

Top-dogs and under-dogs: competition between dogs and sympatric carnivores

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3.1 Introduction

In many natural and semi-natural systems worldwide, dogs (*Canis familiaris*) are an integral part of the carnivore community (Gompper, Chapter 1). Until recently, the role of dogs as mid-sized members of the carnivore guild, and how they shape the structure of native carnivore communities, has garnered little attention. Of late, however, a suite of studies across the world has highlighted several key aspects of the competitive dynamics that occur between dogs and sympatric members of the carnivore community (Table 3.1). These studies have demonstrated that dogs often compete with native carnivores for food, and that smaller carnivores may react to dogs as they would to any other mid-sized predator: with increased vigilance, lowered food intake, avoidance of dog-dominated habitat types, or complete spatial separation. These studies have also shown that the types and intensity of interactions between dogs and subordinate predators are likely influenced by several factors, including, but not limited to:

1. Relative position within the native carnivore community: In several areas dogs are the largest mammalian carnivore and hence assume the role of the apex predator (e.g., Australasia), whereas in others they may be part of a guild of carnivores where they occupy a mesopredator position (e.g., India, Africa). The nature of the interactions of

dogs with sympatric carnivores will depend on their position in the interference hierarchy, with dogs being either at the receiving or giving end of aggressive interactions, or both.

2. Dependence on human-derived food: Interference competition may be seen ultimately as a function of food acquisition. Although most dog populations are heavily dependent on human-derived food (HDF), this is variable depending on their degree of association with humans. Dogs in urban areas are almost completely dependent on HDF, whereas at the other extreme, wild dogs (such as the dingo) and feral dogs are fully dependent on wild-caught food (Vanak and Gompper, 2009b). Thus, it can be assumed that competition with wild carnivores is likely highest in areas where dependence on wild resources is highest.
3. Population density: The competitive effects of dogs can also be influenced by their density and their tendency to form packs. Even without human involvement, packs of dogs are capable of overpowering not just herbivores several times their size (Corbett, 1995), but also carnivores such as foxes, coyotes, and jackals (Vanak and Gompper, 2009b; Van Sittert, 1998). Furthermore, numerical superiority can improve competitiveness in obtaining resources such as carcasses. Thus, competitive ability may be a function of density at the local scale.

Table 3.1 Summary of studies that examine or report the competitive effects of dogs on sympatric carnivores.

Country	Predator guild*, besides dog	Interactions studied	Effect of dogs	Reference
Australia	Large marsupials	Dog (dingo) → thylacine and Tasmanian devil	Direct killing and possibly more efficient resource exploitation, resulting in extinction of both marsupials on the Australian mainland [§]	Corbett 1995; Glen and Dickman 2005; Wroe et al. 2007; Fillios et al. 2012
Australia	Invasive red fox, feral cat, and small to mid-size native predators	Dog (dingo) → fox and cat	Killing, harassment, spatial interference (fox, cat) with corresponding benefit to native species via mesopredator release [#]	Corbett 1995; Glen and Dickman 2005; Mitchell and Banks 2005; Johnson and VanDerWal 2009; Letnic et al. 2009; 2011; 2012; Purcell 2010; Wallach et al. 2010; Brawata and Neeman 2011; Kennedy et al. 2012; Moseby et al. 2012
Brazil	Maned wolf, crab-eating fox, puma, South American coati, crab-eating raccoon, tayra	Dog → Maned wolf	Interference on maned wolf, no evidence of effects on crab-eating raccoon [§]	Lacerda et al. 2009
Brazil	Crab-eating fox, South American coati, crab-eating raccoon, tayra, lesser grison, oncilla, margay	Dog → Crab-eating fox and coati	Evidence of negative association with crab-eating fox and coati, no evidence of effects on tayra and small cats [§]	Espartosa 2009
Chile	Puma, chilla fox, guigna, Molina's hog-nosed skunk, American mink (invasive)	Dog → Chilla fox	Killing, harassment, spatial interference [#]	Silva-Rodriguez et al. 2010a
Ethiopia	Ethiopian wolf	Dog → ← Ethiopian wolf	Outcome of interactions depended on numerical superiority [#]	Atickem et al. 2010
India	Wolf, golden jackal, jungle cat, Indian fox	Dog → Indian fox	Killing, harassment, spatial interference [#]	Vanak et al. 2009; Vanak and Gompper 2010
India	Striped hyena, wolf, jungle cat, Indian fox	Dog → golden jackal	Dominance at carcasses [§]	Aiyadurai and Jhala 2006
Madagascar	Fossa, small-toothed civet, Malagasy civet, ring-tailed mongoose, broad-striped mongoose, small Indian civet, domestic cat	Dog → Fossa and ring-tailed mongoose	Fossa nearly absent from sites with high dog occupancy. Capture rates of fossa decreased as capture rates of dogs increased. Ring-tailed mongoose changed activity patterns when dogs and the invasive small Indian civet were present. No effects reported for other three species analyzed [§]	Gerber et al. 2012; Barcala 2009
Poland	Red fox, domestic cat	Dog → Red fox, cat	Negative association between occurrence of dogs with cats and red foxes [§]	Krauze-Gryz et al. 2012
Spain	Red fox, badger, domestic cat, Egyptian mongoose,	Dog → Badger	Spatial exclusion [§]	Revilla et al. 2001
United Kingdom	Red fox	Dog → Red fox	Killing of adults and pups	Harris 1981
Zimbabwe	Lion, spotted hyena, leopard, black-backed jackal, side-striped jackal	Lion, spotted hyena, leopard → Dog → jackals	Dominance over jackals at carcasses on wildlife reserve peripheries; spatial exclusion of jackals (in communal lands and on commercial farmland peripheries) [#]	Butler 1998; Butler and Bingham 2000; Butler and du Toit 2002; Butler et al. 2004

* Arranged in order of decreasing body size, # Direct evidence, § Indirect or correlative evidence. Arrows indicate direction of dominant interactions.

4. Ranging behavior: The ability of dogs to range widely into natural habitats increases the potential for them to compete with sympatric carnivores not just at the periphery of human settlements but also in native habitats. Vanak and Gompper (2009b) proposed a conceptual model wherein the competitive effects of dogs were affected not just by their densities, but also by their ranging behavior (Figure 3.1). According to this model, the maximum impact on sympatric carnivores is expected from a high-density dog population that also exhibits wide-ranging behavior.

Other than in Australasia, few dog populations are truly independent of humans (Vanak and Gompper 2009b). Ultimately, their close relationship with human society strongly influences all the above factors. Whether dogs are herding dogs, guard dogs, village dogs, farm dogs, or simply household pets determines in large part their ranging behavior, population density, and feeding habits. Close association with human habitation may also provide refugia from top-down interference competition or predation in systems where larger predators exist (Butler et al., Chapter 5).

Here, we review the literature to examine competitive dynamics between dogs and sympatric carnivores as a function of their position in the carnivore community and the type of competition (see Box 3.1).

3.2 Dogs as interference competitors

Predators that share common resources will often show potential to compete with each other, but even if resources are abundant and overlap is minimal, interference competition may still occur via direct aggression and intraguild killing or via cues that drive spatial segregation (Box 3.1). Interference competition between mammalian carnivores is well documented, and it is expected that dogs as abundant mid-sized carnivores will be either recipients of top-down interference or will be the aggressors. However, the competitive dynamics that occur between dogs and sympatric carnivores can be expected to vary considerably across the world as a function of related human densities, land use types, and the place of dogs in the native carnivore community.

3.2.1 Where dogs are top-predators

In many regions of the world, dogs have assumed the role of top-predators for a variety of reasons: the absence of larger mammalian carnivores, the extermination of large carnivores either by humans or other factors, or the restriction of larger carnivores to non-human dominated landscapes (Gompper and Vanak, 2008). Some potential examples of the competitive ability of dogs as top-predators come

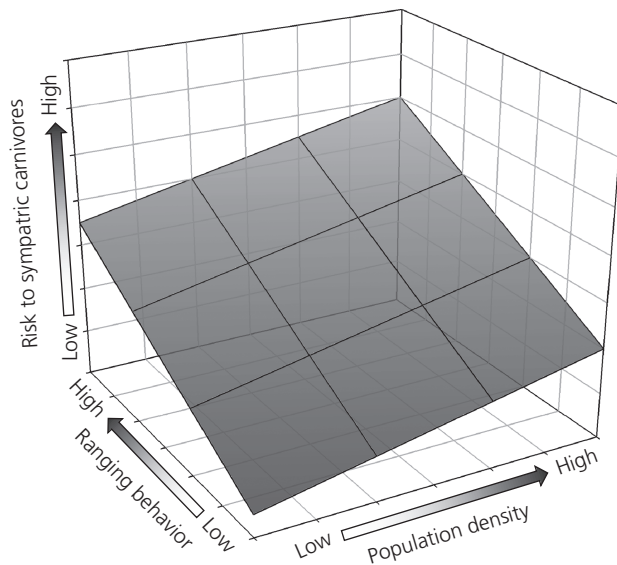


Figure 3.1 Conceptual model of the effect of dog population density and ranging behavior on the risk dogs may pose as interference competitors to sympatric native carnivores. Adapted from Vanak and Gompper (2009b). Reproduced with permission from John Wiley & Sons.

Box 3.1 Competition in its various forms

Within the carnivore guild, sympatric species compete fiercely with each other and this interaction manifests as either a form of: (1) exploitative competition, whereby differences in acquisition of limited resources determine the competitive outcome (Figure 3.2a); or (2) interference competition, whereby direct interactions such as spatial exclusion, harassment, or even intraguild killing determine the outcome (Figure 3.2b). Exploitative competition in carnivores has not been directly demonstrated but can be inferred, especially for species that kleptoparasitize the kills of others. Interference competition and intraguild killing, however, are common among carnivores and there are many well-documented examples of these interactions.

Interference competition

Mechanisms of interference competition usually follow an allometric relationship, with larger carnivores directly dominating smaller ones. Smaller species thus have a strong imperative to minimize interference interactions, especially when there are potentially lethal consequences (Creel et al., 2001; Palomares and Caro, 1999; Ritchie and Johnson, 2009). Studies that examine single or multiple features of interference competition among carnivores are numerous and have been reviewed extensively in the literature (Creel et al., 2001; Glen and Dickman, 2005; Ritchie and Johnson, 2009; Ritchie et al., 2012; Roemer et al., 2009). Here we highlight some of the patterns.

In general, interference competition can affect subordinate competitors in several ways: by limiting spatial distributions (Creel et al., 2001; Ritchie and Johnson, 2009), constraining habitat selection (Mitchell and Banks, 2005;

Vanak and Gompper, 2010; Fisher et al., 2013), or reducing prey encounter rates (Atwood and Gese, 2008; Creel et al., 2001; Palomares et al., 1996; Vanak et al., 2009). In response, subordinate competitors use a suite of spatial and temporal behavioral strategies to minimize encounters with the dominant competitor(s). These include avoiding range overlap altogether, or modifying range use within overlapping home ranges (e.g., Berger and Gese, 2007; Crabtree and Sheldon, 1999; Elmhagen et al., 2002; Fedriani et al., 2000; Gosselink et al., 2003; Tannerfeldt et al., 2002). In these cases, interference competition results in non-overlapping territories, in favor of the dominant competitor.

There are also more subtle spatial and temporal behavioral choices that subordinate competitors make to avoid interference competition. African hunting dogs (*Lycaon pictus*) avoid prey-rich habitat due to the presence of lions (*Panthera leo*) (Creel et al., 2001), thereby incurring a reduction in hunting efficiency. After the reintroduction of wolves (*C. lupus*) into Yellowstone National Park, USA, coyotes (*C. latrans*) 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. Ultimately, interference competition can result in reduced individual fitness and population sizes (Ritchie and Johnson, 2009).

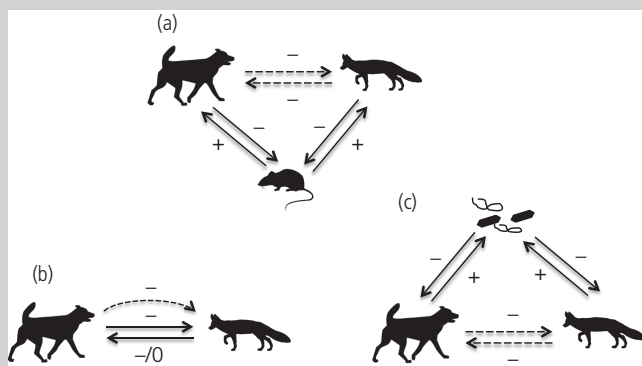


Figure 3.2 Illustrations of exploitative (a), interference (b), and apparent competition (c). Solid arrows denote direct effects, dashed arrows indicate indirect effects, and signs indicate effect on species. Adapted from Glen and Dickman (2005). Reproduced with permission from John Wiley & Sons.

continued

Box 3.1 *Continued***Exploitative competition**

Exploitative competition occurs when species share the same limited resources, and one species can potentially out-compete the other either through numerical or behavioral superiority in acquiring this shared resource (Petren and Case, 1996). Demonstrating the occurrence of exploitative competition between two species requires a number of factors to first be established: (1) reduced survivorship or reproduction as a function of the limited and shared resource; (2) reduced access to the shared resource; and (3) a lack of direct interference (Petren and Case, 1996). Because of this, exploitative competition among carnivores has rarely been demonstrated even though there is extensive evidence of dietary overlap between species. Indeed, exploitative competition has only been experimentally demonstrated in a few plants and animals (Bonaccorso et al., 2007; Dorchin, 2006; Smallegange et al., 2006). Nonetheless, the existence of exploitative competition is a common assumption among carnivore ecologists (Jhala and Giles, 1991; Johnson et al., 1996; Sillero-Zubiri and Gottelli, 1995).

Apparent competition

A third kind of interspecific interaction may also function to explain patterns of carnivore spatial distribution: apparent competition. While interference and exploitation competition are perceived as a function of resource limitation, the outcome of apparent competition results from a third factor indirectly mediating the distribution of apparently competing species (Figure 3.2c) (Holt, 1977; Holt and Lawton, 1994; Price et al., 1998). For example, populations of Sierra Nevada bighorn sheep (*Ovis canadensis californiana*) declined due to predation from mountain lion (*Puma concolor*), whose

numbers were primarily sustained by the more abundant mule deer (*Odocoileus hemionus*). Hence, without factoring in predation by mountain lion, the decline in bighorn sheep appeared to be due to competition with mule deer (Johnson et al., 2013). Similarly, the critically endangered island fox (*Urocyon littoralis*) faced near extinction due to predation by golden eagles (*Aquila chrysaetos*), whose unnaturally large populations were in turn sustained by invasive feral pigs (*Sus scrofa*) (Roemer et al., 2001, 2002). 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. However, apparent competition 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 et al., 2000, 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 and Pickering, 1985; Price et al., 1998; Tompkins et al., 2000). Apparent competition has been documented in many 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., Morris et al., 2004; Power and Mitchell, 2004; Tompkins et al., 2000). Apparent competition via shared parasites may ultimately turn out to be a common and important component of community structure (Hatcher et al., 2006; Holt and Dobson, 2006) but has only rarely been explored as such in carnivore communities (Roemer et al., 2009).

from Australia. Prior to the arrival of the dingo in Australia around 4,000 years ago, the largest mammalian predators were the thylacine (*Thylacinus cynocephalus*) and the Tasmanian devil (*Sarcophilus harrisi*). Both of these marsupial predators disappeared from the Australian mainland after dingoes had become established, the thylacine around 3,500 years ago and the devil within the last millennium (Corbett, 1995). As both species persisted in the absence of dingoes in Tasmania, it has been commonly assumed that their demise on the mainland was caused by competition from the dingo (Corbett, 1995;

Wroe et al., 2007). The evidence is ostensibly compelling. In Tasmania, thylacines (15–35 kg) reportedly hunted kangaroos and wallabies in open forest and woodland areas, pursuing their quarry singly or in pairs at night (Paddle, 2002). They may also have hunted a range of smaller prey (Attard et al., 2011; Wroe et al., 2007). Tasmanian devils (5–15 kg) occupy similar habitats and also pursue wallabies and smaller mammals, but include much scavenged material in their diet (Jones and Barmuta, 1998). Both species probably would have overlapped markedly in these aspects of their resource use with the dingo.

Although dingoes are smaller than the Tasmanian thylacine, at 12–22 kg, their ability to hunt in packs may have given them a competitive edge over the marsupial predators and suppressed their populations via either extreme interference competition or superior exploitation of shared prey (Letnic et al., 2012). Recent evidence further indicates that mainland thylacines were smaller than their counterparts in Tasmania and that mainland females were considerably smaller than dingoes (Fillios et al., 2012). This potentially would have placed mainland thylacines under great pressure, especially from direct interference interactions.

Despite the elegance of this interpretation, the arrival of the dingo coincided with several environmental changes that may have been more detrimental to the marsupials, making it difficult to resolve the competitive impact of the dingo on its own. The mid Holocene experienced intense climatic changes as the continent recovered from the extremes of the last glacial maximum (Brown, 2006). There was also an increase in the human population and in peoples' hunting efficiency due to the adoption of technologies, such as edge-ground and hafted stone tools, that improved considerably on previous weaponry (Johnson and Wroe, 2003; Letnic et al., 2012). Coincident with (and perhaps caused by) these changes, archeological records suggest that people exploited smaller-bodied prey progressively from the mid to late Holocene

(Fillios et al., 2012). As this suite of changes affected the Australian mainland (but Tasmania to a much lesser extent), the arrival of the dingo would have had an additive impact on the mainland populations of the thylacine and devil and may perhaps have delivered the competitive *coup de grace*. The longer tenure of devils in the presence of dingoes on the Australian mainland may have arisen from their ability to exploit carrion and small prey that formed a more minor part of the diet of the dingo; that is, there was perhaps more dietary niche separation and hence less competition between devils and dingoes than between dingoes and thylacines (Corbett, 1995).

As the apex mammalian predator in Australia, dingoes could be expected to dominate in direct encounters with most other predators; moderate to large crocodiles would have ascendancy over them, although their eggs and young still may be vulnerable (Somaweera et al., 2011). No studies have yet addressed whether sympatric predators recognize and avoid cues of the presence of the dingo. There is some evidence that native prey species can distinguish the odor or other cues left by dingoes and domestic dogs and reduce their activity after exposure (Carthey and Banks, 2012; Parsons and Blumstein, 2010); native predators plausibly also would have experienced selection to reduce their risk of an encounter with dingoes.

In many parts of the world with high human population densities, native predators have either been

Box 3.2 Old dogs and new dogs: competition between dingoes and recent dogs

As a general rule, the form of competition that occurs between two species will be the same form of competition that is apparent between conspecifics. Thus, we might expect that interference will be the dominant form of competition between different groups of dogs, with exploitation playing no, or a very minor, role. Studies of wild animals generally bear out this expectation: pairs or packs of dingoes, for example, use howling and scent-marking to defend the boundaries of their territories, and chase intruders if they are detected (Purcell, 2010). There is no evidence for exploitative interactions between packs.

But what if dogs differ from each other in subtle ways? Dingoes and recently introduced domestic dogs co-occur throughout much of Australia and differ in aspects of their size, skull morphology, coloration, behavior, and seasonality of reproduction (Corbett, 1995). Dingoes occur in most parts of the continent except where they are heavily persecuted in the south-east and south-west, whereas wild domestic dogs tend to be most active near townships and settlements. There is some evidence that wild domestic dogs seldom successfully breach the territorial boundaries established by dingo packs, and fare poorly due to interference (Corbett, 1995). Conversely,

continued

Box 3.2 *Continued*

large breeds of domestic dog, such as the Maremma, are being used increasingly on rural properties to protect flocks of sheep from the ravages of dingoes. Termed livestock guardian dogs (LGDs), these large and aggressive animals are allowed to bond with flocks from an early age and are provided with all their food and shelter needs by their human owners. Once trained, they can be very effective in using aggressive interference behaviors to repel dingoes. In one survey of 150 livestock producers, two thirds of respondents indicated that predation from dingoes and other wild dogs ceased after LGDs were put in service; another 30% reported that predation on livestock decreased (van Bommel and Johnson, 2012). In these situations, LGDs are essentially the guardians of their own human-defined territories (usually fences and paddock boundaries) and effectively repel incursions by dingoes via direct interference. Without the continuous resource-subsidy from humans it is not clear whether LGDs would always prevail over dingoes, although interference would almost certainly be the mechanism of competition in any encounters.

Over the long term, any competitive superiority of dingoes over wild domestic dogs may not be sufficient for dingoes

to survive in 'pure' form. Another kind of interaction—hybridization—may doom them. Although wild domestic dogs seldom gain access to dingo packs, they can do so more easily after packs have been fractured by misguided human attempts to control dingo numbers. Such attempts, using poisons, trapping, or shooting, often remove the dominant animals from a pack and may loosen the social and reproductive controls on remaining animals sufficiently that wild dogs then can gain access to the packs (Allen and Gonzalez, 1998; Purcell, 2010). If breeding is successful, hybridization ensues. Recent studies suggest that dingoes in remote regions of Australia have suffered little hybridization, with up to 90% of animals retaining the 'pure' dingo genotype (Newsome et al., 2013), whereas only 15% or less may be 'pure' in more heavily settled and rural areas where dingoes are controlled and wild domestic dogs are more prevalent (Elledge et al., 2009). Hybridization is not usually seen as a form of competition. However, the inexorable supplanting of dingo by dog genes in the present example gives the process the appearance of a strong and highly asymmetrical form of competition.

exterminated or occur at very low densities. Here, free-ranging dogs have become the *de facto* top-predator, and this is reflected in their interactions with the remaining native carnivores. One of the most comprehensive examples of competitive dynamics between dogs and sympatric carnivores comes from the dry grasslands of Maharashtra, India, where dogs interact with native Indian foxes (*V. bengalensis*). Here, dogs are not the largest predator, as the Indian wolf (*C. l. pallipes*) occupies that spot. However, wolves occur at very low densities (Habib, 2007), while dogs occur at very high densities (24 dogs/sq. km; Vanak, 2008; Vanak and Gompper, 2010). Thus, as the most abundant mid-sized carnivore in the landscape, dogs are dominant. Dogs and Indian foxes have low dietary overlap and thus do not appear to compete directly for food. This is due mainly to the fact that dogs subsist almost entirely on HDF such as garbage, human feces, direct feeding, and carrion, whereas foxes subsist almost entirely on rodents, fruit, and invertebrates (Vanak and Gompper, 2009a). Yet, Indian foxes react to dogs as they would to a dominant carnivore. When experimentally

exposed to dogs, foxes reduced food consumption by as much as 70% (Figure 3.3a) and increased time spent in vigilance behavior 15-fold (Figure 3.3b; Vanak et al., 2009). Thus, at the fine scale, Indian foxes showed a strong foraging-vigilance trade-off, but risk-averse behaviors were also seen at larger spatial scales. The odds of foxes using an area decreased rapidly the closer that area was to a dog-dominated habitat. This happened even if these areas were associated with a higher abundance of their main food source (Vanak and Gompper, 2010).

Similar spatial avoidance in response to interference competition is also observed in other parts of the world. In the United Kingdom, the distribution of red foxes (*V. vulpes*) was negatively affected by the presence of high densities of street dogs. These dogs were not only the second most important cause of mortality of cubs, with as much as 15% of cub mortality attributed to dogs, but also killed adult foxes on occasion (Harris, 1981). In South America, three different studies suggest that dogs have negative effects on the occurrence of canids such as the maned wolf (*Chrysocyon brachyurus*), chilla fox (*Lycalopex*

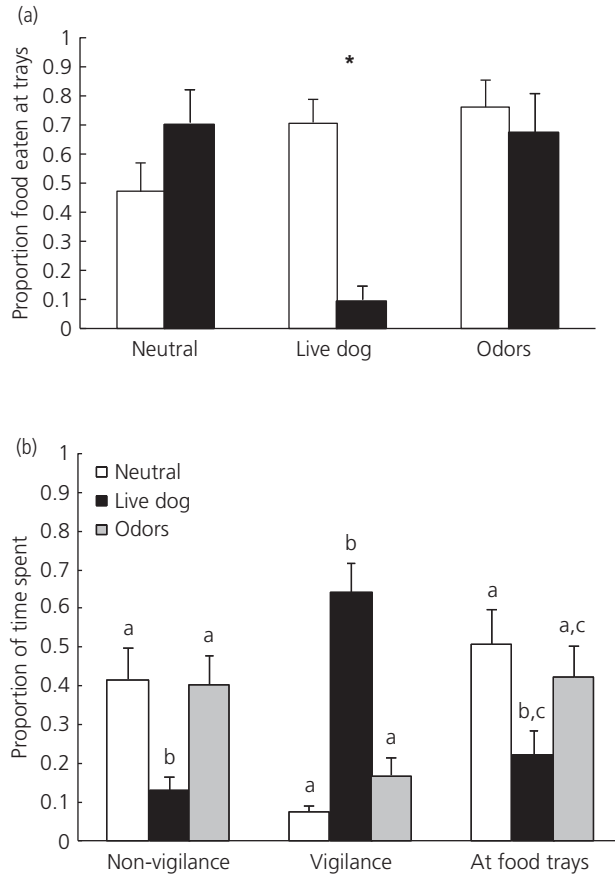


Figure 3.3 Indian foxes, when exposed to the presence of a live dog at experimentally placed food trays, (a) reduced the proportion of food eaten by ~70% compared to a control tray, and (b) increased time spent in vigilance behaviors by 15-fold when compared to trials when only dog odor or a control was placed. The asterisk and letters denote significant difference (Fisher's protected least squares difference $P < 0.05$) among trials for each behavior and error bars represent mean \pm SE, $n = 7$ dens. Reprinted from Vanak et al. (2009) with permission from Springer.

griseus), and crab-eating fox (*Cerdocyon thous*) (Espartosa, 2009; Lacerda et al., 2009; Silva-Rodríguez et al. 2010a). Two of these studies also addressed the effects of dogs on non-canid carnivores such as South American coati (*Nasua nasua*), crab-eating raccoon (*Procyon cancrivorus*), tayra (*Eira barbara*), and small cats (*Leopardus* spp.). Among these species, and with the sole exception of the coati (Espartosa, 2009), there was no evidence of potentially negative effects of dogs (Espartosa, 2009; Lacerda et al., 2009). The fact that canids seem to show stronger responses to dogs than other carnivores is not surprising as interference competition and intraguild killing should be more intense between members of the same family (Donadio and Buskirk, 2006).

Because of the scarcity of directed studies on competition between dogs and sympatric carnivores, the competitive effect of dogs can sometimes only be inferred without a direct link to causality

(see Box 3.3). For example, in Spain the presence of dogs was inversely correlated with an indicator of Eurasian badger (*Meles meles*) presence (Revilla et al., 2001). In Madagascar, the fossa (*Cryptoprocta ferox*) is nearly absent from areas with high dog occupancy (Gerber et al., 2012) and trapping rates of this species decrease as dog trapping rates increase (Barcala, 2009; see Box 3.4). Similarly, the highest densities of the endangered narrow-striped mongoose (*Mungotictis decemlineata*) occur in areas where neither dogs nor people are detected and, in one area, sightings of this species increased after dog removal (Woolaver et al., 2006). These complementary distribution patterns are likely to be common throughout the world, especially in countries where dog densities are largely unregulated in rural areas (Boitani et al., 1995; Krauze-Gryz and Gryz, 2009; Slater et al., 2008; Vanak and Gompper, 2010).

Box 3.3 Competition between dingoes and introduced predators

In contrast to the relative paucity of studies invoking competition between dingoes and native predators, a substantial body of work has focused on interactions between dingoes and the more-recently introduced red fox and feral cat (*Felis catus*). Both predators show varying degrees of dietary overlap with the dingo, although their small size (fox 4–8 kg; cat 3–6 kg) means that they generally hunt smaller prey than their larger counterpart (Cupples et al., 2011; Glen et al., 2011). All three species are broadly sympatric over much of Australia and often co-occur in the same habitat, thus increasing the opportunity for competition. Evidence that competition does indeed occur is derived largely from inverse spatial patterns in the species' abundances. In the case of the fox, several studies have shown that fox numbers and/or activity are suppressed in the presence of the dingo at local, regional, and continental scales (Johnson and VanDerWal, 2009; Letnic et al.,

2009, 2012; Mitchell and Banks, 2005; Wallach et al., 2010). In general these studies also show that where dingoes are abundant, foxes are rare, but where dingoes are scarce or absent, foxes can achieve much higher numbers (Figure 3.4). In the case of the feral cat, evidence for competition is more tenuous. Several studies show negative associations between the numbers of dingoes and cats (Brawata and Neeman, 2011; Kennedy et al., 2012; Purcell, 2010; Wallach et al., 2010), but others show weak patterns or no relationship (Letnic et al., 2009; Newsome, 2001). In contrast to the red fox, which is largely active on the ground, feral cats can climb trees and thus may be better able to avoid direct contact with dingoes. For example, in very barren areas of the Channel Country in western Queensland, the primary refuge sites are tree-lined riparian strips that allow cats to escape ground-active dingoes (Pettigrew, 1993).

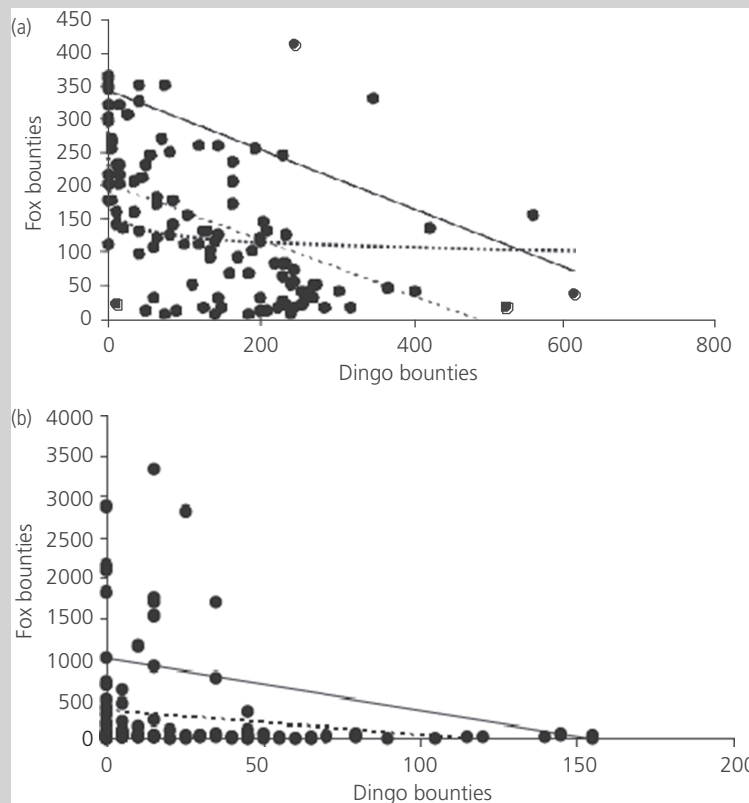


Figure 3.4 Numerical relationship between the dingo and red fox, based on bounty records collected (a) in Queensland in the financial year 1951–52 and (b) in Western Australia in the years 1947–52. Each dot represents the number of bounties paid within 100×100 km grid cells in each state over the bounty collection period. Solid lines show regressions for the 90% quantile of fox abundance against dingo abundance, light dotted lines show significant ($P < 0.05$) least squares linear regressions, and the heavy dotted line in (a) indicates a significant ($P < 0.05$) least squares logarithmic regression. Reprinted from Letnic et al. (2011) with permission from John Wiley & Sons.

continued

Box 3.3 *Continued*

The form of interaction between dingoes and the two smaller predators is almost certainly extreme interference competition. This is suggested by the fact that red fox and feral cat remains are found frequently but only at very low levels in scat or stomach samples of the dingo (Allen and Leung, 2012; Letnic et al., 2012), and observations that both the smaller predators will flee if an encounter with a dingo is imminent (Corbett, 1995; Purcell, 2010). However, the most compelling evidence for extreme interference comes

from observations of dingoes killing but not eating both foxes and feral cats in a large (37 km²) enclosure in treeless habitat in South Australia (Moseby et al. 2012). In this latter study, data derived from GPS collars confirmed that dingoes returned to the carcasses of foxes and cats that they had killed for several hours after the killing, with some dingoes returning again and again over the ensuing days. It is possible that these frequent return visits were to ensure that the smaller predators no longer posed a competitive threat.

Box 3.4 Landscapes of fear: spatial and temporal considerations

There is increasing recognition that predators, including dogs, may influence their prey in subtle ways that are not readily apparent by simply comparing measures of abundance of pairs of interacting species (Creel and Christianson, 2008; Ritchie and Johnson, 2009). This is important, because significant effects of dogs on other species may have been overlooked or dismissed previously due to a focus on abundance patterns only (Johnson and VanDerWal, 2009). Recent studies from two vastly separated regions (Australia and Madagascar) and with different predator communities serve to illustrate this point.

In Australia, dingoes are often killed to minimize their attacks on livestock, and the impact this has on their abundance and behavior, as well as that in turn on a sympatric mesopredator, the feral cat, was examined using remote camera surveys across nine pairs of large Australian rangeland (cattle) properties (Brook et al., 2012). Dingo abundance was generally reduced on properties where dingoes were controlled, but most interestingly dingo behavior varied between sites where dingoes were controlled and where they were not. Uncontrolled dingo populations were crepuscular, similar to their major prey (kangaroos). In populations subject to control, dingoes were less active around dusk, with activity concentrated in the period immediately before dawn. Shifts in feral cat abundance were inversely related to corresponding shifts in dingo abundance, but importantly

there was also a negative relationship between predator visitation rates at individual camera stations, indicating that cats avoided areas where dingoes were most active, and that reduced activity by dingoes at dusk was associated with higher cat activity at dusk. This suggests that dingo control may not only lead to more feral cats (mesopredator release), but also allows cats to optimize their hunting when dingoes are less active (Brook et al., 2012).

In Madagascar, as part of an overall study examining activity patterns of carnivores, the authors found that the fossa selectively used crepuscular hours, but was cathemeral overall (Gerber et al., 2012). Fossas were conspicuously absent from sites where dogs were most abundant and active throughout the diel cycle, and the ring-tailed mongoose (*Galidia elegans*), another native, but smaller-bodied predator, shifted its activity away from its preferred periods in the presence of dogs. Together, these studies highlight that indicators other than abundance, such as spatial and temporal behavioral patterns, should also be considered when determining a predator's ability to affect trophic levels. However, abundance still remains an important consideration, as dogs have even been known to exclude larger-bodied predators, such as wolves, from accessing food; despite their smaller body-size as compared to wolves, dogs overcame this by being more aggressive and occurring in higher numbers than wolves (Boitani et al., 1995).

3.2.2 Dogs as mesocarnivores

In several ecosystems across the world, dogs are sympatric with larger carnivores such as the wolf, leopard (*Panthera pardus*), tiger (*P. tigris*), and bears. In natural systems, mesocarnivores are often

suppressed by the presence of larger competitors (Crooks and Soulé, 1999). Thus, it would be expected that in areas where larger carnivores are present, dogs would be negatively affected. However, because of the lack of directed studies in such systems,

we can only speculate on whether dogs are subject to top-down competitive effects from larger carnivores. What we do know is that in many systems dogs form an important part of the diet of larger carnivores (e.g., leopard; Butler et al., Chapter 5). Thus, it is likely that in such systems dogs will also display avoidance tactics as shown by other meso-carnivores. However, dogs may also be insulated from top-down effects if they can find refuge in human settlements or benefit from human association while ranging into native habitats.

Studies from southern Africa, where dogs have the potential to interact with possibly the greatest number, as well as diversity, of carnivores, well illustrate the complexity of the situations that are possible (Butler and du Toit, 2002; [Butler et al., 2004](#)). Detailed studies of interactions in Zimbabwe between dogs and large wild carnivores in Gokwe Communal Land (GCL) bordering the Sengwa Wildlife Research Area (SWRA) suggested that dogs were inefficient and infrequent predators. Their small group size (mean 1.7) and body mass (mean 15 kg) was reflected in their diet, which consisted of scavenged human refuse, feces and carrion, fruit, and some insects. The vast majority (87%) of this food was gained independently, with 55% of it derived from carrion, particularly mammalian carcasses. Leopards, lions, spotted hyenas (*Crocuta crocuta*), side-striped jackals (*Canis adustus*), and several smaller carnivore species travelled up to 3 km into GCL (Butler, 2000) while dogs were observed up to 3 km within the SWRA independently of people, and up to 6 km with people, and consequently were sympatric with these species in the SWRA–GCL interface. Dogs dominated the carnivore scavenging guild (see Section 3.3.1), but were preyed upon by lions, leopards, and spotted hyenas. Thus, inside wildlife reserves, and on their boundaries with communal lands, dogs were meso-level carnivores and had diverse relationships within a guild of larger and smaller native mammalian and avian species.

In most communal land areas and commercial farmlands where large carnivores are essentially absent, either due to high human population densities or persecution, dogs are the local apex predator. However, in commercial farmland typified by intensive cropping and more extensive cattle

production, dogs occur at very low densities due to the lack of human settlement. As a consequence side-striped and black-backed jackals (*C. mesomelas*) have become the most numerous native carnivore through ‘mesopredator release,’ occurring at high densities relative to natural conditions ([Cumming, 1982](#); [Bingham et al. 1999](#)). Hence within communal lands and where they border commercial farmland, relationships within the carnivore guild are limited to competitive interactions between dogs and jackals.

Both jackal species have omnivorous and opportunistic feeding habits in Africa (Skinner and Chimimba, 2005), and will efficiently scavenge carrion (Richardson, 1980) and human waste ([Bothma et al., 1984](#)), potentially overlapping the dietary niche of dogs. Consequently the ecological relationship between dogs and jackals is characterized by conflict and intolerance, with dogs dominating jackals in aggressive encounters due to their larger size (15 kg versus 8–10 kg for side-striped and 7–8 kg for black-backed jackals). Carcass experiments showed that side-striped jackals are attracted to carrion but do not feed, perhaps avoiding the scavenging dogs present (Butler and du Toit, 2002; see Section 3.3.1). At higher densities, dogs aggressively exclude jackals and jackals may become the subordinate species, avoiding contact with dogs and hence occurring at lower densities in communal lands. Commercial farmland therefore provides a refuge for jackals, which then ‘spill over’ into the peripheries of communal lands.

Competition between dogs and other carnivores may not always follow an allometric hierarchical relationship. In some cases, dogs can out-compete larger carnivores because of numerical superiority via frequency-dependent competition. The outcome of encounters between the endangered Ethiopian wolf (*C. simensis*) and dogs in the highlands of Ethiopia seems to depend on numbers. If wolves outnumber dogs, then the dogs are chased away, and vice-versa ([Atickem et al., 2010](#)). However, the authors concluded that interference competition with dogs was not a major concern for the conservation of Ethiopian wolves, but suggested that this could change in the future as the numbers of people and dogs grow ([Atickem et al., 2010](#); [Laurenson et al., 1998](#); [Sillero-Zubiri and Macdonald, 1997](#)).

3.2.3 Dogs as predators of other carnivores

The killing and eating of one carnivore by another is termed intraguild predation (Polis et al., 1989). Several reviews have highlighted the widespread occurrence of this interaction (Donadio and Buskirk, 2006; Glen and Dickman, 2005; Ritchie and Johnson, 2009). However, we draw the distinction between 'routine' predation, where the victim is killed mainly for consumption, from killing as a form of extreme interference competition, where the victim is not consumed or only partially consumed (see also Butler et al., Chapter 5). There are numerous examples of dogs killing other carnivores, both with and without consumption. For example, in Australia, dingoes have been recorded killing but not eating spotted-tailed quolls (*Dasyurus maculatus*) (Körtner, 2007; Körtner and Watson, 2006), red foxes, and feral cats (Moseby et al., 2012), but more generally they appear to eat or even cache their victims. Other than quolls, large varanids and snakes have been recorded in the diet of dingoes in several studies (e.g., Glen et al., 2011; Pascoe et al., 2012). However, the frequency of occurrence of other predators in dingo scats or stomach samples is usually very low (<1%), and it is seldom clear whether dingoes have killed or merely scavenged these items. One exceptional observation is that of Webb (1996) who saw three dingoes work together to kill and then consume a large (1.5–2 m long) lace monitor (*Varanus varius*).

Evidence of killing by dogs comes from almost everywhere they have been studied, and the list of mammalian carnivore species that are killed by dogs is long. The list includes taxa with a wide range of body sizes from dhole (*Cuon alpinus*) ~18 kg; (Williams, 1935), to civets ~1–6 kg (Ashraf et al., 1993; Dahmer, 2002), small cats ~5 kg (Barashkova and Smelansky, 2011) and mustelids ~1–2 kg (Butler and du Toit, 2002; Maran et al., 2009; Ross et al., 2008). In many cases intraguild killing (and not predation) can be deduced because the carcasses of even small carnivore species are recovered relatively intact. For example, dogs were the presumed cause of direct killing of nearly 29% of Indian foxes that were found dead ($n = 13$) (Vanak, 2008). Similarly, dogs killed 26% of spotted skunks (*Spilogale putorius*) known to have died ($n = 77$) during a study conducted in farmlands in southeast Iowa (Crabb,

1948). Dogs are also frequent causes of mortality for the Geoffroy's cat (*Leopardus geoffroyi*) and culpeo foxes (*Lycalopex culpaeus*) on certain Argentinean ranches (Novaro et al., 2005; Pereira et al., 2010). On the other hand, evidence of consumption comes from analyses of dog diet. One study showed consumption of carnivores such as lesser grison (*Galictis cuja*) and South American coati (Campos et al., 2007), but it was unclear whether dogs killed these carnivores or simply scavenged them. Despite these studies, the quality of the evidence for the importance of dogs as a source of mortality is mixed. In fact, most of the evidence available is constituted by anecdotal reports of single mortalities (see Section 3.5.1). Among these, the most attention-garnering report was the rediscovery of the black-footed ferret (*Mustela nigripes*), when a farm dog brought in a freshly killed individual (Clark, 1987; see Gompper, Preface).

3.3 Exploitative competition

Other than via direct interference competition and associated indirect effects, dogs can also compete with native carnivores exploitatively for food (Box 3.1). Because domestication has rendered dogs less efficient at hunting than wild carnivores (Clutton-Brock, 1995), they are less likely to be effective exploitative competitors (Petren and Case, 1996; Vanak and Gompper, 2009b). However, most populations of dogs are subsidized by humans and thus can attain numerical superiority, allowing them to potentially outcompete native carnivores in acquiring limited resources (as per the abundance-asymmetry hypothesis; Vázquez et al., 2007). Furthermore, the plasticity of dog behavior and the advantages of food security from human subsidies can potentially allow dogs to compete with a wide range of carnivore species, from top-predators such as wolves, lions, and leopards to mesopredators such as jackals and foxes as well as nonmammalian carnivores such as varanid lizards.

Although there are several examples worldwide of dogs killing often substantial numbers of prey and being an important cause of mortality for many species (Ritchie et al., Chapter 2), the evidence for dogs being effective exploitative competitors is not robust. This is mainly due to the fact that most dog

populations are heavily dependent on HDF. Vanak and Gompper (2009b) found that of 21 studies of dog diet, only 5 (23%) reported subsistence on mainly wild-caught food whereas in the rest dogs were either fully or mainly dependent on HDF. Illustratively, all of those five studies were of truly feral dogs (i.e., dogs that were no longer tame or associated with human settlements and food subsidies). Even studies that have specifically examined the potential for exploitative competition between dogs and sympatric carnivores have found little evidence. [Atickem et al. \(2010\)](#) found that dogs in the Ethiopian highlands subsisted almost entirely on HDF, and that wild-caught prey such as rodents constituted a relatively minor part of their diet. The authors thus concluded that dogs are unlikely to be competing with endangered Ethiopian wolves. Similarly, in India, dogs and Indian foxes did not appear to compete directly for food. This was again due mainly to the fact that dogs subsisted almost entirely on HDF such as garbage, human feces, direct feeding, and carrion, whereas foxes subsisted almost entirely on rodents, fruit, and invertebrates ([Vanak and Gompper, 2009a](#)). [Silva-Rodríguez et al. \(2010a\)](#) found similar low levels of overlap in diet between dogs and chilla foxes in southern Chile. On the other hand, [Campos et al. \(2007\)](#) reported high rates of vertebrate consumption by dogs in suburban areas of Brazil. Although these authors suggested that dogs could compete with wild carnivores, there was some uncertainty in this regard since there was no assessment of dietary overlap.

3.3.1 Dogs competing with mammalian and non-mammalian scavengers

Almost all studies that examine the dietary habits of dogs conclude that an important part of their diet is obtained from scavenging human- and non-human generated carcasses of animals. This highly efficient facultative scavenging behavior brings dogs into direct competition with a suite of mammalian and non-mammalian species that are either specialist or opportunistic scavengers. Many of the same factors described previously, such as high population densities, proximity to humans, and 24-hour foraging ability, allow dogs to dominate carcasses, especially near human settlements. For instance, in western

India, dogs dominated cattle carcasses at a village dump throughout the day, preventing scavengers such as golden jackal (*C. aureus*), vultures, and striped hyena (*Hyaena hyaena*) from accessing these resources ([Aiyadurai and Jhala, 2006](#)).

A more detailed investigation into the potential scavenging interactions between dogs and wild carnivores was carried out in Zimbabwe (see Section 3.2.2). At experimental carcasses, [Butler and du Toit \(2002\)](#) found that dogs and vultures were the most successful species in the scavenging guild, which also consisted of eight mammalian and nine avian species. Dogs were the most efficient scavengers, consuming up to 60% of the total carcass biomass, compared to 15% for the vultures. However, the influence of dogs varied along transects. Dogs consumed the majority of carcass biomass 1 km within the communal land, whereas vultures, leopards, lions, and spotted hyenas were the principal scavengers at carcasses placed 1 km inside the wildlife reserve.

These patterns suggest that dogs primarily compete with vultures along the interface of communal lands and wildlife reserves. While most carnivores will scavenge given the opportunity, vultures have evolved specifically as scavengers of mammalian carrion, and the eagle-like vultures (hooded, *Necrosyrtes monachus*, white-headed, *Trigonoceps occipitalis*, and lappet-faced, *Torgos tracheliotus*) will also scavenge carrion and human refuse ([Houston, 1979](#); [Mundy, 1982](#)). Dogs appear to out-compete vultures for four reasons. First, they physically dominate vultures at carcasses, aggressively excluding them from feeding due to their larger body mass (15 kg versus 6.2 kg for lappet-faced vultures, the largest species recorded scavenging; [Houston, 1979](#)). Second, because the experimental carcasses were small (<50 kg, as with the majority of carcasses found in GCL; [Butler and du Toit, 2002](#)), dogs were easily able to defend carcasses against vultures, and consume them quickly. Third, although vultures are attracted to carcasses in GCL, they are more sensitive to human disturbance and reluctant to settle at carcasses near human settlements. The majority of human activity occurs during the day, the only time when vultures forage. Fourth, dogs are active for most of the 24-hour cycle, enabling them to

locate and then consume carrion more efficiently than vultures.

Similar evidence also points to dogs out-competing black vultures (*Coragyps atratus*) in South America. According to Pavés et al. (2008), dogs reduce food availability for vultures by preying and scavenging on South American sea lions (*Otaria flavescens*). Similarly, with the collapse of the vulture population in south Asia, several reports suggest that dog numbers have increased substantially and have replaced vultures as the main scavengers (Prakash et al., 2003).

By being effective scavengers, dogs can potentially out-compete much larger carnivores. For example, in Africa lions and leopards also scavenge opportunistically (Kruuk, 1972; Schaller, 1976; Smith, 1977) and considering that both species prey on dogs (Butler et al. 2004, Chapter 5), they could certainly outcompete dogs during direct interference confrontations. In spite of this, in Zimbabwe dogs were the more efficient scavengers at experimental carcasses owing to their higher numbers, enabling them to locate and consume larger quantities of carrion. Consequently dogs probably do successfully compete with lions and leopards in exploitative terms, but because both felid species are primarily predators (rather than scavengers), the impact of dogs is likely to be minimal. There is little evidence to show that dogs effectively kleptoparasitize recent kills of wild carnivores.

Spotted hyenas present a more complex issue. They are large (up to 86 kg) and highly efficient scavengers, and are able to locate and consume tissue and bones from carcasses of all but the largest species (Richardson, 1980). They often scavenge refuse around human settlements, for example in Ethiopia (Kruuk, 1968), Tanzania (Kruuk, 1972), and South Africa (Pienaar, 1969), but are also highly successful predators in their own right (Kruuk, 1972; Mills, 1990). Given that they prey on dogs in Zimbabwe (Butler et al., 2004), Tanzania (Kissui, 2008), Kenya (Kolowski and Holekamp, 2006) and Ethiopia (Atickem et al., 2010) (see also Butler et al., Chapter 5), they are also likely to dominate dogs in direct competitive encounters involving scavenging. Due to their higher densities, dogs may potentially reduce food supplies for spotted hyenas around human settlements, but this is unlikely to

affect populations within wildlife reserves. The competitive impact of dogs on the smaller and more omnivorous brown (*H. brunnea*) and striped hyenas may potentially be more significant, but no research has been undertaken on this question.

3.3.2 Dogs competing as top-predators

The success of dogs as exploitative competitors seems to depend to a large extent on their association with humans. As mentioned earlier, in the review conducted by Vanak and Gompper (2009b), only 5 of 21 studies of dog food habits showed a primary dependence on wild-acquired food. It is notable that four of these dog populations were fully independent of humans and acted as wild predators. Thus, the true competitive ability of dogs with other carnivores can be assessed in situations where dogs are wild. Such a situation is best seen on a few islands (e.g., Kruuk and Snell, 1981) and on the continent of Australia.

Aside from the thylacine and Tasmanian devil, there is no evidence that any other predatory native species declined or became extinct in Australia following the introduction of the dingo, suggesting that competition between dingoes and extant native species may not be strong. Although contemporary studies generally support this interpretation, there is nonetheless considerable evidence that dingoes share food, habitat, or shelter resources with many native species. Hence, the potential for resource competition exists. Dingoes show some overlap in diet with spotted-tailed and western quolls (*D. geoffroii*); all species prey upon small to medium-sized mammals and birds, although dingoes are capable of hunting much larger prey than the marsupials, especially when in packs (Corbett, 1995; Glen and Dickman, 2008; Glen et al., 2011). It is also possible that the marsupial predators consume the remains of dingo-kills and gain an energetic benefit from doing so (Dickman, 1992). However, good evidence for this is scant; large mammals such as sheep have been identified in the diet of the spotted-tailed quoll, but it is not clear whether these prey had been killed initially by dingoes or had been scavenged after death from other causes (Glen et al., 2011).

Large predatory birds such as wedge-tailed eagles (*Aquila audax*) also share prey including rabbits

(*Oryctolagus cuniculus*) and small to medium-sized macropods with dingoes, as do large reptilian predators, such as varanid lizards (*Varanus* spp.) and salt-water crocodiles (*Crocodylus porosus*) (Glen et al., 2010; Parker et al., 2007; Pascoe et al., 2012; Taylor, 1979). During an irruption of native rodents in central Australia, Pavey et al., (2008) reported a dietary overlap of 88% between dingoes and letter-winged kites (*Elanus scriptus*), which provides considerable potential for food-based competition. Dingoes occupy the same broad range of habitats as native predators (Fleming et al., 2001) and overlap with some species on a fine spatial scale, although a degree of segregation via differential use of habitat components such as trees is usually still apparent (Glen et al., 2011). Dingoes also overlap broadly in their temporal activity with marsupial, some avian, and reptilian predators. However, until simultaneous monitoring of the dingo and native predators is attempted via remote tracking or camera trapping, it will not be possible to quantify patterns of temporal overlap or separation more precisely.

3.4 Apparent competition

The occurrence of apparent competition, wherein patterns of interaction that seem to be the result of competition are actually driven by the distribution and effects of a third species (Box 3.1), has not been robustly demonstrated among carnivores. However, apparent competition between carnivores as a result of shared parasites may be far more common. Several important microparasites of wild carnivores are also enzootic in dog populations and may be readily transmitted to native carnivores (Knobel et al., Chapter 6). For instance, almost all canid species are susceptible to infections from 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). This potential for disease-mediated changes in population densities of carnivores that are sympatric with dogs has been suggested as a form of apparent competition (Vanak and Gompper, 2009b). Prominent examples of the role of dogs as reservoirs of pathogens that significantly impact wild carnivore populations come from species in several carnivore families including canids, felids, hyaenids, phocids, mustelids, viverrids,

and procyonids. The spillover of these pathogens from dogs to wild carnivores and the consequences of these events for the population dynamics of wild carnivores have been reviewed extensively (Cleaveland et al., 2007; Deem et al., 2000; Funk et al., 2001; Laursen et al., 1998; Knobel et al., Chapter 6).

3.5 Conservation implications

3.5.1 Dog impacts on threatened carnivores

Most of the directed studies on the impacts of dogs on carnivores have used non-threatened species as study models (e.g., Silva-Rodríguez et al., 2010a; Vanak and Gompper, 2010). However, dogs have been reported to kill a large number of threatened carnivores (either for consumption or intraguild killing). To our knowledge there is (mostly anecdotal) evidence of dog-caused mortality for at least 14 (23%) of 61 species of extant threatened terrestrial carnivores (Silva, 2012). For example, in Nepal, dogs are thought to be one of the most frequent causes of mortality of the red panda (*Ailuurus fulgens*) (Williams, 2004; Yonzon and Hunter Jr, 1991). In southern India, the death of 10 (of 22 dead) critically endangered Malabar civet (*Viverra civettina*) was attributable to dogs (Ashraf et al., 1993). In Estonia, dogs killed 4 of 54 European minks (*Mustela lutreola*) that had been released as part of a mink restoration program (Maran et al., 2009). In different areas of the world, local people inform that dogs have killed threatened carnivores such as the Andean cat (*Leopardus jacobita*), guigna (*L. guigna*), Darwin's fox (*Lycalopex fulvipes*), smooth-coated otter (*Lutrogale perspicillata*), and southern river otter (*Lontra provocax*) (Espinosa-Molina, 2011; Hon et al., 2010; Lucherini and Merino, 2008; Silva-Rodríguez and Sieving, 2011; Soler et al., 2004). Other examples of threatened carnivores with evidence of killing by dogs include the black-footed ferret (Clark, 1987), dhole (Williams, 1935), narrow-striped mongoose (Hawkins, 2008; Woolaver et al., 2006), marine otter (*L. felina*) (Pizarro-Neyra, 2008), marbled polecat (*Vormela peregusna*) (Dulamtsen et al., 2009), and Cozumel raccoon (*Procyon pygmaeus*) (McFadden et al., 2010). Considering the relative paucity of studies on free-ranging dogs, it is very likely that the proportion

of species of conservation concern killed by dogs is much higher.

From the information available, the picture that emerges is that although the most compelling evidence supporting the impacts of dogs come from non-threatened carnivores such as the Indian fox ([Vanak and Gompper, 2010](#)), the same kind of problem may be affecting species that are critically endangered, such as the Malabar civet, the Cozumel raccoon, or Darwin's fox. Research directed at understanding the effects of dogs on both the distribution and population dynamics of endangered carnivores is urgently needed, but in the interim, the information available on common species could, under the precautionary principle, inform decision-making ([Silva, 2012](#)).

3.5.2 Dogs and human–carnivore conflict

Under certain conditions, the presence of dogs may be beneficial for conservation. Human–carnivore conflicts are one of the main threats for carnivore conservation worldwide ([Inskip and Zimmermann, 2009](#); [Treves and Karanth, 2003](#)) because the economic losses from livestock depredation lead to intolerance of wild carnivores. Livestock-guarding dogs are most commonly used to mitigate this conflict ([VerCauteren et al., Chapter 9](#)). In such cases, the function of dogs is to keep native carnivores away from livestock. Hence, the negative correlation between the distribution of carnivores and dogs in many studies ([Espartosa, 2009](#); [Silva-Rodríguez et al., 2010a](#); [Vanak and Gompper, 2010](#)) may ultimately help in reducing carnivore mortality associated with human–wildlife conflict, and therefore benefit conservation in the long run ([González et al., 2012](#)).

In Australia, where the dingo is the 'top-dog,' much evidence has emerged in recent studies that this carnivore provides a net benefit to native wildlife by suppressing the impacts of the red fox and perhaps also the feral cat ([Glen and Dickman, 2005](#); [Letnic et al., 2012](#)). However, as dingoes also cause livestock losses in rangeland areas, their management for conservation needs to be balanced against mitigating their effects in production landscapes. Intriguingly, one of the most promising means

of doing this is to use domestic dogs as livestock guardians, to keep dingoes away from rangeland enterprises (Box 3.2; [van Bommel and Johnson, 2012](#)).

Although dogs can help reduce human–carnivore conflict, they can also intensify it. Just as for other carnivores, dogs prey on livestock, but distinguishing between losses caused by dogs and those by other carnivores is a difficult task. Despite the difficulty involved in the correct determination of cause of death, carnivores such as wolves are often blamed for losses that could have been caused by dogs ([Cozza et al., 1996](#)). For example, in northern Spain, wolves were blamed for 94% of the attacks on domestic animals ([Cozza et al., 1996](#)). Paradoxically, in the same area and during the same time period, dogs were more abundant than wolves. Furthermore, sheep represented 36% of prey items found in dog scats versus only 3% in wolf scats, thus suggesting that the actual impacts of wolves may have been overestimated ([Echegaray and Vilà, 2010](#)). These identification problems are a major issue for carnivore conservation, because they may lead to unjustified persecution of carnivores, and may increase the cost of compensation strategies to reduce human–carnivore conflicts ([Cozza et al., 1996](#); [Echegaray and Vilà, 2010](#); [Sundqvist et al., 2008](#)). Another situation where high densities of dogs can inadvertently trigger human–carnivore conflict is when they are prey for larger carnivores. As described by [Butler et al. \(Chapter 5\)](#), dogs are killed and often consumed by several species of large carnivores. In cases where the dog is a beloved pet or a prized animal, this causes resentment towards the presence of large carnivores and can be a major impetus for predator removal programs. Thus, it appears that dogs may be beneficial in mitigating human–carnivore conflict, but only in a narrow set of conditions where they are fully under human supervision.

3.5.3 Dogs as a large-scale edge effect

A body of evidence is starting to accumulate on the existence of large-scale edge effects as a function of human-driven activities ([Laurance, 2000](#)). Contrary to previous evidence, edge effects are not confined

to just <150 m from a habitat edge, but can potentially extend up to 5 km from a disturbance edge (Laurance, 2000; Murcia, 1995). As shown above (Section 3.2.2), in Zimbabwe dogs were found 3 km within a wildlife reserve independently of their owners, and 6 km with people, and clearly modified the scavenging guild up to 1 km within the wildlife reserve. This study also demonstrated that dogs were the most common carnivore along the wildlife reserve boundary, occurring with a frequency six-fold greater than the most common wild carnivore, the leopard. Fragmentation and the loss of habitat, along with increasing human populations, have resulted in an ever-increasing proportion of natural areas subject to anthropogenic edge effects. Several recent studies have now proposed that domestic carnivores such as dogs and cats can constitute a large-scale edge effect (Torres and Prado, 2011).

Apart from these directed studies, a number of general faunal surveys across the world have noted that dogs are among the most commonly detected carnivore species (Table 3.2) in several natural areas with close proximity to human habitation. Dogs may be detected as far as 10 km from the nearest human habitation (and much further away in Australia), and thus the likely impacts they can have are not necessarily confined to short distances from human settlements. For most of the surveys and studies listed in Table 3.2, examination of the effects of dogs on other species was not their primary goal. Thus, the information gathered from across these studies is heterogeneous with regard to detail, and is intended to be purely illustrative. What emerges is that dogs are quite commonly detected in several surveys. Given the scope for negative interactions between dogs and native species discussed above and elsewhere in this book, there appears to be a legitimate cause for concern. There is thus not only a need for more directed research on the extent to which dogs can be viewed as an edge effect, but also for general surveys to explicitly report the presence of domestic carnivore species.

3.5.4 Dog management for conservation

The competitive dynamics between dogs and sympatric carnivores described above can clearly be

problematic for conservation, particularly when dogs occur in and around protected areas (e.g., [Lacerda et al., 2009](#); [Srbek-Araujo and Chiarello, 2008](#); [Torres et al., 1996](#); [Vanak and Gompper, 2010](#)). However, not all dogs are likely to be equal in their effects on carnivores. As postulated by Vanak and Gompper (2009b), the competitive ability of dogs is likely to be influenced by their population size and ranging behavior. The larger the population of dogs, and the wider ranging their behavior, the more likely they are to either directly or indirectly influence other carnivore species. Thus, to negate the possible deleterious effects of dogs on carnivores, it is necessary to not only reduce population size, but also restrain free-ranging behavior. Priority should be given to male dogs, since they have larger home ranges than females (Butler et al., Chapter 5) and travel greater distances when rabid (Knobel et al., Chapter 6), and therefore may be likely to interact more frequently with wild carnivores. Most of the emphasis on free-ranging dog populations worldwide has thus far been on reducing the potential for zoonotic diseases, in particular rabies. Even in cases where dogs have been implicated as the source of pathogens causing widespread mortality in carnivores, the emphasis has been on reducing the transmission potential via vaccination (e.g., [Cleaveland et al., 2007](#)), rather than on population control or restricting ranging-behavior.

Mitigating the risk of pathogen transmission does not, however, reduce the possibility of other kinds of dog-wildlife interactions ([Vanak and Gompper, 2010](#)). As discussed above, these depend on population size and ranging behavior. Therefore, controlling dog-wildlife interactions, particularly in the vicinity of conservation areas, must involve a multi-pronged approach. Pathogen transmission risk can be mitigated through vaccination, and the biotic potential of the population can be reduced via lethal control and sterilization. In areas of conservation concern, control measures must also include the removal of un-owned dogs, restriction of free-ranging activity (particularly among males), improvement of feeding, and a strong emphasis on responsible dog ownership ([Vanak and Gompper, 2010](#); [Silva-Rodríguez and Sieving, 2011](#)). These management approaches must be implemented in a sustained and integrated manner for a long-term solution.

Table 3.2 Summary of a sample of surveys that recorded dogs in natural habitats as an example of a large-scale edge effect. We have excluded studies of dingoes from Australia as they are naturalized predators in the system and may not be considered as an edge effect.

Region	Habitat	Detection method	Frequency of detection relative to other carnivores	Distance from human habitation (km)	Reference
Europe					
Spain	Agricultural matrix	Transects (spotlight)	Red fox > dog > cat > others	Variable	Sobrino et al. 2009
Spain	Woodland	Camera traps	Cat > dog > fox > others	< 0.4	Fandos et al. 2012
Portugal	Mediterranean farmlands	Sign detection in transects	Red fox > dog > Egyptian mongoose > Eurasian badger > cat > Eurasian otter > weasel ~ European polecat ~ stone marten > genet	Variable	Pita et al. 2009
Asia					
Taiwan	Rainforest and secondary forest	Camera traps	Dogs detected, frequency not reported	2–10	Chen et al. 2010
Malaysia	Rainforest	Transects and camera traps	Dogs, jungle cats, and common palm civet frequently detected	<1	Sanei and Zakaria 2011
India	Grassland and plantation	Camera traps and track plots	Indian fox > dog > others	1–3	Vanak and Gompper 2007
North America					
USA	California sage scrub, annual grassland, chaparral, and oak woodland	Camera traps	Coyote > bobcat > dog > striped skunk > raccoon > gray fox > puma > others	Dogs associated with urban percentage but not with distance to edge	Ordeñana et al. 2010
USA	Deciduous/coniferous forests	Camera traps, Scent stations	Albany Pine Bush Preserve (APB): Cat > coyote ~ raccoon > dog > others. Adirondack sites: dogs not detected.	APB: Close to suburban and urban development	Gompper et al. 2006
South America					
Brazil	Atlantic forest	Camera traps	Dog > ocelot > crab-eating raccoon > puma > coati > crab-eating fox > others	0–1.1 from forest edge. A dog detected 0.9 from residence.	Srbek-Araujo and Chiarello 2008
Brazil	Cerrado	Track stations	Maned wolf > dog > crab-eating raccoon > crab-eating fox > coati ~ puma ~ tayra	Associated to edge of National Park (< 1)	Lacerda et al. 2009
Chile	Temperate rainforest	Camera traps and track stations	Dog > guigna > Darwin's fox > Southern river otter > others	Variable	Farias and Jaksic 2011
Chile	Temperate rainforest	Camera traps	Dog > skunk > guigna ~ puma ~ chilla fox	Variable	Silva-Rodriguez et al. 2010b
Africa					
Zimbabwe	Woodland savannah	Transects (tracks on sand, experimental carcass observation, wildlife monitoring transects)	Dog > leopard > side-striped jackal > lion > spotted hyena	3 (independent of humans), 6 (with humans)	Butler and du Toit, 2002; Butler et al. 2004

3.6 Further research

This review highlights the general lack of studies on the competitive dynamics between dogs and sympatric carnivores, both in terms of geographic representativeness as well as the range of species that are affected. Indeed, barely a handful of studies from Asia, Africa, and South America have directly examined these competitive dynamics. Even when direct aggression and intraguild predation can be detected among competing species, the subtler indirect effects of exploitation and apparent 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. Hence, it is clear that there are major gaps in directed research on the effects of dogs on sympatric carnivores worldwide, but particularly in Asia, Europe, and Africa, which together have the largest populations of dogs as well as a wide array of native carnivore species.

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