Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management

Alistair S. Glen* and Chris R. Dickman

Institute of Wildlife Research, School of Biological Sciences A08, University of Sydney, NSW 2006, Australia

ABSTRACT

Mammalian carnivore populations are often intensively managed, either because the carnivore in question is endangered, or because it is viewed as a pest and is subjected to control measures, or both. Most management programmes treat carnivore species in isolation. However, there is a large and emerging body of evidence to demonstrate that populations of different carnivores interact with each other in a variety of complex ways. Thus, the removal or introduction of predators to or from a system can often affect other species in ways that are difficult to predict. Wildlife managers must consider such interactions when planning predator control programmes. Integrated predator control will require a greater understanding of the complex relationships between species.

In many parts of the world, sympatric species of carnivores have coexisted over an evolutionary time scale so that niche differentiation has occurred, and competition is difficult to observe. Australia has experienced numerous introductions during the past 200 years, including those of the red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*). These species now exist in sympatry with native mammalian predators, providing ecologists with the opportunity to study their interactions without the confounding effects of coevolution.

Despite an increasing body of observational evidence for complex interactions among native and introduced predators in Australia, few studies have attempted to clarify these relationships experimentally, and the interactions remain largely unacknowledged. A greater understanding of these interactions would provide ecologists and wildlife managers world-wide with the ability to construct robust predictive models of carnivore communities, and to identify their broader effects on ecosystem functioning. We suggest that future research should focus on controlled and replicated predator removal or addition experiments. The dingo (*Canis lupus dingo*), as a likely keystone species, should be a particular focus of attention.

Key words: carnivore, competition, keystone species, intraguild predation, trophic cascade, mesopredator release, predator management, dingo, red fox, feral cat, quoll.

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* Address for correspondence: Tel: +612 9351 8679; Fax: +612 9351 4119, E-mail: aglen@bio.usyd.edu.au

I. INTRODUCTION

The deleterious effects of introduced mammalian carnivores in Australia are well documented. The red fox (*Vulpes vulpes*) and the feral cat (*Felis catus*) have been implicated in the decline and extinction of a vast array of native fauna, especially mammals, since European settlement (e.g. Rolls, 1969; Burbidge & McKenzie, 1989; Dickman, 1996*a, b*; Smith & Quin, 1996). In addition, foxes, dingoes (*Canis lupus dingo*) and feral dogs (*C. l. familiaris*) are significant predators of livestock and are therefore major pests of the grazing industry (Rolls, 1969; Saunders *et al.*, 1995; Glen & Short, 2000; Fleming *et al.*, 2001).

Studies on the impacts of introduced predators on Australia's native wildlife have focused primarily on direct predatory impacts (e.g. Kinnear, Onus & Bromilow, 1988; Priddel, 1989; Kinnear, Onus & Sumner, 1998; Mahon, 1999; Kinnear, Sumner & Onus, 2002). However, several authors have suggested that introduced predators may also impact upon native species through competition for resources such as food, territories and den sites (e.g. Edgar & Belcher, 1995; Morris, Orell & Brazell, 1995; Dickman, 1996*a, b*), or through the introduction and spread of diseases and parasites (e.g. Caughley, 1980; Dickman, 1996*a, b*; Molsher, 1999). In addition, emergent evidence suggests that introduced predators may themselves be limited by competition and/or predation from other members of the mammalian carnivore guild (e.g. Marsack & Campbell, 1990; Short & Smith, 1994; Newsome *et al.*, 1997; Molsher, 1998, 1999; Molsher, Newsome & Dickman, 1999; Newsome *et al.*, 2001).

There is a considerable body of theoretical and empirical work addressing interactions within trophic guilds outside Australia (e.g. Paine, 1966; Polis, Myers & Holt, 1989; Doncaster, 1992; Estes, 1996; Holt & Polis, 1997; Palomares & Caro, 1999; Fedriani *et al.*, 2000; Creel, 2001; Gosselink *et al.*, 2003). However, little research has been conducted in systems where one or more predators have been recently introduced. In Australia, where cats and foxes are relative newcomers in ecological terms, systems have probably not yet reached new stable states, and the potential for further decline among their native competitors and prey is therefore very real. Indeed, the dingo was introduced to the Australian mainland some 3500–4000 years ago (Gollan, 1984; Corbett, 1995) and co-occurred with the thylacine (*Thylacinus cynocephalus*) for perhaps 500 years and with the Tasmanian devil (*Sarcophilus harrisii*) for some 3000 years (Archer & Baynes, 1972; Archer, 1974) before the native species disappeared. Even then, mainland extinction of these native marsupials coincided with shifts in human hunting technology (Johnson & Wroe, 2003). Given the ecological and economic impacts of introduced carnivores in Australia, an understanding of their effects, and of the processes that limit their populations, is clearly essential.

Wildlife managers often target one species at a time for management, neglecting to consider the indirect effects that their actions may have on other pest species. For example, removal of a predator may release other pest species from predation or competition. This review is a first step in being able to predict such effects, and is therefore important for wildlife managers. In addition, the Australian situation is of special interest from a theoretical point of view. Over an evolutionary timescale, competition often causes species to adapt to separate niches, so that its effects are no longer observable (Arthur, 1982), except in unusual situations where competition is 'suspended' (Dickman, 1986*c*). Where one or more species of competitor is a recent arrival, a window of opportunity exists to study competition before such adaptation occurs (Clode & Macdonald, 1995; Blackwell & Linklater, 2003).

Here, we review the evidence for complex interactions among native and introduced mammalian carnivores in Australia, and discuss this in the context of examples from other continents. The implications for management of vertebrate pests both within and outside Australia are also discussed.

II. DEFINITIONS

Competition: competition may occur within or between species, when individuals deprive others of resources, thus reducing their growth, survivorship or fecundity (Begon, Harper & Townsend, 1986). The mechanisms of competition can be broadly classified into exploitation or interference, although these can be divided more finely (Schoener, 1983). Exploitation competition occurs when organisms use resources, thus depriving others of those resources (Fig. 1A). By contrast, interference competition occurs when individuals are directly antagonistic towards others (e.g. by fighting or production of chemical deterrents), thereby excluding them from a contested resource (Schoener, 1983; Sih *et al.*, 1985) (Fig. 1B). The effects of interference competition may be particularly significant among carnivores due to their physical and behavioural adaptations for killing (Dickman, 1991; Creel, Spong & Creel, 2001).

Intraguild predation: we follow the definition of Polis *et al.* (1989), which describes intraguild predation as 'the killing and eating of species that use similar, often limiting, resources and are thus potential competitors.' This definition excludes cases of interspecific killing in which the victim is not consumed. Thus, intraguild predation constitutes both predation and extreme interference competition (Fig. 1C).

Trophic cascade: numerous definitions, some general and some more specific, have been offered for trophic cascades. The term refers to predator–prey interactions whose effects
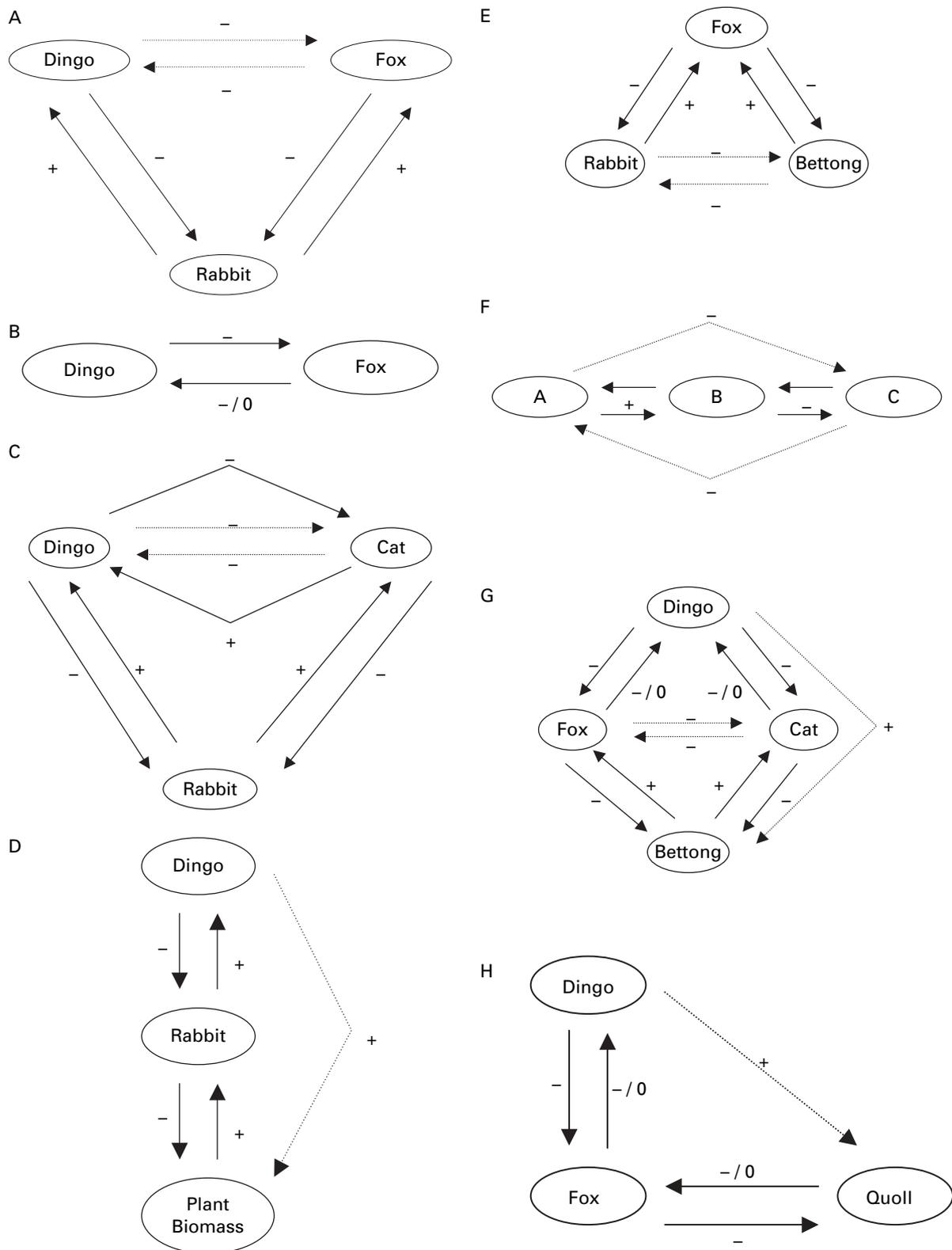
Fig. 1. Illustrated examples of a number of simple and complex interactions. Solid arrows denote direct effects; broken arrows denote indirect effects and signs ($+$, $-$, 0) indicate effect on species. (A) exploitation competition, (B) interference competition, (C) intraguild predation, (D) trophic cascade, (E) apparent competition *via* a shared predator, (F) apparent competition within a single trophic level, (G) keystone predation, (H) indirect commensalism. Species names used in each example represent documented or postulated examples of the respective interactions in Australia. Adapted from Connell (1990) and Morin (1999).

extend (or *cascade*) down through more than one level in a food web so that plant biomass is ultimately affected by changes in predator abundance, *via* a series of intermediate links (Paine, 1980; Pace *et al.*, 1999; Schmitz, Hambäck & Beckerman, 2000) (Fig. 1D). Polis *et al.* (2000) recognised two levels of trophic cascades. Species-level cascades occur within a subset of the community so that changes in predator numbers affect one or a few plant species. Community-level trophic cascades are more complex and profound, causing plant biomass to be redistributed throughout the system.

Mesopredator release: this describes an increase in the abundance of subordinate predators following the removal of a dominant predator which previously held the subordinate species in check (Soulé *et al.*, 1988). Such an occurrence may constitute one link in a larger trophic cascade.

Apparent competition: this is most commonly a situation in which two or more alternative prey species limit each other's abundance, not because they compete directly for resources, but because each prey species helps to maintain the density of shared predators, thereby indirectly maintaining predation pressure on the other (Holt, 1977) (Fig. 1E). An alternative form of apparent competition was described by Connell (1990) as involving three species within the same trophic level (Fig. 1F).

Keystone species: originally, this term referred to a predator that facilitated the coexistence of potentially competing prey species. By preying upon and hence suppressing the dominant competitor, the keystone predator indirectly allowed the subordinate competitors to persist (Paine, 1966, 1969) (Fig. 1G). The term has come to be used much more broadly, and now refers to a species that has disproportionately large effects on the community or ecosystem relative to its own abundance (Heywood, 1995; Power *et al.*, 1996). Thus, a keystone species need not be a predator, but may exert strong effects through a variety of processes such as pollination, seed dispersal or alteration of the abiotic environment (Power *et al.*, 1996).

Indirect commensalism: this describes a situation in which a dominant predator or competitor suppresses a subordinate one, indirectly benefiting competitors of the subordinate species (Fig. 1H).

Native and introduced predators: for the purposes of this discussion, the dingo, having existed in Australia for some 3500–4000 years prior to European settlement (Gollan, 1984; Corbett, 1995), is treated as native. This reflects the management objectives of conservation agencies, which seek to conserve the dingo as part of Australia's natural heritage. The cat and the fox arrived much more recently in Australia (Rolls, 1969; Abbott, 2002), and are defined as introduced.

III. EVIDENCE FOR INTERACTIONS

(1) Interactions between native and introduced carnivores

Introduced predators may impact on native ones *via* intraguild predation (Fig. 1C), introduction or spread of disease, or by competition for resources (Fig. 1A, B). Wiens (1989) outlined types of evidence that indicate interspecific competition. Where the distributions of two species appear to be mutually exclusive, this may be taken as weak evidence of competition. A stronger case is presented if overlap in resource use is demonstrated, and an even stronger case if it can be shown that the use of resources by one species reduces their availability to the other. Finally, if one or both species is negatively affected by the presence of the other (e.g. in terms of reduced abundance, growth or fecundity), and alternative hypotheses are not consistent with observed patterns, a convincing case exists for competition (Wiens, 1989). Unequivocal evidence can be obtained from well-designed removal studies, in which reciprocal removal of putative competitors results in increased abundance and resource use of the remaining species. There is sufficient evidence from existing studies to present a strong case for the existence of competition between native and introduced predators in Australia.

Numerous authors have noted the potential for competition from cats and foxes to impact upon Australian native mammalian predators. These suggestions are often speculative, and based on the high degree of overlap in resource use observed between introduced predators and their native counterparts. For example, it has been posited that quolls (*Dasyurus* spp.) are likely to experience competition from cats for food and den sites (Dickman, 1996*a, b*; Jones & Barmuta, 1998; Molsher, 1999). Quolls are the most similar Australian genus to cats in terms of diet, and are sympatric with cats throughout their distributions (Dickman, 1996*b*). (Four species of quoll occur in Australia, and a further two in New Guinea.) Molsher (1999) found that the diet of spotted-tailed quolls (*Dasyurus maculatus*) in central-western New South Wales overlapped sufficiently with the diet of cats to suggest potential for exploitation competition. Quolls also have overlapping habitat and den requirements with those of cats (Godsell, 1982; Dickman, 1996*b*; Oakwood, 2002).

Niche overlap also occurs between quolls and foxes, which consume similar prey (e.g. Alexander, 1980; Mansergh & Belcher, 1992; A. Glen, unpublished data), and probably have similar preferences for dens and shelter sites (Johnson & Roff, 1982; Godsell *et al.*, 1984; Mansergh & Marks, 1993; Watt, 1993; Edgar & Belcher, 1995; Coman, 1995). Belcher (2000) noted that the ability of the spotted-tailed quoll to climb trees and rock faces may provide some niche differentiation between this species and foxes. Such vertical partitioning may provide a refuge from predators or competitors. For example, Nellis (1989) reported that black rats (*Rattus rattus*) persisted on a Caribbean island following the introduction of the Indian mongoose (*Herpestes auropunctatus*) by switching to arboreal habitats, while bridled quail doves (*Geotrygon mystacea*) changed from nesting on the ground to nesting in low trees. However, if quolls are forced in the presence of foxes to restrict their activity to arboreal or rocky habitats, this may severely limit their access to potential prey and shelter sites, thus causing them to persist at lower densities.

Individual eastern (*Dasyurus viverrinus*), northern (*D. hallucatus*) and spotted-tailed quolls use large numbers of dens, and rarely if ever share dens with conspecifics except when

mating (Godsell *et al.*, 1984; Watt, 1993; Oakwood, 2002; Belcher & Darrant, 2004). Indeed, competition for dens may be a limiting factor for eastern quolls (Godsell, 1982). It is likely, therefore, that a large number of suitable den sites is required for an area to support high densities of these species. If the choice of den sites is restricted by competition from, or the need to avoid, introduced predators, this could have a marked effect on the population densities of quolls, as was the case for the arctic fox (*Alopex lagopus*) following invasion of its range by red foxes (Hersteinsson *et al.*, 1989; Kaikusalo & Angerbjörn, 1995).

As well as observations of niche overlap, further evidence of impact comes from instances where the historical pattern of decline of native predators has coincided with the arrival of cats and foxes (Jones *et al.*, 2003). For example, the decline of the western quoll (*Dasyurus geoffroii*) in central Australia coincided with the arrival of foxes (Johnson & Roff, 1982), as did the decline of the eastern quoll in South Australia (Wood-Jones, 1923). The rate of decline in quolls has been much slower in fox-free areas (the northern tropics and Tasmania) than that observed elsewhere in Australia (Oakwood, 1997; Jones *et al.*, 2003). Similarly, Rolls (1969) noted that declines of the eastern and spotted-tailed quolls occurred shortly after the release of cats, and Dwyer (1983) proposed that the New Guinea quoll (*Dasyurus albopunctatus*) may have declined since the introduction of cats to its range. However, Johnson, Burbidge & McKenzie (1989) claimed that cats may not have caused declines of quolls, noting a long period of coexistence prior to the arrival of foxes. The impacts of cats appear to be inconsistent, but can act in concert with a range of other variables such as alteration of habitat, leading in some instances to decline or extinction of native taxa (Oakwood, 2000; Burbidge & Manly, 2002).

In addition to the speculative arguments presented above, direct evidence for the impacts of introduced predators comes from increases in the abundance of native predators following the removal of foxes. Morris *et al.* (1995) reported increased abundance of the western quoll following poison baiting for foxes, with no concurrent increase in an adjacent, unbaited area. These authors attributed the observed response to reduced competition for food and reduced predation, particularly on young quolls.

Several authors have recorded intraguild predation (Fig. 1C) or competitive killing of native mammalian predators by cats and foxes. For example, Serena, Soderquist and Morris (1991) and Morris *et al.* (2003) cited predation by foxes and cats as a major source of mortality for the western quoll. Körtner & Gresser (2002) recovered carcasses of two spotted-tailed quolls that had been partially eaten by foxes, and Banks (1997) found hair from a spotted-tailed quoll in fox faeces. Similarly, Oakwood (2000) found that predation by cats, as well as by native predators, was a major source of mortality for the northern quoll. Cats and foxes also prey upon the mulgara (*Dasycercus cristicauda*), which is itself a predator of small mammals and therefore a potential competitor of cats and foxes (Mahon, 1999; Dickman, 2003).

On a global scale, Palomares & Caro (1999) found that the red fox was second among the canids (after the grey wolf, *Canis lupus lupus*) as a killer of other carnivores. For example, red foxes in Europe have been observed to prey directly on arctic foxes (Frafjord, Becker & Angerbjörn, 1989) and pine martens (*Martes martes*) (Lindström *et al.*, 1995). The effects of competitive aggression by red foxes can be significant, particularly where they act in concert with other factors. For example, on islands or at the edge of their distribution, populations of arctic foxes may be driven to extinction by the red fox (Bailey, 1992; Hersteinsson & Macdonald, 1992).

The dingo is the largest terrestrial carnivore in Australia and, unlike its smaller marsupial counterparts, appears to assert predatory and competitive dominance over both cats and foxes. Numerous studies report direct predation by dingoes on foxes and cats. Marsack & Campbell (1990) observed four instances of dingoes feeding on fresh fox carcasses, saw one dingo carrying a freshly killed fox, and also witnessed one unsuccessful attempt at predation. During the same study, fox remains were present in the guts of 6.1 % of 49 dingoes sampled, and 2.4 % of 82 dingo faeces. Cat remains were also found in the gut of one dingo (2 %), and in one faecal sample (1.2 %). Consumption of cats by dingoes has also been reported by Newsome, Catling & Corbett (1983), Lundie-Jenkins, Corbett & Phillips (1993), Thomson (1992), Corbett (1995) and Paltridge (2002). In addition, Pettigrew (1993) reported that an adult cat fitted with a radio collar was killed by a dingo. This pattern is mirrored in North America where coyotes (*Canis latrans*) kill and eat both bobcats (*Felis rufus*) and grey foxes (*Urocyon cinereoargenteus*) (Fedriani *et al.*, 2000).

As well as killing cats and foxes, dingoes may also have exploitative effects (Fig. 1A), particularly when food is limited (Lundie-Jenkins *et al.*, 1993; Corbett, 1995; Dickman, 1996 b). Dietary overlap is considerable, with rabbits (*Oryctolagus cuniculus*) being a staple prey for all three species where they are available (Catling, 1988; Corbett, 1995; Saunders *et al.*, 1995; Molsher *et al.*, 1999; Mitchell & Banks, 2005). However, in some circumstances, dingoes can benefit cats by providing a source of carrion. For example, during a drought in central Australia, cats regularly scavenged carcasses killed by dingoes (Paltridge, Gibson & Edwards, 1997). Although paradoxical, this situation is not uncommon in other systems. Macdonald (1987), Dickman (1992 a), Creel (2001) and Switalski (2003) illustrate a number of similar examples from Europe, Africa and North America in which dominant competitors kill or steal prey from subordinate ones, but the subordinate predator may also benefit by scavenging carcasses killed by the dominant one.

There is abundant evidence from the patterns of distribution of dingoes, foxes and cats to suggest that dingoes can suppress populations of their smaller competitors. Perhaps the most compelling evidence is that of Newsome *et al.* (2001), who measured the relative abundance of foxes on either side of the dingo fence, which excludes dingoes from much of south-eastern Australia while high densities remain to the north and west of the fence. Indices of fox abundance based on spotlight counts and spoor counts at waterholes were 20.6 and 7.1 times higher, respectively, in the absence than in the presence of dingoes. Cats were at similarly low densities on either side of the fence (Newsome *et al.*, 2001).

Using a passive activity index, Newsome *et al.* (1997) found an inverse relationship between dingo and fox activity in Kosciuszko National Park and Nadgee Nature Reserve

in south-eastern Australia. Given that both species occupy similar habitats, this may reflect a relationship between the densities of the two species, resulting either from avoidance [foxes often avoid dingoes at shared resources such as watering points (Lundie-Jenkins *et al.*, 1993)], or from killing of foxes by dingoes. Alternatively, animals may alter their level of activity or use of roads according to the presence of their confamilials. Further investigation is required to clarify this relationship (Newsome *et al.*, 1997).

In central Australia's Tanami Desert, foxes were rare or absent until recently, possibly due to exclusion by dingoes. Control of dingoes may have allowed invasion of the area by foxes (Short, Kinnear & Robley, 2002). Lundie-Jenkins *et al.* (1993) also reported the absence of foxes from their central Australian study area until dingoes were removed by poisoning. A single fox was then believed responsible for the extinction of a local population of endangered rufous hare-wallabies (*Lagorchestes hirsutus*). A similar situation has occurred in North America, where expansion in the distribution of coyotes has been attributed to the decline of the grey wolf (Mech, 1970).

In addition to these specific instances, many authors have made the general observation that foxes are scarce where dingoes are abundant, or *vice versa* (e.g. Thompson, 1983; Jarman *et al.*, 1987; Johnson *et al.*, 1989; Smith & Quin, 1996; McRae, 2004). However, the occurrence of the two species is not mutually exclusive, and Catling & Burt (1995) noted that fresh dingo and fox tracks were often recorded side by side. It is possible that foxes tolerate dingoes more readily in densely vegetated forest areas, such as those studied by Catling & Burt (1995), because of the greater ease of avoidance or evasion once detected where structural refugia are available (e.g. Finke & Denno, 2002).

It has also been noted that cats can increase in density following the removal of dingoes (Lundie-Jenkins *et al.*, 1993; Pettigrew, 1993; Christensen & Burrows, 1995). Using data presented by Catling & Burt (1994), Dickman (1996*b*) calculated that there was a negative correlation between the abundance of dingoes and feral cats in southern New South Wales. By contrast, Smith & Quin (1996) found that patterns of distribution suggested tolerance of cats by dingoes. The relationship between the two species may be affected by extraneous factors. For example, interactions may be stronger in open habitats where it is difficult for cats to avoid dingoes (Pettigrew, 1993; Dickman, 1996*b*; Edwards *et al.*, 2002). A similar dichotomy was reported in south-east Africa, where kleptoparasitism by spotted hyenas (*Crocuta crocuta*) on African wild dogs (*Lycaon pictus*) was more frequent in open than in densely vegetated habitats (Creel, 2001).

There is also evidence to suggest that small native predators in Australia may face competition from introduced species. For example, considerable niche overlap has been observed between insectivorous dasyurids in the genus *Antechinus* and the introduced black rat, which has similar dietary and habitat preferences to those of *Antechinus* (Cox, 1997; Cox, Dickman & Cox, 2000). Competitive interactions have also been demonstrated between the insectivorous dunnart (*Sminthopsis griseoventer boullangerensis*) and the introduced house mouse (*Mus domesticus*), with populations of

the former species increasing up to fourfold when numbers of the mouse were reduced (Dickman, 1992*b*).

(2) Interactions among native carnivores

There is evidence of past and present competitive interactions among a range of Australian mammalian predators. This includes patterns of distribution, historic and prehistoric patterns of decline, morphological evidence, and ecological comparisons of sympatric native carnivores, as well as observations of direct interactions between species.

Dingoes are thought to have caused the prehistoric extinction on the Australian mainland of the thylacine and the Tasmanian devil (Burbidge & McKenzie, 1989; Corbett, 1995; Smith & Quin, 1996; Jones *et al.*, 2003, but see also Johnson & Wroe, 2003). Corbett (1995) described two possible mechanisms by which dingoes may have facilitated the demise of thylacines and Tasmanian devils; the superior adaptability hypothesis and the disease hypothesis. The former states that the social structure of dingoes conferred on them a competitive advantage over their less socially cohesive rivals. Packs of predators should enjoy greater success than individuals in hunting large prey and protecting carcasses from competitors (e.g. Eaton, 1979; Corbett, 1995). The disease hypothesis posits that dingoes introduced a pathogen (possibly toxoplasmosis) to Australia which decimated populations of thylacines and Tasmanian devils. However, there is no direct evidence implicating dingoes in the arrival of any new pathogens (Corbett, 1995).

The extent to which the dingo now serves as an ecological analogue of the thylacine and Tasmanian devil is a matter of contention. As a scavenger of large carcasses, the devil is likely to have been replaced to a large extent by the dingo, which is a generalist predator and scavenger (Johnson & Wroe, 2003). However, the former role of the thylacine is less clear as the species was extirpated before its ecology was studied. Jones & Stoddart (1998) concluded that the thylacine was most likely a predator of medium-sized vertebrates. However, Johnson & Wroe (2003) argue that the greater body size and wider gape of the thylacine relative to the dingo identify the species as a hunter of large prey.

The relationships between dingoes and the four Australian species of quolls are complex and poorly understood. The differences in body size between the taxa and the partially arboreal habits of the quolls are likely to provide a degree of niche separation. However, a number of studies provide evidence of interference competition (Fig. 1B) between the two taxa. For example, in the northern tropics of Australia, dingoes were a major source of mortality for northern quolls, although carcasses were left uneaten (Oakwood, 2000). These observations suggest extreme interference competition. In addition, remains of spotted-tailed quolls have been identified in the scats of dingoes and domestic dogs (Brunner & Wallis, 1986), possibly indicating intraguild predation, although it is also possible that the remains were scavenged. As well as predation, Belcher (1995) suggested that spotted-tailed quolls may suffer kleptoparasitism from dingoes. Conversely, Edgar & Belcher (1995) stated that discarded dingo kills provide additional food

for quolls. Quolls could also benefit from the presence of dingoes if dingoes suppress populations of cats or foxes (Fig. 1 H). Similarly in Fennoscandia, arctic foxes apparently benefited from the presence of wolves by scavenging from their kills, and because wolves may have suppressed numbers of the red fox prior to their own decline (Hersteinsson *et al.*, 1989). Further examples are presented by Mech (1970) and Hersteinsson & Macdonald (1982).

In studies of sympatric dasyurid carnivores in Tasmania, Jones (1997, 1998) and Jones & Barmuta (1998, 2000) found considerable evidence of interspecific competition. Tasmanian devils, spotted-tailed quolls and eastern quolls showed character displacement in the strength of the canine teeth and size of the temporalis muscle, suggesting that competition has occurred among these guild members over an evolutionary time scale (Jones, 1997). That competition still occurs was evidenced by dietary overlap, patterns of relative abundance, and interactions at carcasses, which indicated hierarchical dominance (Jones, 1998; Jones & Barmuta, 2000).

Dietary overlap among species was dependent on sex and age class. Thus, female and sub-adult Tasmanian devils showed significant overlap with male spotted-tailed quolls, and female spotted-tailed quolls overlapped with male eastern quolls. The degree of overlap was also affected by seasonal variations in the diets (Jones & Barmuta, 1998). Where dietary overlap was greatest, habitats were partitioned. This caused different prey to be encountered, thereby reducing competition; a situation termed niche complementarity (Jones & Barmuta, 2000). For example, between adult male spotted-tailed quolls and adult devils, strong vertical partitioning of habitat was found, and the diet of adult male quolls contained a much higher proportion of arboreal prey than that of adult devils (Jones & Barmuta, 2000).

Interactions between Tasmanian devils and spotted-tailed quolls at carcasses revealed that adult devils are dominant and can displace quolls from a carcass (Jones & Barmuta, 2000). The vulnerability of spotted-tailed quolls to klepto-parasitism increases if they kill prey too large to consume quickly (Jones & Barmuta, 2000). Unlike exploitation competition, interference of this kind can have a severe impact even when live prey are abundant (Creel, 2001).

Spotted-tailed quolls are the least abundant of the three sympatric carnivores in Tasmania, with densities five times lower than those of the Tasmanian devil (Jones & Barmuta, 1998). These authors suggested that the low abundance of spotted-tailed quolls may have resulted from a combination of exploitation and interference competition, as well as possible predation by owls and devils. Hair of spotted-tailed quolls and eastern quolls was found in devil faeces, but it was not known whether this reflected intraguild predation or scavenging by devils (Jones & Barmuta, 1998). An opportunity currently exists to evaluate this hypothesis of competition, as Tasmanian devil populations have crashed over large areas due to an outbreak of an unidentified disease (Jones, 2003).

Among the smaller native predators, competitive interactions have been demonstrated among species of *Antechinus* and between *A. stuartii* and the common dunnart (*Sminthopsis murina*). In a series of field experiments, Dickman (1986 *a*, *b*, 1988) showed that controlled removal of the larger (50 g) dusky antechinus (*A. swainsonii*) triggered increases in juvenile survival and population size of the smaller (20 g) agile antechinus (*A. agilis*), as well as shifts in its arboreal activity, ground-level movements, habitat use and diet. These shifts allowed the agile antechinus to exploit resources formerly used by its larger congener and, in particular, to gain access to rich terrestrial microhabitats that contained its preferred invertebrate prey. By contrast, removals of *A. agilis* had limited effects on the demography and resource use of the dusky antechinus, suggesting that competition was strongly asymmetrical. In the case of *A. stuartii* (35 g) and *S. murina* (20 g), Fox (1982) observed shifts in the habitats used by the smaller species in the presence of the larger, and later showed that the two species overlapped in their diets (Fox & Archer, 1984). In staged encounters between the two species in captivity, the dunnart has been shown to avoid the antechinus, and interference appears to be the mechanism by which competition occurs (Righetti, Fox & Croft, 2000). Few other examples of competition among small native predators have been described (Dickman, 1984).

(3) Interactions among introduced carnivores

There is abundant experimental and anecdotal evidence pointing towards competitive interactions between foxes and cats in Australia. This evidence comprises patterns in relative abundance, overlap in resource use, changes in the abundance, diet or habitat use of cats following removal of foxes, and occasional observations of possible intraguild predation.

Exploitation competition is likely to occur between foxes and cats, particularly when food is limited (Dickman, 1996 *b*). Both are opportunistic predators (Coman, 1973; Jones & Coman, 1981) and have overlapping diets (Triggs, Brunner & Cullen, 1984; Catling, 1988; Molsher, 1999; Molsher *et al.*, 1999; Risbey, Calver & Short, 1999). In addition, Molsher (1999) noted overlap in the home ranges and habitat use of cats and foxes, and concluded that there was a high potential for exploitation competition. Both Molsher (1999) and Risbey *et al.* (1999) suggested that foxes are the dominant competitor and may limit populations of cats.

Patterns of distribution further suggest exclusion of cats by foxes (Smith & Quin, 1996), and a number of studies have reported increased numbers of cats following the removal of foxes. For example, Short *et al.* (1995) reported a substantial increase in the abundance of cats after meat baits were used to remove foxes. Subsequently, Risbey *et al.* (2000) obtained spotlight counts of cats before and after fox removal, with concurrent monitoring in an untreated area. Spotlight counts of cats tripled in the baited area, but did not change in the unbaited area. Christensen & Burrows (1995) also reported an increase in cats of more than fourfold in the twelve months following fox and dingo removal in central Australia. However, cats also increased more than twofold in an unbaited area during the same period. Above-average rainfall probably contributed to the increases (Christensen &

Burrows, 1995; Burrows *et al.*, 2003). A similar result was obtained in North America by Engeman *et al.* (2000), who found increased bobcat activity when coyote numbers were reduced.

Molsher (1999) studied the diet, home range and habitat use of cats following fox removal. Cats consumed significantly more carrion following fox removal, suggesting that foxes had previously limited cats' access to carcasses by interference. Habitat use by cats also changed as fox numbers were reduced, with cats making more frequent use of open habitats, which contained high densities of rabbits (Molsher, 1999). Where foxes were left uncontrolled, the home ranges of cats and foxes overlapped. However, there was no overlap in the core areas of the home ranges of cats and foxes, and six of eight cats were trapped outside fox core areas (Molsher, 1999). This suggests that cats avoided the areas most frequently used by foxes; a result that was supported by temporal analysis of radio telemetry data. Simultaneous radio-tracking of cats and foxes showed that cats kept significantly further from foxes than they did from each other. Foxes also tended to keep further from cats than from each other, but this difference was not significant. Anecdotal observations of interactions between the two species suggested that they tolerated each other at distances of 50 m or more. At closer distances, displacement or aggression occurred, the fox usually being dominant. These observations suggest that cats actively avoid foxes, but not *vice versa* (Molsher, 1999).

These results are consistent with patterns found in the United States for coyotes and red foxes. Harrison, Bissonette & Sherburne (1989) trapped nine foxes outside the territories of coyotes and a further two within a 2 km buffer around core coyote territory, but no foxes were trapped in coyote core areas. Radio telemetry revealed that fox home ranges were located in the spaces between coyote ranges, with some overlap, and only occasionally were foxes radio-located in core coyote ranges. Further, within areas of spatial overlap between coyotes and foxes, there was considerable temporal separation. Coyotes were the dominant predator, displacing foxes from areas of preferred habitat (Harrison *et al.*, 1989). Exclusion of foxes by coyotes has also been documented by Voigt & Earle (1983), Sargeant, Allen & Hastings (1987) and Gosselink *et al.* (2003). Similarly, Johnson & Franklin (1994) found strong spatial separation in the home ranges of grey (*Dusicyon griseus*) and culpeo foxes (*D. culpaeus*) in southern Chile, attributing the observed pattern to interference competition by culpeo foxes.

Several studies have also revealed evidence of competitive killing or consumption of cats by foxes. For example, Molsher (1999) reported that three of eight cats whose cause of death could be determined had been killed by foxes. Due to decomposition, it could not be determined whether any of the carcasses had been partially consumed by foxes. However, during the same study, Molsher (1999) found no cat remains in 598 fox scats and stomachs. Conversely, Risbey *et al.* (1999) found a cat's paw in the gut of a fox. The absence of insects or their larvae suggested that the cat had not been consumed as carrion, but had probably been subject to intraguild predation (Risbey *et al.*, 1999). Cat remains have also been found in the diets of foxes by Coman (1973), Brunner *et al.* (1991) and Paltridge (2002).

IV. IMPLICATIONS FOR PREY POPULATIONS

Clearly, the various interactions that occur between mammalian predators can have significant effects on their behaviour, distribution and abundance. In turn, these can lead to profound effects on prey populations. For example, Risbey *et al.* (2000) investigated the response of small mammal and reptile populations to different levels of cat and fox activity. Where both foxes and cats were controlled, small mammal captures doubled. Where foxes were controlled but cats were not, small mammal captures declined by 80 % over five years, and where foxes and cats were left uncontrolled, no consistent trend was observed in small mammal captures (Risbey *et al.*, 2000). These authors concluded that populations of small mammals were limited by cat predation, and the effect was stronger where foxes were removed. Cats may have increased in abundance after fox removal through mesopredator release (*sensu* Soulé *et al.*, 1988) (Fig. 1 G). Alternatively, the spotlight counts may have reflected increased activity of cats rather than increased abundance. Whichever explanation is correct, the result was decimation of prey populations. Similarly, de Tores *et al.* (1998) found evidence of increased predation by cats on native prey, including the endangered brush-tailed bettong (*Bettongia penicillata*), following fox control. Comparable results have been reported in North America, where local extinctions of coyotes appear to have caused mesopredator release of foxes, skunks and domestic cats, leading to decline or local extinction of their prey (Estes, 1996).

Dingoes may also have an indirect positive effect on populations of some native prey by limiting densities of cats and foxes. For example, Pettigrew (1993) suggested that the net effect of dingoes on populations of the endangered greater bilby (*Macrotis lagotis*) was positive because, although dingoes prey occasionally on the bilby, they suppress populations of cats and foxes more strongly. Further evidence in support of this notion comes from Smith & Quin (1996), who studied the historical decline of conilurine rodents in Australia. These authors found a significant negative correlation between the abundance of dingoes and the number of local conilurine extinctions. Further, conilurine species whose ranges fall largely inside the range of the dingo have contracted less than those in whose ranges dingoes are scarce, whereas contractions and local extinctions were positively correlated with the abundance of foxes. In areas with few foxes, cats were also strongly implicated in local conilurine declines (Smith & Quin, 1996). However, loss or modification of habitat may also have contributed to conilurine declines. Similarly, Short & Smith (1994) observed that in areas of north-eastern New South Wales where endangered medium-sized mammals such as the parma wallaby (*Macropus parma*) persist, dingoes are often abundant and foxes scarce. Such observations point towards the dingo as a potential keystone species (Fig. 1 G). However,

controlled and replicated experiments involving the removal or introduction of dingoes are required to confirm this.

V. IMPLICATIONS FOR PREDATOR MANAGEMENT

The evidence reviewed above shows that the effects of one predator are unlikely to operate in isolation, but will usually influence, and be influenced by, the suite of co-occurring predators in the system. Removal of one predatory species (such as occurs typically during pest management programmes) may lead directly or indirectly to increases in another, and the effects upon prey species may ultimately be negative. Thus, a number of authors have stressed the importance of integrated pest control, arguing that managing each pest species in isolation can be ineffective or even counter-productive. Risbey *et al.* (1999) speculated that control of cats could benefit native prey populations at Shark Bay, whereas fox control could lead to competitive release of cats and therefore increased predation on small mammals, birds and reptiles. Similar suggestions have been made by Martin, Twigg & Robinson (1996) and Newsome *et al.* (1997).

Management strategies need to consider the complex inter-relationships between sympatric predators and their prey, and many Australian authors have recommended integrated pest control programmes in which foxes, cats and rabbits are controlled in a co-ordinated fashion (e.g. Newsome, 1990; Lundie-Jenkins *et al.*, 1993; Dickman, 1996*b*; Smith & Quin, 1996; Molsher, 1999). The introduced rabbit is inextricably linked to the abundance of dingoes, cats and foxes, for which it is a staple prey (Catling, 1988; Saunders *et al.*, 1995; Corbett, 1995). Thus, although it is itself not a predator, the rabbit warrants inclusion in discussions of predator management, and will be considered here.

Rabbits often support populations of cats and foxes, thereby contributing to the suppression of native prey (Pech *et al.*, 1992; Pech, Sinclair & Newsome, 1995; Saunders *et al.*, 1995; Dickman, 1996*a*; Newsome *et al.*, 1997). This situation constitutes apparent competition (*sensu* Holt, 1977) (Fig. 1E) between rabbits and native herbivores. For example, rabbits are thought to have supported populations of foxes and cats in the Tanami Desert in central Australia, leading in turn to increased predation on the endangered rufous hare-wallaby (Lundie-Jenkins *et al.*, 1993). Rabbits may also facilitate increases in cat populations following fox control (Risbey *et al.*, 2000). By allowing predators to persist at high densities even after native prey have been driven to scarcity, rabbits can facilitate the extinction of native prey populations; a situation termed 'hyperpredatory extinction' (Smith & Quin, 1996).

Clearly, the rabbit is of great importance in sustaining predator populations in many parts of Australia. Not surprisingly then, there have been many instances where the control of rabbits has apparently contributed to reductions in cat and fox populations. For example, in South Australia's Flinders Ranges, the introduction of rabbit

calicivirus in 1995 decimated rabbit populations, and probably contributed to subsequent reductions in cat and fox numbers (Holden, 1999; Holden & Mutze, 2002). Conversely, crashes in rabbit populations (for example, due to drought) have led in some instances to intensified predation on alternative native prey (Newsome, Parer & Catling, 1989). Thus, a simple 'bottom-up' approach, whereby the primary prey (rabbits) are controlled in order to reduce densities of predators, may lead to a period of increased predation on secondary prey (Johnson *et al.*, 1989). Where threatened populations of native prey exist, such a situation could potentially cause local extinction. Once again, this emphasises the importance of an integrated approach in which rabbits and introduced predators are controlled simultaneously. Such was the case in Western Australia, where rabbits were historically controlled by poison baiting. Foxes, which fed on the poisoned rabbit carcasses, were killed by secondary poisoning. In the early 1970s, the myxoma virus was introduced to control rabbits, and poison baiting ceased. Fox numbers soared and marsupial populations crashed (Newsome, 1993). Similarly, poisoning of rabbits in New Zealand has caused secondary poisoning of introduced predators including stoats (*Mustela erminea*), ferrets (*Mustela furo*) and cats (Alterio, 1996).

Control of rabbits is desirable not only to increase the effectiveness of predator control programmes. Rabbits are themselves a serious agricultural and ecological pest in Australia, causing damage to pasture and native flora, and possibly competing with livestock and native herbivores alike (Williams *et al.*, 1995). Control of mammalian predators without concurrent rabbit control has the potential to cause explosions in rabbit densities (Banks, Dickman & Newsome, 1998; Banks, 2000), with subsequent negative impacts on vegetation and wildlife. This is an example of a species-level trophic cascade, as defined by Polis (1999) and Polis *et al.* (2000) (Fig. 1D).

Where integrated pest control is not practicable, managers must consider whether it is appropriate to implement control programmes for individual pest species. This will be dependent on the suite of other species present, and the purpose of conducting the pest control. In some cases, it may be preferable to conduct no pest control, rather than embark on an expensive exercise that may fail to reduce (or may even increase) the damage caused by releasing other pest species from competition or predation (Johnson *et al.*, 1989; Dickman, 1996*b*).

As well as presenting some challenges for wildlife managers, interactions among predators may also provide useful alternative approaches to pest control. For example, introduction of dingoes (or cessation of dingo control) may provide indirect benefits to biodiversity through the suppression of cats, foxes and rabbits (Johnson *et al.*, 1989; Newsome, 1990; Lundie-Jenkins *et al.*, 1993; Short & Smith, 1994). However, such a strategy would require that pest species were at low densities to begin with; either naturally or through intervention (Newsome, 1990).

Palomares *et al.* (1995) and Palomares & Caro (1999) also noted that conserving larger predators can aid in the control of smaller ones. For example, conserving the Spanish lynx (*Lynx pardinus*) should reduce the effects of the red fox and the

Egyptian mongoose (*Herpestes ichneumon*) on prey populations. An analogous situation occurs in California, where coyotes exclude the introduced red fox from their home range, but do not exclude the endangered San Joaquin kit fox. Therefore coyotes may slow or prevent invasion of kit fox habitat by the red fox (Ralls & White, 1995).

Although the focus of the present review is on mammalian carnivores, it should be noted that avian predators may also be involved in competitive and predatory interactions with terrestrial ones. For example, the wedge-tailed eagle (*Aquila audax*) is a predator of medium-large vertebrates including rabbits and small macropods (Brooker & Ridpath, 1980; Richards & Short, 1998). As such, it is likely to compete for food with cursorial predators. *A. audax* also preys upon cats and foxes (Brooker & Ridpath, 1980), thereby exerting intraguild predation. Conservation of large raptors may therefore be beneficial in suppressing rabbits, cats and foxes.

VI. CONCLUSIONS

(1) It is clear from the evidence reviewed here that interactions within the mammalian carnivore guild are common, widespread and can be profound in their effects. While the strength of competitive and other interactions between species may have abated in many situations due to coevolution, areas remain where recent invasions or introductions have occurred and new equilibria have not been reached. The comparatively recent arrival of one or more predator(s) provides an opportunity for ecologists to study the effects of competition without the confounding influence of coevolution. In Australia, two such recent arrivals, the red fox and the feral cat, occur widely and appear to interact with each other and with native carnivores in a variety of complex ways. Australia therefore harbours a wealth of opportunities to develop and test theories of species interactions (Blackwell & Linklater, 2003).

(2) The importance of testing hypotheses of keystone species has been emphasised for a number of years (e.g. Power *et al.*, 1996). However, few studies have attempted to do so in Australia, despite an ever-increasing body of evidence that top-order predators can have profound effects on ecosystems (e.g. Risbey *et al.*, 2000; Newsome *et al.*, 2001; Morris *et al.*, 2003). Large-scale, controlled, replicated experiments are required involving the removal of predators from (or introduction to) systems to test putative interactions. Such studies must monitor the direct and indirect impacts of predators across all trophic levels. Design of such experiments is discussed in Dickman (1996*b*). The importance of these studies to conservation and agriculture in Australia renders them a matter of priority. Specifically, there is abundant evidence that the dingo fulfils the role of a keystone predator in many systems, limiting the abundance of subordinate predators such as cats and foxes. This hypothesis of keystone predation requires rigorous experimental testing.

(3) A further generality which becomes apparent from this review is that interactions between carnivore species vary with context. Simple pair-wise interactions may be strongly influenced by extraneous factors such as habitat type, with open habitats apparently affording greater opportunity for antagonism. Interactions are also affected by the suite of co-occurring predators. It is intuitively appealing for the observer to search for simple patterns in the relationships between pairs of species. Although some generalisations can be drawn from this approach, these will rarely explain all observed interactions. For example, the exclusion of foxes by dingoes is apparent from observations of their broad-scale distribution, but exceptions to this rule are easily found on a local scale (e.g. Catling & Burt, 1995). It is likely that the interaction is real, but that its strength depends on such factors as habitat type, degree of human interference and the distribution and abundance of prey species.

(4) Although there is abundant evidence of complex interactions among mammalian carnivores, in the vast majority of systems, these are poorly understood. The bulk of our knowledge is based on observational studies, or at best on experimental studies with minimal replication. There is an urgent need for clarification of these relationships through detailed examination and rigorous experimental testing. For the wildlife manager, it is essential that complex interactions are given greater consideration when planning predator control programmes. The need for integrated control, as opposed to treatment of each species in isolation, is imperative, and this must be driven by a greater understanding of the complex relationships between species.

VII. FUTURE RESEARCH

As stated above, future research should focus on testing putative interactions with controlled, replicated experiments which manipulate the densities of predators. Here, we make some more specific suggestions. Firstly, because interactions among predators appear to be moderated by structurally complex habitat, initial experiments should be conducted in open areas such as the Australian arid zone, where effects are likely to be more easily detectable. For example, a dingo removal experiment might be conducted in central Australia. Alternatively, an introduction experiment might be conducted by re-routing sections of the dingo barrier fence or by releasing dingoes into large, purpose-built predator enclosures. Such experiments would need to monitor the abundances of foxes, feral cats, rabbits and native prey before and after manipulation of dingo density. Similarly, the impacts of foxes on cats and quolls should be clarified by controlled, replicated fox removal experiments. The knowledge gained from experiments in open habitats could then be used to design experiments capable of detecting more subtle interactions in forested habitats, such as the eastern coastal ranges of Australia. Experiments might also investigate systems where foxes are initially abundant and cats scarce, and *vice versa*, in order to tease out the intricacies of three-way interactions.

In all of the above experiments, the likely subordinate predators should be monitored using radio collars fitted with mortality sensors. This will help to clarify the mechanism of

any observed impact. If interspecific killing is responsible, freshly-killed carcasses can be located, whereas spatial or temporal avoidance between predators can be detected by changes in movement patterns. The diets of all predatory species should also be monitored before and after manipulations are conducted, thereby allowing detection of exploitative effects.

VIII. ACKNOWLEDGEMENTS

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