

Dogs *Canis familiaris* as carnivores: their role and function in intraguild competition

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ABSTRACT

1. Dogs *Canis familiaris* are the world's most common carnivore and are known to interact with wildlife as predators, prey, competitors, and disease reservoirs or vectors.
2. Despite these varied roles in the community, the interaction of dogs with sympatric wild carnivore species is poorly understood. We review how dogs have been classified in the literature, and illustrate how the location and ranging behaviour of dogs are important factors in predicting their interactions with wild prey and carnivores.
3. We detail evidence of dogs as intraguild competitors with sympatric carnivores in the context of exploitative, interference and apparent competition.
4. Dogs can have localized impacts on prey populations, but in general they are not exploitative competitors with carnivores. Rather, most dog populations are highly dependent on human-derived food and gain a relatively small proportion of their diet from wild prey. However, because of human-derived food subsidies, dogs can occur at high population densities and thus could potentially outcompete native carnivores, especially when prey is limited.
5. Dogs can be effective interference competitors, especially with medium-sized and small carnivores. Dogs may fill the role of an interactive medium-sized canid within the carnivore community, especially in areas where the native large carnivore community is depauperate.
6. Dogs can also be reservoirs of pathogens, because most populations around the world are free-ranging and unvaccinated. Diseases such as rabies and canine distemper have resulted in severe population declines in several endangered carnivores coexisting with high-density dog populations. Dogs can therefore be viewed as pathogen-mediated apparent competitors, capable of facilitating large-scale population declines in carnivores.
7. Based on this information, we propose conceptual models that use dog population size and ranging patterns to predict the potential for dogs to be intraguild competitors. We discuss how interactions between dogs and carnivores might influence native carnivore communities.

Keywords: *Canis familiaris*, carnivore community, free-ranging dog, human-subsidized predator, interference competition, intraguild predation

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INTRODUCTION

Dogs *Canis familiaris* are the world's most common carnivores, introduced by humans across the globe (Wandeler *et al.*, 1993). Throughout the world, most dogs engage in some form of

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free-ranging behaviour irrespective of whether they are owned. In the course of this free-ranging activity, dogs interact with wildlife at multiple levels, including as predators (Kruuk & Snell, 1981; Campos *et al.*, 2007), prey (Edgaonkar & Chellam, 2002), competitors (Butler, du Toit & Bingham, 2004; Vanak, Thaker & Gompper, 2009), and disease reservoirs or vectors (Cleaveland *et al.*, 2000; Funk *et al.*, 2001; Butler *et al.*, 2004; Fiorello, Noss & Deem, 2006). Despite this, the impact of dogs on natural environments has not been well documented, and we know little about the nature and ecological impact of interactions between dogs and sympatric carnivores.

Growing evidence documenting competitive dynamics between wild carnivores suggests that intraguild competition affects the persistence and abundance of carnivore populations and thus can have dramatic consequences for the structure of carnivore communities (Karanth & Sunquist, 2000; Linnell & Strand, 2000; Creel, Spong & Creel, 2001; Caro & Stoner, 2003). When sympatric carnivore populations compete for resources, this competition results in spatial patterns such as complete or partial exclusion of at least one species and scattered interspecies territories (Johnson, Fuller & Franklin, 1996; Creel *et al.*, 2001). Larger carnivores suppress populations of other guild members by direct predation for food and through two forms of interspecific competition: (i) exploitative competition, whereby asymmetric competitive abilities in obtaining limited resources explain patterns of species co-occurrence; and (ii) interference competition, whereby patterns of species co-occurrence result from direct interactions such as spatial exclusion, harassment, or at an extreme, direct mortality, known as intraguild predation (Case & Gilpin, 1974; Palomares & Caro, 1999; Laundré, Hernandez & Altendorf, 2001). Exploitative competition in carnivores has not been directly demonstrated, but can be inferred in cases where competitors such as lions *Panthera leo* and hyaenas *Crocuta crocuta* kleptoparasitize cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus*, resulting in appreciable hunting costs (Creel *et al.*, 2001). On the other hand, interference competition and intraguild predation are common among carnivores, and there are many well-documented examples of these phenomena. For example, intraguild predation by lynx *Lynx pardinus* on mongooses *Herpestes ichneumon* and genets *Genetta genetta* results in clear interspecific habitat segregation in the Doñana National Park in south-western Spain (Palomares & Delibes, 1994). In Africa, cheetahs have been observed to avoid lions, even though this may lead to them using habitat with lower prey availability (Creel *et al.*, 2001).

Interference and exploitation competition are ultimately perceived as a function of food limitation, and thus researchers interested in carnivore community structure generally focus first on patterns of prey availability. However, a third interspecific interaction may also function to explain patterns of carnivore spatial distribution: apparent competition. Apparent competition is not a form of true competition. Rather it represents an outcome in which the distribution of putatively competing species is mediated indirectly by a third factor, such as a shared predator or shared parasite (Holt, 1977; Holt & Lawton, 1994; Price, Westoby & Rice, 1998). In other words, patterns of interaction that seem to be the result of competition are actually driven by the distribution and effects of a third species. For example, the replacement of red squirrels *Sciurus vulgaris* by grey squirrels *Sciurus carolinensis* in the UK appeared initially to be an example of interference competition (Wauters & Gurnell, 1999), but later work suggests that the replacement is mediated by parapox virus; the differential sensitivity of the two host species to the virus allows one species to act as a reservoir for the parasite, which in turn results in population decline of the second host species (Rushton *et al.*, 2000; Tompkins, White & Boots, 2003). Patterns conforming to apparent competition may also occur among carnivores, although the process of apparent competition is rarely formally

suggested because researchers are generally knowledgeable about the potential for pathogens to be driving the observed interspecific interactions (Roemer, Gompper & Van Valkenburgh, 2009)

Given these strong intraguild interactions between carnivores, it is striking that the effect of one of the most common carnivores, the dog, on sympatric native carnivores has received little attention. In this review, we discuss the potential for dogs to act as intraguild competitors with other carnivores in the context of exploitative, interference and apparent competition. Our ultimate goal is to assess how dogs and native carnivores interact, and how the addition of dogs to a landscape might influence native carnivore communities.

Classifying free-ranging dogs

Modern dogs evolved from the grey wolf *Canis lupus*, and current evidence suggests a single origin in Asia (Savolainen *et al.*, 2002). The domestication process resulted in a change in body size and cranio-dental configuration (Clutton-Brock, 1995; Coppinger & Schneider, 1995). As a result of these morphological changes, dogs are capable of consuming and surviving on a wide range of food types, from scavenged human-derived garbage to mammalian prey that may be several times their body mass. However, the socio-ecology and diet of dogs vary with their dependence on humans, and this in turn affects their competitive interactions with wild carnivores. For example, MacDonald & Carr (1995) observed distinct differences in the social organization of free-ranging dogs that lived in villages and those that occupied the more rural areas. Village dogs defend territories and are mostly solitary with some loose social grouping. On the other hand, 'sylvatic' dogs lead a more 'wolf-like' existence, often forming packs and occasionally roaming alone (Boitani *et al.*, 1995). Although village dogs are entirely dependent on human-derived food, the free-ranging 'sylvatic' dogs are more opportunistic and supplement their diet with wild-derived foods, even though they are not cooperatively hunting (Boitani *et al.*, 1995; MacDonald & Carr, 1995).

Indeed, the dependence of dogs on human-derived materials (HDM), which we define as including scavenged human food refuse, crops, livestock, farmed animals and human faeces, as well as food directly fed to dogs, is typical for the vast majority of free-ranging dog populations for which diet has been studied. Although many studies have shown that dogs kill and feed on wildlife, these studies have been mainly prey-focused, examining the mortality of particular prey species as a function of dog predation (e.g. Lowry & McArthur, 1978; Yanes & Suárez, 1996; Manor & Saltz, 2004). Such studies give an incomplete picture of dog foraging ecology. A reliance on HDM, even when wildlife is also killed and consumed, is more common (Butler & du Toit, 2002; Atickem, 2003; Butler *et al.*, 2004; Vanak, 2008; Vanak & Gompper, 2009). Given that several studies have, however, revealed the ability of dogs to subsist on a diet comprised solely of wildlife (Kruuk & Snell, 1981; Triggs, Hans & Cullen, 1984; Campos *et al.*, 2007), the reliance on HDM may be a function of the opportunistic nature of dogs and learned behaviour rather than more definitive ecological constraints.

The variance in the diet of dogs may also be a function of location and the extent to which dogs range freely. In much of the developed world, dogs are confined, remaining indoors or constrained to a proscribed outdoor area by the owner. However, dog populations often range freely in urbanized regions of both developed and less developed countries (Beck, 1975; Oppenheimer & Oppenheimer, 1975; Daniels & Bekoff, 1989; Pal, 2003). In rural areas of most of the world, much of a dog's daily activity involves unconfined movements, even when the dog is owned or affiliated with specific human habitations. Several efforts have been made to categorize dogs, and most authors agree that these categories are flexible and that dogs

may fall into more than one category or switch categories (Nesbitt, 1975; Daniels & Bekoff, 1989; Green & Gipson, 1994; Boitani *et al.*, 1995; MacDonald & Carr, 1995). We describe some of the most commonly used categories below:

1. **Owned dogs:** dogs that are owned and restricted in movement to a proscribed 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 status of the broader dog population (Fiorello *et al.*, 2006; Banks & Bryant, 2007; Koster, 2008; Lenth, Knight & Brennan, 2008).
2. **Urban free-ranging dogs:** dogs that are not owned by humans but are commensals, subsisting on garbage and other HDM as their primary food source (Beck, 1975). They usually do not come into contact with wildlife, except in urban parks (Banks & 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 proscribed outdoor area. These include (but are not limited to) 'stray' dogs and owned farm and pastoral 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 & Carr, 1995; Vanak, 2008).
5. **Feral dogs:** dogs that are completely wild and independent of HDM as food sources (Nesbitt, 1975; Green & Gipson, 1994).
6. **Wild dogs:** dingoes, feral dogs and their hybrids in Southeast Asia and Australasia that have a history of independence from humans and are no longer considered domesticated (Corbett, 1995; Sillero-Zubiri, Hoffmann & Macdonald, 2004).

To determine how location and ranging play a role in the diet of dogs, we reviewed studies ($n = 21$) of dog ecology that included some description of the location, diet and ranging of a population of dogs. We categorized dogs' locations as: (i) urban, if they were in cities or suburbs with high human densities and had little or no contact with wildlife habitat; (ii) rural, if the dogs were in villages or farmland with low human densities and had moderate contact with wildlife habitat; or (iii) wild, if the dogs lived in native habitats with no human contact. Ranging behaviour was categorized as: (i) limited, if the dogs had home ranges of <100 ha or were confined to particular neighbourhoods or villages; (ii) wide-ranging, if the dogs had home ranges of >100 ha or moved freely between villages and in the surrounding landscape; or (iii) feral, if the dogs were free-ranging and avoided human association. Based on description and dietary analyses, we classified the diet of dogs as: (i) human-dependent, if the entire diet consisted of HDM, either from direct feeding or through scavenging of human refuse; (ii) opportunistic, if the diet consisted mainly of HDM but included some portion of wild-caught food; and (iii) wild, if the majority of the diet consisted of wild-caught food.

We excluded fully confined dogs in any location under the assumption that they pose no direct threat to wildlife. Although some authors describe urban populations of dogs as free-ranging or feral, these dogs have a limited range, often as small as 0.26 km² (Beck, 1975). Adequate information on certain combination of categories was lacking (urban and wide-ranging, urban and feral, wild and limited range), and we suspect that dog populations fitting these categories are absent or rare.

Of the studies that were included in this review, all examples of urban dogs indicate that they have a limited range and have diets that are entirely human-dependent (Fig. 1). As

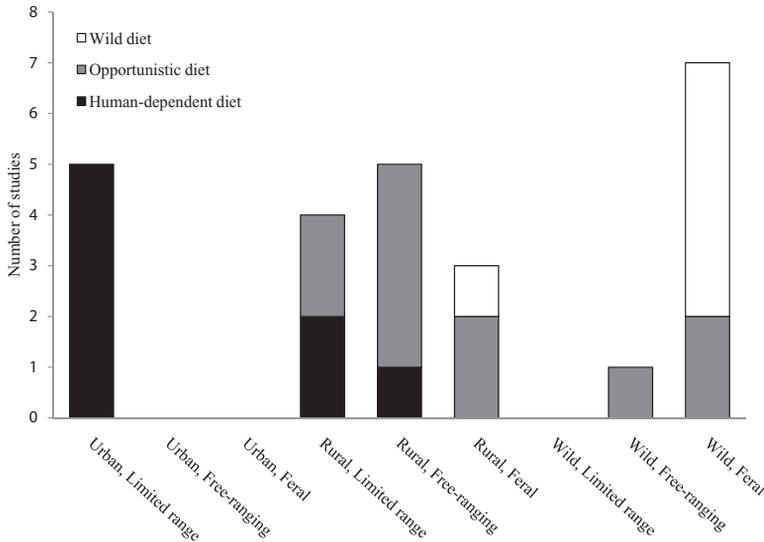


Fig. 1. Numbers of studies (total $n = 21$) in which the location (urban, rural, wild), ranging behaviour (limited, wide-ranging, feral) and diet (human-dependent, opportunistic, wild) of dogs are reported. List of sources: *Urban, Limited range*: (Fox, 1975; Oppenheimer & Oppenheimer, 1975; Rubin & Beck, 1982; Daniels, 1983; Daniels & Bekoff, 1989); *Rural, Limited range*: (Berman & Dunbar, 1983; Daniels & Bekoff, 1989; MacDonald & Carr, 1995; Meek, 1999); *Rural, Wide-ranging*: (MacDonald & Carr, 1995; Meek, 1999; Butler & du Toit, 2002; Atickem, 2003; Manor & Saltz, 2004; Vanak, 2008); *Rural, Feral*: (Gipson & Sealander, 1976; Kamler, Ballard & Gipson, 2003a; Campos *et al.*, 2007); *Wild, Wide-ranging*: (Daniels & Bekoff, 1989); *Wild, Feral*: (Scott & Causey, 1973; Kruuk & Snell, 1981; Taborsky, 1988; Boitani *et al.*, 1995; Yanes & Suárez, 1996; Mitchell & Banks, 2005; Glen, Fay & Dickman, 2006).

ranging of rural dogs increases, their diets become more opportunistic and less human-dependent. For example, five of eight feral dog populations are almost entirely dependent on wild-caught food (Fig. 1). Thus, the diet of dogs is closely linked to their location and ranging behaviour. As dogs range farther into natural areas, it is also more likely that they will encounter native carnivores and will interact with them as predators, prey and competitors.

Dogs as predators and prey of native carnivores

Many large carnivores kill and consume smaller carnivores (Palomares & Caro, 1999; Donadio & Buskirk, 2006). Being opportunistic foragers, dogs are also known to include smaller carnivores in their diet. For example, in an examination of feral dog diet in Brazil, remains of small carnivores such as coati *Nasua nasua* and lesser grison *Galictis cuja* were found in dog scats (Campos *et al.*, 2007), although it is unclear what percentage of these was scavenged. In general, there is very little information on the role of dogs as intraguild predators, although this is likely to be more than an occasional occurrence. This is evident from several studies of Australian wild dogs in which the remains of red foxes *Vulpes vulpes* are regularly found in dog scats, suggesting that dogs are actual predators of these animals (Newsome *et al.*, 1983; Marsack & Greg, 1990).

Dogs can also form an important prey item in the diets of several carnivores, especially those living close to humans. For instance, leopards *Panthera pardus*, lions and hyaenas in Africa are known to regularly consume dogs. In Zimbabwe, Butler *et al.* (2004) reported that

53% of all confirmed dog kills were by these carnivores. Wolves in Finland consumed almost all dogs that they killed, although food acquisition may not have been the primary motive for predation (Kojola *et al.*, 2004). Coyotes *Canis latrans* in urban and rural areas of North America regularly kill pet dogs (Grinder & Krausman, 1998). In India, several studies have shown dogs to be an important component of leopard diet (Mukherjee & Sharma, 2001; Edgaonkar & Chellam, 2002; Singh *et al.*, 2007). High dog densities may even be responsible for increased leopard–human conflict in some areas if leopards come into greater contact with humans in the process of hunting dogs close to human habitation (Athreya, 2006; Athreya *et al.*, 2007).

Dogs as exploitative competitors

Exploitative competition occurs when species share the same limited resources, and one species can potentially outcompete the other either through numerical or behavioural superiority in acquiring this shared resource (Petren & Case, 1996). Exploitative competition among carnivores has rarely been demonstrated even though there is extensive evidence of dietary overlap between species. This is because demonstrating the occurrence of exploitative competition between two species requires a number of factors to be established first (Petren & Case, 1996), including (i) reduced survivorship or reproduction as a function of the limited and shared resource; (ii) reduced access to the shared resource; and (iii) a lack of direct interference. Indeed, exploitative competition has only been experimentally demonstrated in a few plants and animals (Dorchin, 2006; Smallegange, van der Meer & Kurvers, 2006; Bonaccorso *et al.*, 2007). Nonetheless, the existence of exploitation competition is a common assumption among carnivore ecologists (Jhala & Giles, 1991; Sillero-Zubiri & Gottelli, 1995; Johnson *et al.*, 1996).

It is unclear whether dogs are effective competitors with other carnivores for wild-caught food in most natural environments. There is little evidence in the literature that pressure from dog predation on wild prey is high enough to decrease prey availability for native large carnivores. Scott & Causey (1973) found no evidence of predation on deer by rural free-ranging dogs. Similarly, Lowry & McArthur (1978) noted that dogs were responsible for only 12 deer deaths in the Couer d'Alene drainage, Idaho, USA, in 1975. Although deer remains were found in 15.5% of 58 dog stomachs analysed in south-eastern Quebec, it is not possible to determine how much of this prey may have been scavenged (Bergeron & Pierre, 1981). However, several other studies have shown that dogs can have significant localized impacts that can lead to a decrease of some prey populations (e.g. Iverson, 1978; Kruuk & Snell, 1981; Barnett & Rudd, 1983; Taborsky, 1988; Genovesi & Dupre, 2000). For example, dogs are one of the main contributors to a declining kid-to-female ratio in mountain gazelles *Gazella gazella* in Israel (Manor & Saltz, 2004).

Despite the potential for negative impacts of dogs on prey communities, it is still unclear whether exploitative competition can occur between dogs and wild carnivores. For example, Atickem (2003) found low overlap between sympatric free-ranging dog and Ethiopian wolf *Canis simensis* diet based on scat analysis, and concluded that exploitative competition may not be an important interaction between these two species. Food habits of free-ranging dogs and Indian foxes *Vulpes bengalensis* reveal a similar pattern, wherein dogs have low dietary overlap with foxes, since dogs are heavily dependent on HDM and foxes consume mainly wild-caught food (Vanak, 2008; Vanak & Gompper, 2009). Dietary studies of wolves at the same study site in India (Habib, 2007) also indicate a lack of resource overlap with dogs.

The lack of dietary overlap between dogs and wild carnivores is not surprising because, with a few exceptions (Mitchell & Banks, 2005; Glen, Fay & Dickman, 2006; Campos *et al.*,

2007), most dog diets are composed principally of HDM (Green & Gipson, 1994; Butler & du Toit, 2002; Atickem, 2003; Vanak, 2008; Vanak & Gompper, 2009). Butler *et al.* (2004) suggest this as a major reason that dogs may be ineffective competitors with wild carnivores. However, a caveat to this suggestion is that, because of human subsidies, free-ranging dogs can reach high population densities (Daniels & Bekoff, 1989; Butler *et al.*, 2004), and can therefore have a large numerical effect on native prey by keeping predation pressure constant on prey populations.

One notable situation in which dogs effectively compete with other carnivores is when dogs are the top predator in the ecosystem. The extensive studies of food habits of Australian wild dogs (dingoes, feral dogs and their hybrids) show that dogs depend almost exclusively on wild-caught food, including macropods, small marsupials, rodents and other small vertebrates and invertebrates (Newsome *et al.*, 1983; Corbett & Newsome, 1987; Marsack & Greg, 1990; Glen & Dickman, 2005; Mitchell & Banks, 2005; Glen & Dickman, 2008). Because of this dependence on wild-caught food, dingoes compete with both native marsupial carnivores and introduced eutherian carnivores. The introduction of the dingo into Australia is also believed to have ultimately contributed to the extinction of the thylacine *Thylacinus cynocephalus* and the extirpation of the Tasmanian devil *Sarcophilus harrisii* from mainland Australia (Dickman, 1996), thus changing the structure of the native carnivore community. The extinct thylacine and the dingo may have had high dietary niche overlap and therefore high levels of competition (Wroe *et al.*, 2007). In the modern context, dingoes compete with introduced carnivores such as red foxes and feral cats *Felis catus*. Several studies demonstrate high niche overlap between dingoes and foxes (Pianka's index = 0.69 to 0.94; Mitchell & Banks, 2005; Glen *et al.*, 2006) as well as between dingoes and native marsupial carnivores, such as the spotted tailed quoll *Dasyurus maculatus* (Pianka's index = 0.66; Glen & Dickman, 2008). At the level of the individual, exploitation competition may favour wild carnivores, such as foxes, over dogs. However, given the large numbers of dogs in some areas, exploitation at the population level may ultimately favour dogs over wild carnivores.

Furthermore, dogs may be effective exploitative competitors with native carnivores in situations where dogs and native carnivores compete for the use of HDM. For example, dogs scavenge and thus may indirectly compete with native carnivores by reducing the carcass biomass available. Butler *et al.* (2004) observed free-ranging dogs on the periphery of a wildlife reserve in Zimbabwe and found that dogs dominated vultures at domestic and wild animal carcasses and were effective, although subordinate, competitors for carcasses with lions, leopards, spotted hyaenas and side-striped jackals *Canis adustus* (Butler & du Toit, 2002). Similarly, Ethiopian wolves may be denied potential food resources, as ungulate carcasses are quickly monopolized by dogs (Sillero-Zubiri & Macdonald, 1997). This pattern of scavenging was also observed in western India, where livestock carcasses on the periphery of villages were dominated by dogs and thus were less available for golden jackals *Canis aureus* (Aiyadurai & Jhala, 2006).

Dogs as interference competitors

Interference competition is manifested by direct interactions such as spatial exclusion, harassment, or at an extreme, mortality by intraguild predation (Holt & Polis, 1997). In response to interference competition, the subordinate competitor uses one of two strategies to reduce encounters with dominant competitor(s): avoiding range overlap, or modifying range use to reduce interactions while still allowing for home range overlap. For example, grey and red foxes avoid areas where coyotes are present (Fedriani *et al.*, 2000; Gosselink *et al.*, 2003), coyotes avoid wolf territories (Crabtree & Sheldon, 1999; Berger & Gese, 2007), and Arctic

foxes *Alopex lagopus* avoid red fox territories (Elmhagen, Tannerfeldt & Angerbjorn, 2002; Tannerfeldt, Elmhagen & Angerbjorn, 2002). In these cases, interference competition results in non-overlapping territories, in favour of the dominant competitor.

There are also more subtle spatial and temporal behavioural choices that subordinate competitors make to avoid interference competition. African hunting dogs avoid prey-rich habitat because of the presence of lions (Creel *et al.*, 2001), thereby incurring a reduction in hunting efficiency. After the reintroduction of wolves into Yellowstone National Park, USA, coyotes reduced foraging and increased vigilance when they were in wolf territories (Switalski, 2003). Kit foxes *Vulpes macrotis* are known to use several anti-predatory tactics, such as multiple diurnal den use and habitat partitioning, to avoid interference competition with coyotes (Nelson *et al.*, 2007). These examples demonstrate that the mere presence of a dominant competitor results in risk aversion that is manifested by the reduced use of areas that would otherwise be selected for.

Examples demonstrating that sympatric carnivores alter their habitat use and behaviour to avoid competition from dogs when dogs are the dominant species are emerging from Australia and India. In New South Wales, Mitchell & Banks (2005) found high overall dietary niche overlap between foxes and dingoes, but foxes avoided bait stations that were previously visited by dingoes even though the species overlapped spatially at the landscape level. Indices of fox abundance were also lower in areas where dingoes were present than in areas inside dingo-proof fences (Newsome, Lunney & Dickman, 2001). Foxes avoiding dingoes at shared resources (Lundie-Jenkins, Phillips & Jarman, 1993) and the fact that dingoes may actually kill foxes result in the observed inverse relationship between dingo and fox activity patterns (Mitchell & Banks, 2005).

These general patterns of intraguild interactions are expected to exist between free-ranging dogs and native carnivores elsewhere in the world, even when dogs are not the top predator in the ecosystem. For example, in the presence of a dog, Indian foxes significantly reduced visitation rates to experimentally manipulated rich food sources; reduced consumption of food; and increased vigilance behaviour (Vanak *et al.*, 2009). Vanak & Gompper (2009) also noted lower levels of HDM in the diets of Indian foxes than in the diets of dogs and speculated that the presence of dogs may prevent foxes from accessing HDM resources. The reactions of foxes to dogs were similar to those of red foxes to golden jackals described by Scheinin *et al.* (2006); this strengthens the argument that dogs are perceived as intraguild predators by smaller carnivores (Vanak, 2008; Vanak *et al.*, 2009). Such aversion of dogs is not limited to small carnivores, as dogs may deter wolves from accessing garbage dumps in Italy, simply by their presence in larger numbers (Boitani *et al.*, 1995).

Although direct interactions between dogs and other carnivores are only rarely observed, even the temporary presence of dogs can affect wild carnivore activity and landscape use. Recent studies have shown avoidance or change in activity patterns by carnivores in multiuse recreation areas used by humans with dogs (George & Crooks, 2006; Lenth *et al.*, 2008; Reed & Merenlender, 2008). In these studies, measures of carnivore presence were compared in areas without recreation trails and in areas with trails that were used by humans and companion dogs. George & Crooks (2006) reported that the probability of detecting bobcats *Lynx rufus* decreased with increasing human activity (due to dog walkers), and that bobcats displayed temporal displacement in areas used by hikers, bikers and dogs. However, the presence of dogs could not be separated from that of humans in this study, and therefore the results do not imply a direct effect of dogs alone. A more direct relationship between bobcat use of habitat and dog presence was shown by Lenth *et al.* (2008), who found lower numbers of bobcat detections in wildlife areas where dogs were allowed to roam freely than in areas

where dogs were prohibited. However, the same study also showed that red fox detections were higher in areas used by dogs, which the authors suggest may be due to the generalist nature of the red fox and its propensity to tolerate human presence for access to anthropogenic resources.

The most extreme form of interference competition is the killing of the subordinate competitor, the phenomenon known as intraguild predation. Intraguild predation can be categorized into cases in which the species is killed and consumed and cases in which it is not consumed (Palomares & Caro, 1999). It is intriguing when the subordinate species is not consumed after intraguild predation (Palomares & Caro, 1999; Amarasekare, 2002), as this suggests that the dominant species is directly reducing numbers of the putative resource competitor (Roemer *et al.*, 2009). Interference competition without consumption has been well documented among mammalian Carnivora (Palomares & Caro, 1999; Donadio & Buskirk, 2006).

Dogs have been reported to suffer from intraguild predation without consumption by larger carnivores. Dogs are killed by wolves (Boitani & Zimen, 1979; Zimen & Boitani, 1979; Fritts, Paul & Paul, 1989; Jhala, 1993; Pulliainen, 1993; Naughton-Treves, Grossberg & Treves, 2003; Jethva & Jhala, 2004; Kojola *et al.*, 2004; Habib, 2007), coyotes (Howell, 1982; Bider & Weil, 1984; Timm *et al.*, 2004), mountain lions *Puma concolor* (Torres *et al.*, 1996) and bears *Ursus* spp. (e.g. Lott, 2002; Goldenberg, 2008). In most cases these dogs may be free-ranging or confined pets which are attacked in the vicinity of human habitation, or they may be hunting or companion dogs that are attacked in wild habitats (Kojola & Kuittinen, 2002).

Conversely, we know less about the extent of dogs killing wild carnivores without consumption as these cases have only been reported anecdotally. Trained dogs have been used to hunt red foxes in the UK, other parts of Europe, and elsewhere since the 16th century (Itzkowitz, 1977; Orendi, 2007), but the killing of foxes, jackals and other carnivores by free-ranging dogs in the wild is only occasionally reported. For example, Pils & Martin (1974) reported an attack on a red fox den in Wisconsin, USA, by 'three free-roaming mongrel dogs' which resulted in the death of a lactating female. Dogs have killed kit foxes (Ralls & White, 1995) and Indian foxes (Vanak, 2008). Three feral dogs were observed killing a coyote in Kansas, USA (Kamler *et al.*, 2003b), and farm dogs were responsible for killing 20 of 77 eastern spotted skunks *Spilogale putorius* that were found dead (Crabb, 1948). Dahmer (2001, 2002) reported the killing of 11 small Indian civets *Viverricula indica* by stray dogs in Hong Kong between 1998 and 2002. One of the more famous anecdotal reports of dogs killing carnivores led to the rediscovery of the black-footed ferret *Mustela nigripes* in Wyoming, USA, when a farm dog brought in a freshly killed individual of the putatively extinct species (Miller, Reading & Forrest, 1996). In most of the above cases the dogs did not consume their quarry.

Dogs as apparent competitors

Apparent competition among carnivores may result from one carnivore subsidizing the presence of another carnivore, and thus also putatively reducing the density of other sympatric carnivore species. For example, feral cats in Australia can better survive droughts by scavenging from dingo kills (Paltridge, Gibson & Edwards, 1997), and this subsidy gives them an advantage over native marsupial carnivores such as quolls (Glen & Dickman, 2005). On the other hand, apparent competition among carnivores is more likely to result from shared parasites than from shared predators. Shared parasites may be an important driver in structuring assemblages of species (Rushton *et al.*, 2000; Tompkins, Draycott & Hudson,

2000a; Tompkins *et al.*, 2003). This kind of interspecific interaction is a form of apparent competition because the parasite–host interactions result in the appearance of a competitive dynamic (Holt, 1977; Holt & Pickering, 1985; Price *et al.*, 1998; Tompkins *et al.*, 2000b). Apparent competition has been documented in several taxa, ranging from bacteria and insects to birds and large mammalian predator–prey communities. In general, the rarer or more susceptible host species is reduced or eliminated as the parasite increases in the less susceptible or more abundant reservoir host (e.g. Tompkins *et al.*, 2000a; Morris, Lewis & Godfray, 2004; Power & Mitchell, 2004). Apparent competition via shared parasites may ultimately turn out to be a common and important component of community structure (Hatcher, Dick & Dunn, 2006; Holt & Dobson, 2006) but has only rarely been investigated in carnivore communities (Roemer *et al.*, 2009).

Many important microparasites of carnivores are shared by multiple species; several of these are enzootic in dog populations and may be transmitted to native carnivores (Fiorello *et al.*, 2004). Such spillover events may be common, but the extent to which they lead to epidemics in wild species is unclear. For instance virtually all canid species are highly susceptible to rabies virus, canine distemper virus (CDV) and canine parvovirus (CPV), and in some cases these three viruses are primary drivers of carnivore population dynamics (Cleaveland *et al.*, 2007). We suggest that this spillover can be considered in light of apparent competition and can shape local guild structure.

The role of dogs as reservoirs of pathogens that could have a significant impact on wild carnivore populations came into the spotlight when a series of rabies and CDV epidemics affected African wild dogs, lions, hyenas and jackals in the Serengeti in 1994 (Funk *et al.*, 2001; Cleaveland *et al.*, 2007). Since then, several studies have indicated that pathogen spillover resulting from interactions between wild carnivores and dogs has led to significant population declines in a wide range of species from several carnivore families including canids, felids, hyaenids, phocids, mustelids, viverrids and procyonids. These spillover events have been reviewed extensively (Laurenson *et al.*, 1998; Deem *et al.*, 2000; Funk *et al.*, 2001; Cleaveland *et al.*, 2007). For example, the critically endangered Ethiopian wolf population suffered a severe population decline due to outbreaks of rabies transmitted from dogs (Sillero-Zubiri, King & MacDonald, 1996; Whitby, Johnstone & Sillero-Zubiri, 1997; Randall *et al.*, 2006). Similarly, spillover of CDV from dogs to lions in Tanzania (Roelke-Parker *et al.*, 1996; Cleaveland *et al.*, 2000) and rabies from dogs to African wild dogs (Gascoyne *et al.*, 1993; Kat *et al.*, 1995) resulted in epidemics and population crashes. Notably, there is very little documented competition for resources among these species in the above cases and yet, due to shared parasites, dogs were the cause of large-scale mortality in sympatric carnivore species.

Conservation practitioners have attempted, with mixed success, to mitigate some of these effects by vaccination programmes aimed at the reservoir (dogs) or the susceptible hosts (wild carnivores). For example, mass vaccination of dogs around the Serengeti–Mara Ecosystem against rabies was sufficient to control rabies in dogs (Cleaveland *et al.*, 2007). However, vaccination of African wild dogs against rabies in the Serengeti was less successful and the population went locally extinct (Woodroffe *et al.*, 2004; Cleaveland *et al.*, 2007). On the other hand, reactive vaccination of Ethiopian wolves as well as a mass vaccination of dogs met with greater success in reducing the occurrence of rabies that had spilled over from dogs (Haydon *et al.*, 2006; Randall *et al.*, 2006). Such examples clearly illustrate how dogs can harbour shared parasites that sometimes result in widespread epidemics and population declines in species of conservation concern, in patterns similar to those expected under a framework of apparent competition. These case studies also reiterate the importance of dogs as an integral

part of diverse ecosystems and why it is important to consider the role of dogs in the management and conservation of native carnivore populations.

CONCEPTUAL MODELS OF RISKS POSED BY DOGS TO WILD CARNIVORES

Dogs pose variable levels of risk to sympatric carnivores when they are exploitative, interference and apparent competitors. Although a range of characteristics, such as the location and degree of complexity of the sympatric carnivore community, can affect the competitive risk posed by dogs, based on the literature reviewed above, two characteristics are particularly predictive. Population density and ranging behaviour are fundamental predictors of ecological impact for any competitor. We conclude this review with conceptual models that predict the level of risk dogs may pose to (or the level of competitive advantage they may have over) sympatric native carnivores under the three types of competition discussed above. For conceptual simplicity, we separate the effects of dogs for each form of competition, but we acknowledge that dogs are often simultaneously exploitative, interference and apparent competitors of native carnivores.

Exploitative competition

In general, dogs are poor exploitative competitors of wild carnivores. However, human-subsidized dog populations can become large and thus can potentially outcompete native carnivores for a limited prey base. We expect that the effects of exploitative competition are driven primarily by population density, with ranging behaviour having a lesser effect (Fig. 2a). Regardless of how widely dogs range, individually they will not outcompete native carnivores for wild-caught food because wild-caught food is less important for dogs than is HDM. However, as dog population density rises, the combined effect of large population size with moderate to high ranging behaviour may have moderate competitive effects, especially where native carnivore populations are relatively small.

Interference competition

Dogs are potential interference competitors, especially for medium-sized and small carnivores. We predict that the ranging behaviour of dogs has a greater effect on their ability to be interference competitors than the size of the population, as the former mediates the extent to which dogs have the potential to interact indirectly with most wild carnivores. Even at low population densities, wide-ranging dogs can be effective interference competitors (Fig. 2b), because ultimately interference competition is manifested in interactions between individuals. However, as population size increases, there is an additive effect with ranging behaviour on the competitive risk posed by dogs, as larger numbers of wide-ranging dogs can collectively compete with a larger section of the carnivore community, especially with the small and medium-sized carnivores, which make up the bulk of the carnivore community (Roemer *et al.*, 2009).

Apparent competition

Pathogen-mediated apparent competition is perhaps the largest threat that sympatric carnivores face from dogs. While exploitative and interference competition affects individuals, the effects of apparent competition due to shared parasites can be felt at the population level because initial parasite transmission from dogs to native carnivores can be amplified by subsequent intraspecific transmission in native carnivore populations. Dogs can be excellent apparent competitors, particularly when they occur at high population densities (Fig. 2c).

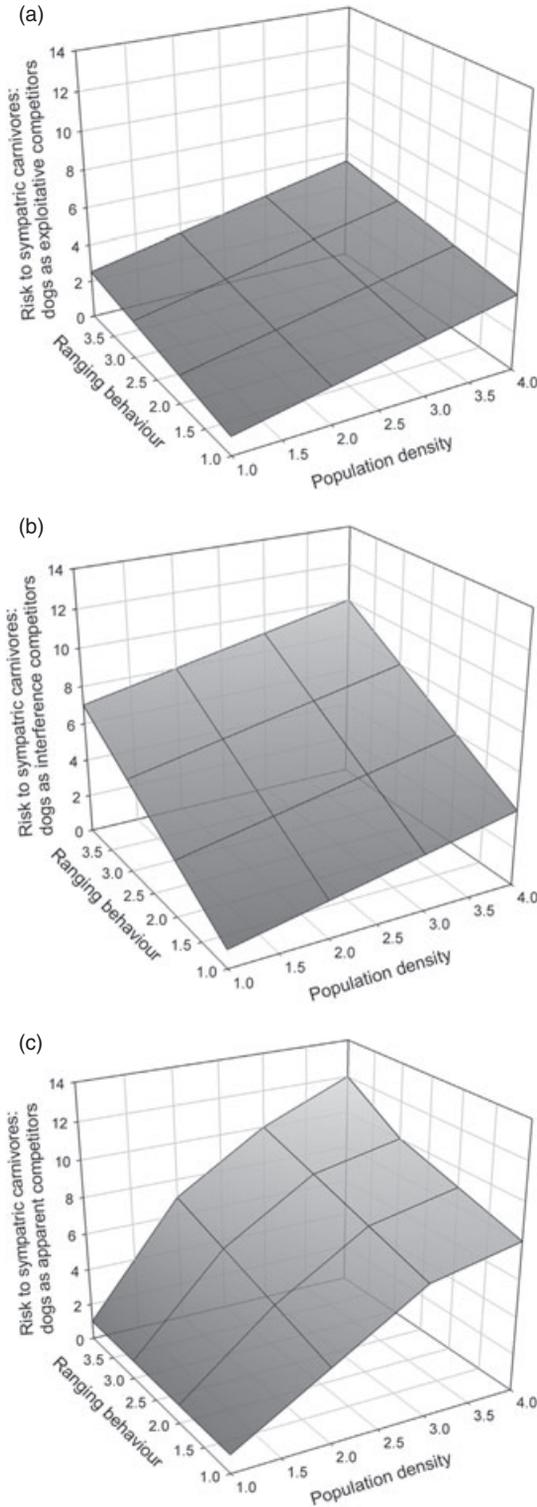


Fig. 2. Conceptual models of the effect of dog population density and ranging behaviour on the competitive risk that dogs may pose to sympatric native carnivores in terms of (a) exploitative competition, (b) interference competition and (c) apparent competition. Scales are arbitrary and depict magnitude of effect.

Because a minimum threshold population density is likely to be required for pathogens to remain enzootic in unvaccinated dog populations, low densities of dogs are unlikely to have a large effect, irrespective of their ranging behaviour. However, once the minimum threshold population density for pathogen reservoir status (enzootic status) is achieved, ranging behaviour becomes more important. An unvaccinated wide-ranging dog that is part of a high-density, infected population has a high chance of coming into contact with carnivores or of leaving infective materials in the environment.

CONCLUSIONS AND FUTURE RESEARCH

Dogs, by virtue of their close association with humans, are distributed worldwide. Although they may differ morphologically from wolves because of the domestication process, they still retain characteristics that make them potentially important members of the carnivore guild. Dogs are also generally subsidized by humans wherever they exist and are therefore insulated from food scarcity. They are also shielded from intraguild feedback mechanisms (such as intense predation by larger carnivores) by safe refuges in human habitations. These direct and indirect subsidies can result in high-density populations of free-ranging dogs even in rural areas where native carnivore communities are relatively intact. For example, Butler & Bingham (2000) report a population of at least 1.36 million dogs in Zimbabwe's communal lands, with an annual growth rate of 6.5%. Even in developed countries such as the USA, dog populations can be locally abundant (150 dogs/km² in Newark, New Jersey; Daniels, 1983; 431 dogs/km² on portions of Navajo reservation lands in Arizona; Daniels & Bekoff, 1989). The combined effect of large population sizes and free-ranging behaviour is problematic for conservation practitioners when these enhanced dog populations influence species of conservation concern.

The aim of future research should be to elucidate spatial and behavioural interactions between dogs and wild carnivores. We know that carnivores can dramatically influence the distribution and density of co-predators through direct and indirect competition (Palomares & Caro, 1999; Caro & Stoner, 2003). Even when direct aggression and intraguild predation can be detected among competing species, the subtler indirect effects of interference competition may sometimes escape notice. The various competitive roles of dogs are still largely unknown. As discussed in this review, dogs may have large-scale effects on native carnivores despite not competing strongly for food. Because dogs can range widely into wild habitats, they may extend the deleterious human-associated edge effects into areas of conservation concern. Carnivores in habitats outside protected areas may be especially vulnerable to these effects. Although it is increasingly recognized that free-ranging dogs are a matter of serious concern, there are still few sustained large-scale initiatives to address this problem.

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