Dogs as predators and trophic regulators

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CHAPTER 2

Dogs as predators and trophic regulators

Euan G. Ritchie, Christopher R. Dickman, Mike Letnic, and Abi Tamim Vanak

2.1 Introduction

There is increasing interest in the ecology of dogs, the world's most abundant carnivore (estimated 700 million–1 billion worldwide) (Hughes and Macdonald, 2013; Silva-Rodríguez and Sieving, 2012; Vanak and Gompper, 2009a; Gompper, Chapter 1). Like other large-bodied predators, dogs have important functional roles in structuring and maintaining ecological communities (Letnic et al., 2012; Ritchie and Johnson, 2009; Vanak and Gompper, 2009a), but they are also a regular source of conflict with humans due to their negative effects on people and their enterprises, for instance through their roles in disease transmission and the killing of livestock and wildlife (Baker et al., 2008; Hughes and Macdonald, 2013; King et al., 2012; Ritchie et al., 2012; Van Bommel and Johnson, 2012; Young et al., 2011). Indeed, some of the negative effects of maintaining dogs in the landscape have led to considerable recent debate about their management, most notably for dingoes, whose structuring role in Australian ecosystems may be comparable to that of wolves (*Canis lupus*) in North American settings (Allen et al., 2011a; Houston et al., 2010b, 2013; Fleming et al., 2012; Letnic et al., 2011a; Mech, 2012; Johnson and Ritchie, 2013).

Despite their controversial effects, global ubiquity, and significant ecological roles, dogs and their ecological impacts remain surprisingly poorly understood. In particular, we know little about how dogs influence other species across environmental gradients (from wild to urban) and how their influence varies between different 'types' of dogs (see Box 2.1). This lack of information is concerning, as in some parts of the world dogs, and in particular free-ranging dogs, have declined substantially due to direct human persecution and active management programs, whereas in other parts they have increased considerably, benefiting from human food and shelter subsidies (Gompper and Vanak, 2008; Ritchie et al., 2012; Vanak and Gompper, 2009b).

To better understand the consequences of changes in the distribution and abundance of dogs we require information on the roles dogs have in ecosystems, and how these vary both within and between types of dogs and different environmental contexts. Such information is also critical for scenarios where efforts are necessary to effectively manage or conserve free-ranging dogs. With this in mind, we review what is known about the predation pressure that is exerted by dogs and how this may influence trophic patterns of communities. We have deliberately chosen not to focus extensively on the theory regarding predators (including dogs) and their effects, as this is covered in detail by other recent reviews (Letnic et al., 2012; Prugh et al., 2009; Ritchie and Johnson, 2009; Ritchie et al., 2012; Vanak and Gompper, 2009a); instead we present an overview of recent work concerning the ecological roles of dogs as predators.

We based this review mainly on the primary literature that examines patterns of predation by dogs. We also used anecdotal reports from the popular press and other media to determine the range of species that are preyed upon by dogs and the extent of predation pressure. We identified several factors that contribute to the extent of predation pressure by dogs on wildlife. These range from population

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Box 2.1 A problem of definitions: ecological functions versus the identities of predators

Before we can define and understand the ecological roles of dogs, we must be clear about what we actually mean by a dog. This may seem obvious, as most people would have no problem identifying a dog from either a direct observation or from a picture, but in fact the issue of definition is far more complex. Importantly, the way dogs are defined directly influences the way they are managed (Claridge and Hunt, 2008; Glen, 2010). Uncertainty as to what defines a dog exists in two contexts: (1) taxonomic and (2) at the level of association and dependence on humans. Such difficulties in definitions are evident by examining the dingo, a naturalized canid of mainland Australia. Dingoes are referred to as invasive by some and native by others, having arrived in Australia less than 5,000 years ago (Savolainen et al., 2004; but see Oskarsson et al., 2012). Like large canids elsewhere (Gottelli et al., 1994), dingoes have undergone hybridization to varying degrees with dogs introduced to Australia over the past several centuries (Radford et al., 2012; Savolainen et al., 2004). 'Pure' dingoes are therefore regarded as rare in many parts of the continent and dingoes, feral dogs, and their hybrids are all frequently referred to collectively as wild dogs (Letnic et al., 2012), and managed similarly as pests, with the ultimate goal being extermination. In the absence of combined genetic and ecological information about 'dingoes,' it is difficult to ascertain whether previous studies (e.g., Johnson and Vanderwal, 2009; Johnson et al., 2007; Letnic et al., 2009b; Wallach et al., 2009, 2010) actually provide information on dingoes only, or dingoes, feral dogs, and their hybrids. If it is the latter, then it is difficult to ascertain the extent to which the ecology of these dog types differs according to their genetics (Claridge and Hunt, 2008).

Coupled with this problem of taxonomic and genetic identity is the variation in association and dependency of dingoes with humans. A review by Vanak and Gompper (2009a) places dogs under one of six categories: owned dogs, urban free-ranging dogs, rural free-ranging dogs, village dogs, feral dogs and wild dogs (e.g., dingoes, feral dogs, and their hybrids).

1. Owned dogs: Dogs that are owned and restricted in movement to a prescribed outdoor or indoor area. Although the potential for these dogs to interact with wildlife is limited, they can nonetheless have an effect on wildlife when they accompany humans into natural areas or if their unvaccinated status enhances the disease reservoir competency of the broader dog population (Banks and Bryant, 2007; Fiorello et al., 2006; Koster, 2008; Lenth et al., 2008).
2. Urban free-ranging dogs: Dogs that are not owned by humans, but are commensals, subsisting on garbage and other human-derived material (HDM) as their primary food source (Beck, 1975). They usually do not come into contact with wildlife, except in urban parks (Banks and Bryant, 2007; Lenth et al., 2008).
3. Rural free-ranging dogs: Dogs that are owned or peripherally associated with human habitations, but are not confined to a prescribed outdoor area. These include (but are not limited to) 'stray' dogs and owned farm and grazing companion dogs whose daily activity pattern may involve ranging that can bring them into contact with wildlife, especially when human habitations border wildlife reserves or other natural areas (Butler et al., 2004; Vanak, 2008).
4. Village dogs: Unconfined dogs that are associated with human habitations in rural environments, but rarely leave the immediate vicinity of the village (Macdonald and Carr, 1995; Vanak, 2008).
5. Feral dogs: Dogs that are completely wild and independent of human-derived food sources (Green and Gipson, 1994; Nesbitt, 1975).
6. Wild dogs: Dingoes and their hybrids in South-east Asia and Australasia that have a long history of independence from humans and are no longer considered domesticated (Corbett, 1995; Sillero-Zubiri et al., 2004).

Yet with the exception of urban free-ranging dogs, dingoes and their hybrids could actually fit all of these categories, as they are sometimes owned by people in urban and rural environments, they occur on the fringes of rural properties and aboriginal communities, and they also occur as completely wild populations that are entirely independent of humans (Hamilton, 1972; Letnic et al., 2012; Smith and Litchfield, 2009). These observations illustrate the difficulty in categorizing dogs, and raise questions about their ecological roles and to what degree we can generalize about dogs. With such classification complexity in mind, we assert that regardless of the name ascribed to a dog type and the categorization of where and how it lives, it is most important to focus on the ecological function of dogs within the spatial and temporal context of where they have been studied.

density and ranging behavior to the diversity and size of prey species available, and the presence and abundance of other sympatric and potentially competing predators.

2.2 Dog diet: influence of location and ranging behavior

Dogs are generalist and opportunistic predators, and their flexibility in this regard is illustrated in Figure 2.1. Between global regions, dog diet is highly variable and changes according to the resources that are locally available. In some cases the diets of dogs at a local scale may be dominated by one or two food types (e.g., human-derived materials (HDM) and vegetation in India or mammals in Zimbabwe; Figure 2.1). However, this does not imply that dogs are specialized with respect to their diets, but simply that they are able to capitalize on different food sources where and when these foods are abundant. This dietary plasticity is a major contributing factor to the success of dogs and their ability to survive in a diverse range of environments. In general, the diets of free-ranging dogs tend to contain a high proportion of vegetation (including fruits), HDM, and mammals, with birds, reptiles, amphibians, fish, and insects being less common prey items. As a comparison, the diet of dingoes contains a very high percentage of mammals and birds. Diet may be specialized further within a particular food class. As an example, in a comprehensive review of the diet of dingoes across Australia (Corbett, 1995), which included 12,802 diet samples collected between 1966 and 1986, 72% of prey identified were mammal. This mammal prey category was further subdivided, and comprised 20.3% large mammals, 29.7% small mammals, and 50% medium-sized mammals. This shows that dingoes have high consumption rates of medium-sized mammals.

The impact of dogs on wildlife is not only dependent on the size of their potential prey, but also, and perhaps more importantly, on the mean encounter rate between dogs and wildlife. It is clear that some categories of dogs (such as feral, wild dog, and rural free-ranging) can potentially have greater impacts on wildlife than others (such as urban or village dogs). The relationship between ranging behavior, location, and diet was explored by Vanak and Gompper (2009a). They found that all examples of urban dogs had a limited range and diets that were entirely human-dependent (Figure 2.1). However, as ranging behavior increased and the location of

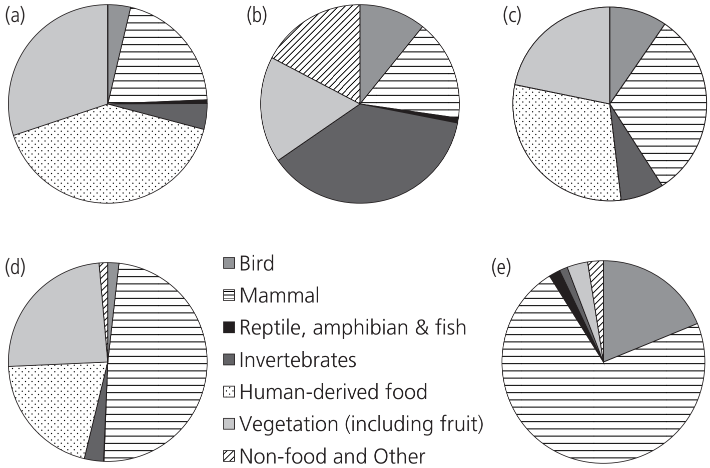

Figure 2.1 A comparison of rural dog diets derived from five studies on four continents. (a) Free-ranging dogs in India (Vanak and Gompper, 2009b); (b) Free-ranging dogs in Brazil (Campos et al., 2007); (c) Free-ranging dogs in Chile (Silva-Rodríguez et al., 2010); (d) Free-ranging dogs in Zimbabwe (Butler et al., 2004); (e) Dingoes in Australia (Corbett, 1995).

dogs became more rural, their diets become more opportunistic and less human-dependent. For example, five of eight (~63%) feral dog populations were almost entirely dependent on wild-caught food. Vanak and Gompper (2009a) concluded that the diet of dogs was closely linked to their location and ranging behavior, such that as dogs ranged farther into natural areas, they were more likely to have an impact as predators on wildlife.

2.3 Predation by dogs and its effects

In environments where predator guilds are largely intact and relatively diverse (e.g., parts of Asia, Africa, and North America), dogs often assume the roles of smaller-bodied and subordinate mesopredators, due to the presence of larger (apex) predators such as wolves and large cats (*Puma concolor* and *Panthera* spp.) (Butler et al., 2004; Dalerum et al., 2009; Ritchie and Johnson, 2009). However, when the predator guild is severely depleted or absent altogether, dogs can function as the top-predator. For example, in Australia, the ~15–20 kg dingo is similar in body size to the New World coyotes (*C. latrans*), and not considerably larger than Old World golden jackals (including the subspecies now considered a wolf species; Rueness et al., 2011) and side-striped jackals (*C. aureus* and *C. adustus*, respectively). Dingoes are considered the apex terrestrial predator due to the early extinction of much larger-bodied native carnivores, such as the marsupial lion (*Thylacoleo carnifex*) (Johnson, 2006; Wroe et al., 2005). Indeed, the situation in Australia reflects an overall trend whereby, due to the dramatic reduction or extinction of many larger predators around the globe (Estes et al., 2011), dogs now fulfill the role of apex predators in many environments. In addition to these influences, supplementation of the diet of dogs by humans may serve to exacerbate (through hyper-predation and diet switching) or potentially reduce the impact on wildlife by dogs (Silva-Rodríguez and Sieving, 2011, 2012; Vanak and Gompper, 2009a).

Dogs may suppress prey by killing them (lethal) or through instilling fear (non-lethal), which may cause changes in prey behavior, physiology, and habitat use (Clinchy et al., 2013; Ritchie and Johnson, 2009). Here, we explore these lethal and non-lethal effects of dogs in the context of their position in the carnivore guild, their population size, and their dependence on humans. We also draw a distinction between individual and population-level effects of dogs on prey. For example, a change in the behavior or the death of a prey animal has obvious effects on that individual, but if the animal would not have survived or its death allowed increased survival or reproduction of surviving members of its population, it is possible that no population-level effects would occur. That is, while changes in prey demography due to predation by dogs may alter population growth rates (e.g., because prey of different age or sex classes may differ in reproductive output), more generally a simplified framework for considering the risk that dogs represent to prey populations is that for predation to influence prey population size, mortality must be additive to existing causes of mortality rather than compensatory to those sources.

Examples of the impact of dogs on wildlife, according to their categorization and local context, are further explored in Table 2.1 below. What emerges from these studies is that dogs have the capacity to impact a range of wildlife species (often mammals and birds), via direct predation of individuals as well as through harassment and disturbance that results in lowered breeding success. It is also apparent that dogs, whether owned, un-owned, or wild, and whether restrained or free-ranging, may significantly impact other species across landscape gradients from urban settings to rural and wild habitats.

2.3.1 Direct killing

Dogs are capable of killing significant numbers of individuals of species, across a range of taxa and body sizes (see Vanak et al., Chapter 3; Young et al., 2011). For example, approximately 10,000 saiga antelope (*Saiga tatarica*) were reportedly killed annually by dogs in Kazakhstan (Sludskii, 1962). However, the extent of predation pressure exerted by dogs on prey populations varies considerably across studies. In some cases, no or low evidence of predation is found (e.g., Lowry and McArthur, 1978; Scott and Causey, 1973) or it is not possible to verify if dogs were the primary predators or scavengers (e.g., Bergeron and Pierre, 1981). Nonetheless,

Table 2.1 Examples of the impacts of dogs on prey according to dog categorization and habitat.

Type of dog	Location of study	Habitat	Major prey	Effects on prey	Reference
Owned	Australia	Suburban forest patches	None: human-provided	Reduced bird abundance and richness	(Banks and Bryant, 2007)
Urban free-ranging	New Zealand	Coastal	None: human-provided	Reduced shorebird breeding success	(Lord et al., 2001)
Rural free-ranging	Malaysia	Plantations	Wildlife	Reduced abundance	(Azhar et al., 2013)
Rural free-ranging or village	Australia	Forest and heath	Medium-large macropods	Harassment and killing; reduced abundance	(Meek, 1999)
Feral	New Zealand	Forest	Kiwi	Reduced population	(Taborsky, 1988)
Wild	Australia	Forest	Medium-large macropods	Elevated (compensatory) reproduction and reduced population size	(Robertshaw and Harden, 1986)

several studies have shown that dogs can have significant localized impacts that lead to decreases in some prey populations (Barnett and Rudd, 1983; Genovesi and Dupre, 2000; Iverson, 1978; Kruuk, 1972; Taborsky, 1988; Azhar et al., 2013).

Dogs may also limit species not only by killing adults, but also by affecting reproductive success. A study of the nesting success of freshwater crocodiles (*Crocodylus johnstoni*) in northern Australia (Somaweera et al., 2011) demonstrated that 72% of nests were opened by predators, and dingoes were responsible for 98% of these disturbances in one part of the study region and 54% in the other. Dogs are one of the main contributors to a declining kid/female ratio in mountain gazelles *Gazella gazella* in Israel (Manor and Saltz, 2004), and in a study of chiru (*Pantholops hodgsonii*), dogs killed 19 mostly young individuals that were malnourished and impeded by deep snow near a highway in Qinghai, China (Schaller, 1998). Similarly, dogs also have been reported to chase young argali *Ovis ammon* (Fedosonko and Blank, 2005) which, through increased energy expenditure and elevated stress levels, has the capacity to negatively impact argali condition, growth, and survival. However, the occurrence and severity of such effects remains to be determined for most species.

Elevated levels of predation such as those above may have severe consequences for some prey populations. In the Caicos Islands, an initial estimated population of 5,500 rock iguanas (*Cyclura carinata*) was nearly extirpated due to predation by both dogs and cats, *Felis catus* (Iverson, 1978), while in New Zealand a single dog was estimated to have killed at least 500 North Island brown kiwi (*Apteryx mantelli*) in a population of just 900 (Taborsky, 1988). Populations of rare species are likely to be particularly susceptible and less able to cope with dog predation, as small and isolated populations may not be able to recover due to insufficient reproduction and immigration that could compensate for dog-induced mortality.

Elevated levels of predation occur in another situation that can potentially exacerbate the negative impact of dogs on prey populations still further. In some situations the rate of killing by dogs greatly exceeds that necessary to meet the needs of the predator for food, and so prey carcasses frequently are not consumed after being killed. This has been termed 'surplus killing' (Kruuk, 1972). Two key reasons for surplus killing of prey by dogs include: (1) ineffective predator responses on the behalf of prey, particularly for species that have not coevolved with dogs and hence interactions with dogs are novel encounters for which prey are unlikely to exhibit effective anti-predator responses; and, (2) dogs have the ability to defend multiple kills due to their tendency to hunt and live in groups, which allows hunting to continue despite sufficient food often being available from an initial kill (Short et al., 2002). Short et al. (2002) noted in their study that they found no instances of surplus killing by cats, whereas it was a common feature of hunting by both red foxes (*Vulpes vulpes*) and dingoes. However, it remains conjectural whether this difference in hunting behavior between cats, foxes, and dingoes is widespread and consistent. Indeed, it is important to note that dogs do not always exhibit surplus killing, even for easily accessible prey (Kruuk and Snell, 1981).

Where surplus killing does occur the impacts of dogs on wildlife can be strong. In the example of dog predation on kiwis noted above, Taborsky (1988) commented that the presumed killing of 500 birds over a period of just 6 weeks would have met the energetic requirements of the single dog many times over. He also reported finding carcasses of kiwi that had been bitten but not eaten. In another example, Shepherd (1981) reported the killing of 83 red kangaroos (*Macropus rufus*) near a water hole over a 7-week period by a group of just 5 dingoes. Dingoes are known to target smaller individuals (juveniles and females) of sexually size-dimorphic prey, such as macropods (Grigg et al., 1989), as has also been found for wolves and their prey (Stahler et al., 2006). In Shepherd's (1981) study, 96% of the kangaroos killed were juveniles but, regardless of their size, their combined mass would have been more than enough to support the food requirements of the dingoes; indeed, many animals had been killed and not consumed at all, while others had been consumed only in part. Given that dogs often target juveniles and females, it is possible that relatively few individuals may be able to impact and suppress populations (Ritchie and Johnson, 2009). Wild and feral dogs in many parts of the world are notorious for their disproportionately intense attacks on livestock (e.g., Mech and Boitani, 2003; Short et al., 2002). In these situations prey are often aggregated, unable to run far owing to their confinement in a paddock, and may show inappropriate responses to the presence of dogs. These factors may combine to elicit continued killing behavior that ceases only when no further prey are conspicuous (Short et al., 2002).

2.3.2 Non-lethal effects

In a camera trapping study in Chile, Silva-Rodríguez and Sieving (2012) found that the probability of dog attacks (>85%) on a forest ungulate, pudu (*Pudu puda*), and the lethality of these attacks (50%), was high. These attacks are presumed to have invoked fear of dogs in pudu and explain why pudu distribution models are best explained by the probability of dog presence. In another study, Banks and Bryant (2007) investigated the responses of birds in suburban woodland sites to the presence of dogs. They found that the simple act of a person walking with a dog on a leash caused a 41% reduction in numbers of individual birds and a 35% reduction in species richness compared with control sites where no walking occurred; people walking alone induced less than half the disturbance compared with when they were walking a dog. This study showed further that dog-induced disturbance to birds was similar in areas where dog-walking occurred regularly compared to areas where it was not allowed, thus suggesting that birds did not become habituated to dog presence and could be at risk of long-term population declines.

Limited work has investigated the indirect effects of generalized disturbance by dogs (Weston and Stankowich, Chapter 4). It is clear from studies such as that by Lord et al. (2001), which found that off-leash dog walking disturbs shorebirds on their breeding nests, that the potential for indirect impacts on reproductive success is high if the prey species perceives dogs as a predation risk. Such effects have the capacity to alter the trophic structure of communities by causing lower-order predators (e.g., shorebirds) to avoid areas of habitat through fear (Laundre et al., 2001), which in turn may benefit smaller prey and/or the competitors of those species affected.

2.4 Human facilitation of dog predation of wildlife

The role of humans in mediating dog predation of other species is a critical consideration when attempting to manage dog populations and for conserving biodiversity. In some cases, ready supplies of food for dogs may serve to reduce impacts. Silva-Rodríguez and Sieving (2011) found that dogs preyed on most endemic and threatened mammals in their study region in Chile, but that the probability of dogs eating these prey was higher for poorly fed than adequately fed dogs. While these results suggest that feeding dogs may be an easy way to reduce their impacts on wildlife, there may be an unexpected and long-term negative consequence of such actions. By feeding dogs, which inevitably leads to sustaining dog populations at levels beyond their natural carrying capacity, humans may assist in maintaining constant and high predation rates on prey, which may become compounded during times when dogs have reduced access to human food and switch their diets to hunt native animals (Butler et al., 2004; Daniels and Bekoff, 1989).

In addition to human food subsidies for dogs, but far less understood, are the effects that habitat modification may play in mediating dog access to, and capture of, prey. Silva-Rodríguez et al. (2010) observed that the impact of dogs on pudu appeared to be exacerbated by roads that allowed dogs to increase their access to protected areas of forest. Habitat change (e.g., more roads, fragmentation, increased edge habitats) may serve to increase dog predation and threaten biodiversity by providing dogs with easier and more open access to hunt in otherwise complex habitats (Paschoal et al., 2012; Torres and Prado, 2010).

2.5 Ecosystem-wide effects of dogs

The non-consumptive effects of dogs on prey species are not restricted to their primary prey and competitors. For example, in the Strzelecki Desert of Australia, dingoes suppress the abundances of smaller invasive red foxes and in turn provide the dusky hopping mouse (*Notomys fuscus*) with refuge from predation by foxes (Letnic et al., 2009a). In areas where dingoes are present, hopping mice are less likely to occur in predator scats, are more abundant and forage less apprehensively (Figure 2.2; Letnic and Dworjanyn, 2011). These findings provide evidence that dingoes, through their suppression of fox populations, create a safer environment for hopping mice where the frequency of fatal encounters with foxes is reduced and the non-consumptive effects of foxes are lower.

The direct killing by dogs, or the fear dogs induce, may have strong negative effects on species depending on the environmental context and the identities of species comprising the faunal assemblage. The effects of dogs, however, go beyond just their direct predatory effects on individual species, and may extend to whole communities and ecosystems. At this broader ecosystem scale, the ecological effects of dogs become more complex and may include both negative and positive effects on the abundances and phenotypes of other species. Positive effects for some species can arise because dogs suppress the abundances and shape the activity patterns of smaller carnivores and herbivores. This suppression of smaller carnivores and herbivores by dogs can result in increases in the abundance and biomass of vegetation and small prey. Thus dogs can induce ecosystem-wide trophic cascades and indirectly facilitate increases in the abundances of species at lower trophic levels within the same food chain.

For example, in Australia, recent research has shown that dingoes, through their suppression of

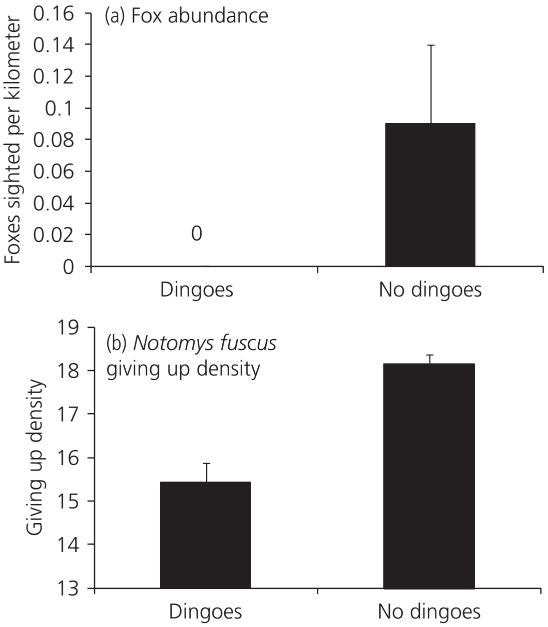

Figure 2.2 The presence of dingoes may alter the occurrence of smaller carnivore species as well as those taxa fed on by these smaller predators. (a) The abundance of red foxes, *Vulpes vulpes*, in areas where dingoes were present and where dingoes were rare. (b) The giving up density of dusky hopping mice, *Notomys fuscus*, determined using foraging trays where dingoes were present and rare. Lower giving up densities in the presence of dingoes indicate that *N. fuscus* foraged less apprehensively. Redrawn from Letnic and Dworjanyn (2011). Reproduced with permission from John Wiley & Sons.

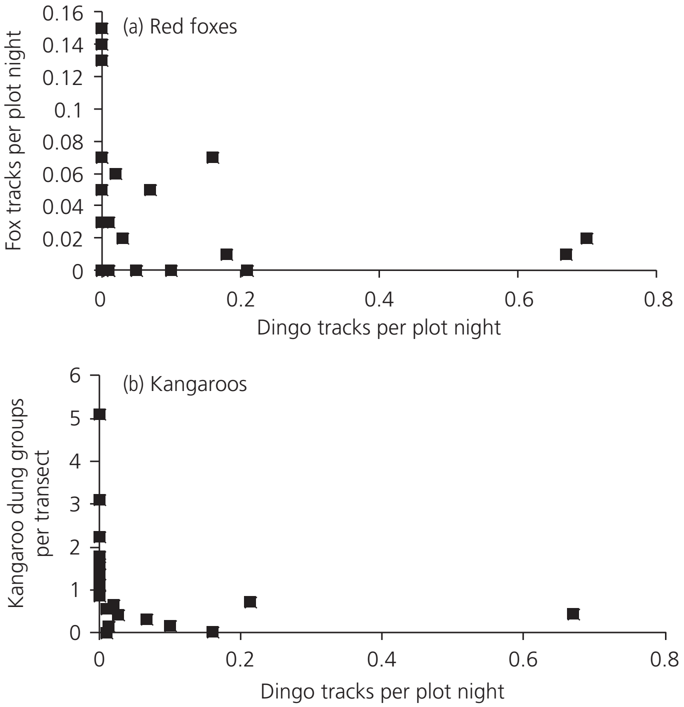

Figure 2.3 Dogs often have strong, nonlinear effects on the abundances of their competitors and prey. For example, plots of abundance indices of dingoes versus those of (a) red foxes, *Vulpes vulpes*, and (b) kangaroos, *Macropus* spp., in desert regions of Australia display threshold relationships which suggest that even low density populations of dingoes have strong suppressive effects on the abundances of mesopredators and herbivores. Redrawn from (a) Letnic et al. (2011b) and (b) Letnic and Crowther 2013. Reproduced with permission from John Wiley & Sons.

smaller predators and herbivores (Figure 2.3), induce ecosystem-wide trophic cascades with a net positive effect for biodiversity conservation (Letnic et al., 2012) (Figure 2.4). Within the last 200 years, two novel invasive predators have been introduced to the continent: the red fox and the domestic cat (Johnson, 2006). These species have been implicated in a large number (>20 species) of native mammal extinctions (Johnson, 2006). Comparisons of ecosystem attributes in areas where dingoes are actively controlled or not controlled (Figure 2.5) indicate that the impacts of these mesopredators are moderated by the presence or absence of dingoes (Johnson et al., 2007; Letnic et al., 2009b). Where studied, dingoes appear to suppress both cats and foxes, through the direct killing of individuals, but also by dingoes causing these subordinate predators to avoid them both spatially and temporally (Brook et al., 2012; Johnson and VanDerWal, 2009; Kennedy et al., 2012; Letnic and Dworjanyn, 2011). In addition, dingoes have been shown to be very effective at suppressing herbivore populations, contributing to more available food and shelter for native prey (Letnic et al., 2009b; Pople et al., 2000; Wallach et al., 2010). Together, the limiting effects of dingoes on cat, fox, and herbivore populations have been shown to protect smaller native prey, with native mammals in particular achieving higher diversity and abundance where dingoes are common (Letnic et al., 2012; Ritchie and Johnson, 2009; Ritchie et al., 2012; Wallach and O'Neill, 2009; Wallach et al., 2009, 2010).

Despite the benefits for biodiversity of dogs such as the dingo, in most other cases dogs appear to have significant detrimental effects. In Europe, for example, the common practice of dog walking may impact the European Nightjar *Caprimulgus europaeus* (Langston et al., 2007) and, as mentioned above, Banks and Bryant (2007) showed that bird diversity was reduced by more than one third and abundance by ~40% in woodland areas where dogs are walked. Where dogs are human-subsidized it would appear they frequently have negative effects.

Many studies, including a large number of those mentioned above, report the impact of dogs on prey species as measured and inferred primarily through

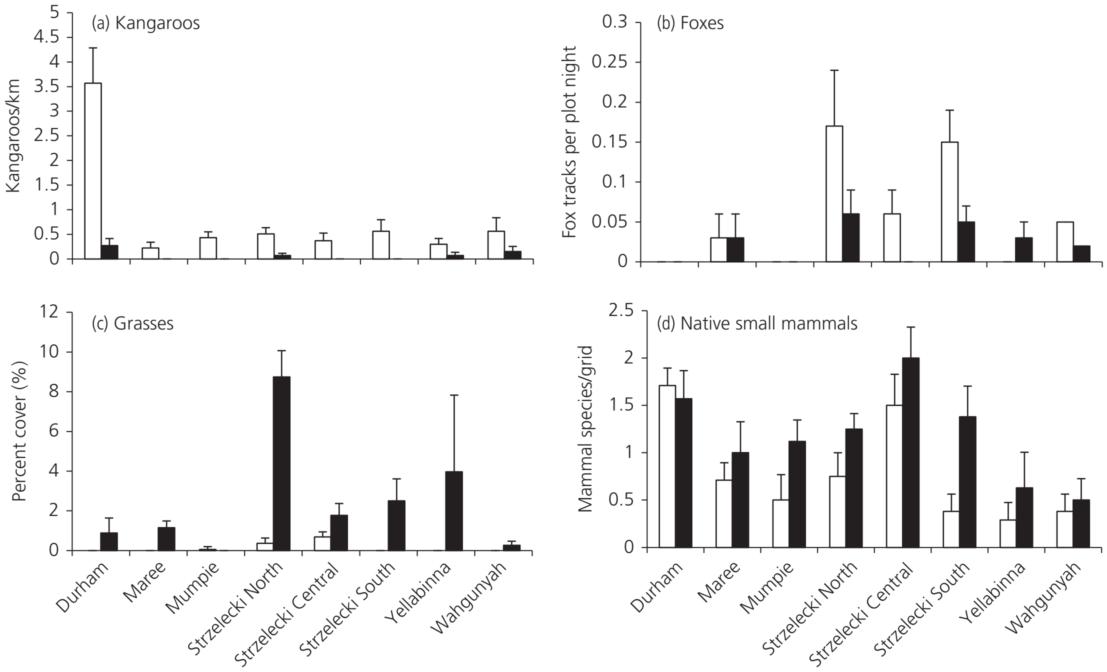

Figure 2.4 Evidence that dingoes induce a community-wide trophic cascade is provided by a comparison of the abundances of kangaroos, red foxes, and grasses and the species richness of small mammals at eight paired study sites situated on either side of the dingo fence in arid Australia (Letnic et al., 2009b). Within each pair of sites, dingoes were common in one (black bars) and rare in the other (white bars). Kangaroos and foxes were more abundant in the absence of dingoes. Grasses, the preferred forage of kangaroos, were more abundant in the presence of dingoes. Small mammals are subject to high rates of predation by foxes. Small mammal communities were more species rich in the presence of dingoes.

dog–wildlife habitat associations and dog diet (Hughes and Macdonald, 2013; Vanak and Gompper, 2009a; Young et al., 2011). With few exceptions what remains largely unknown and should be of concern is:

1. Whether dog predation on wildlife is additive (total annual mortality rate that is greater than what would occur without the predation) or compensatory (a population's total mortality remains unchanged because the other, presumably natural, causes of mortality, such as intraspecific competition for food, decrease to compensate for reduced density caused by dogs' predation; see Ritchie and Johnson, 2009).
2. Whether dogs are the principal drivers of decline for particular species, or whether they are contributing to the final decline or extinction of populations and species only because they have already been heavily impacted by other causal agents, such as habitat loss and disease. This is, in essence, a formulation of Caughley's contrast of small population versus declining population paradigms (Caughley, 1994).

There is no question dogs can pose a severe risk to species that are already threatened due to their low population sizes, but to assess the true impacts of dogs on other species, and hence to ensure appropriate biodiversity conservation and management, there is an urgent need for studies that address these two points.

2.6 Future research

From our review it is clear that dogs, spanning both wild and urban environments, interact with and affect biodiversity through a variety of important pathways. Most importantly, this occurs by dogs acting as predators or competitors within communities. In doing so, in some cases, they may contribute to the decline of already rare and threatened

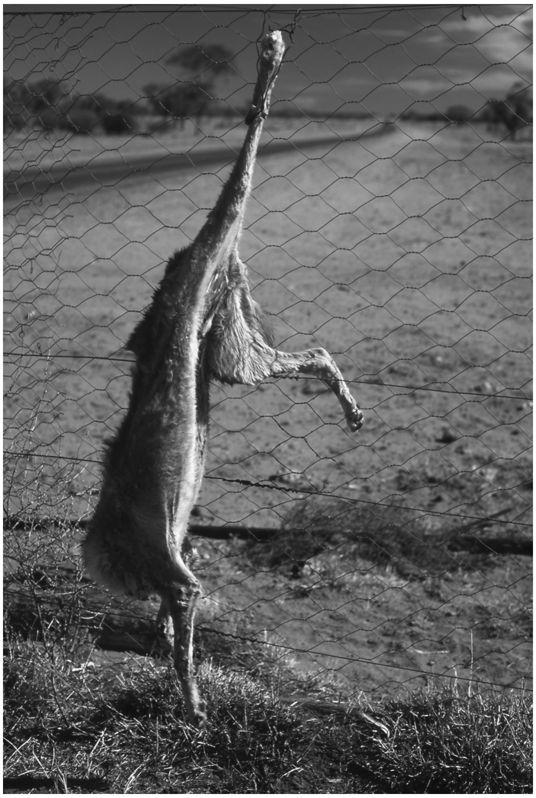

Figure 2.5 A dingo left to hang on Australia's dingo barrier fence. This sight is common across much of arid Australia, with conflict occurring between cattle and sheep production and dingoes. Dingoes are known to prey on livestock, sometimes causing significant economic damage (photo courtesy of Mike Letnic).

species, or indeed of common species. But in other instances, conversely, through their suppression of other predators (including invasive species) and herbivores, dogs may help to protect and promote biodiversity, maintaining the resilience of ecosystems. It is therefore difficult to generalize about the trophic roles and ecological functions of dogs, as they are environmentally and temporally context dependent.

Humans have important roles in either facilitating or reducing the effects of dogs on other wildlife. Through anthropogenic changes to habitat and the supply of food provided to dogs, humans may make areas more or less suitable for dogs, with concomitant effects on wildlife. However, despite dogs being the most widespread and abundant carnivores worldwide, there are surprisingly few studies of their ecology. Indeed, the impacts of cats are far better known (Fitzgerald and Turner, 2000; Loss et al., 2013; Medina et al., 2011; Woinarski et al., 2011), with this species being listed in the 100 worst invasive species globally (Lowe et al., 2004). Given the difficulty of working on cats, due to their largely solitary and cryptic nature and their generally lower abundance than dogs globally, it is surprising we know so little about dogs, including basic information such as their diets, hunting behavior, and whether they impact native species to the same or greater degrees as do other non-native species. There are many key questions that remain to be answered in regards to dogs, and below we suggest what we consider to be urgent research priorities.

First, determine more broadly the importance of differences in dog categories (Box 2.1). How do such differences influence the functional roles of dogs within similar environments? Further, how do the behaviors of these different categories of dogs differ? The dingo provides an excellent model system in which to examine these questions, given the large area and range of environments in which it occurs, and its complex Holocene and recent history. Determining the answer to these questions has strong implications for how we should manage the dingo and other dog populations worldwide.

Second, more work needs to be done comparing dog populations from across the world, in both similar and different environments. Do dogs in South America, North America, Asia, Europe, Australia, and Africa behave in similar ways? Much could be learned from such comparisons and the ensuing knowledge would aid a global synthesis about dogs and their roles as trophic regulators. At present we have too few studies to do this.

Third, more experimental work on dogs (dog removals or dog additions) is needed to establish their effects, as the majority of work to date has been largely observational and correlative.

Finally, a greater focus on dog behavior is required, rather than just focusing on the effects of dogs in relation to their abundance. Dogs may affect other species in sublethal ways as these species respond to perceived predation risk. These indirect and subtle effects are only just beginning to be appreciated. Given the densities of dogs in many parts of the world, their perception as a predatory risk by other members of the animal community suggests that they may alter community structure even when not having a significant direct predatory effect.

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