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Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey?

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The mesopredator release hypothesis (MRH) predicts that a reduced abundance of top-order predators results in an increase in the abundance of smaller predators due to the cessation of intraguild predation and competition. In turn, small prey preferred by mesopredators are predicted to benefit from the suppressive effects of top-order predators on mesopredators. In support of the MRH a growing body of evidence shows that Australia's largest terrestrial predator, the dingo (*Canis lupus dingo*, body mass of 15–25 kg), might suppress the abundance of the smaller invasive red fox (*Vulpes vulpes*, body mass of 3.5–7.5 kg). Foxes are implicated in the declines of native rodents and marsupials in arid Australia; where foxes are rare, native prey species are more likely to persist. However, the mechanism by which dingoes suppress fox populations and benefit native mammal species is not well understood. We used scat analysis and prey selectivity indexes to examine the potential for dietary competition between dingoes and foxes at 3 arid sites. Dietary overlap between dingoes and foxes was high ($\geq$85%) at all sites. Dingoes and foxes preferentially selected identical prey types in greater proportion to their relative abundance at all sites, but foxes tended to consume smaller prey than dingoes. Dingoes consumed more large- (>999 g) and medium-sized (100–999 g) mammals, and foxes consumed greater numbers of smaller (<100 g) mammals. At 2 sites rabbits were the most frequently occurring prey for both predators and were consumed in greater proportion than their abundance. The extensive dietary overlap and preferential selection by the predators for the same prey suggest that considerable potential exists for dietary competition between these predators. Fox remains found in dingo scats provided evidence of intraguild predation. Our results support the notions that dingoes could suppress fox populations through both dietary competition and direct killing and that this suppression of foxes could benefit small prey.

Key words: competition, dietary overlap, intraguild predation, mesopredator release hypothesis, prey selectivity

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Top-order predators can have an important role in structuring ecosystems by the regulation of their prey or competitors, or both (Beschta 2003; Crooks and Soulé 1999; Estes et al. 2004; Ripple et al. 2001). The cessation of regulatory interactions between a top-order predator and smaller predators (mesopredators) can lead to an increase in mesopredator abundance (Rayner et al. 2007; Trewby et al. 2008). This phenomenon is termed mesopredator release (Ritchie and Johnson 2009; Soulé et al. 1988). Mesopredators tend to occur at higher population densities and prey on smaller species than top-order predators (Ritchie and Johnson 2009). Consequently, an overabundance of mesopredators can have devastating consequences for their prey (Berger et al. 2008; Crooks and Soulé 1999; Rayner et al. 2007; Soulé et al. 1988).

One way in which top-order predators suppress mesopredator populations is through interspecific competition for food or other resources, such that growth, survivorship, or fecundity of the smaller predators is reduced (Glen and Dickman 2005). Competition can be divided broadly into exploitive competition, where competition for the use of resources occurs, and interference competition, whereby individuals are directly antagonistic toward others such that they exclude others from a contested resource (Glen and Dickman 2005). Dominant predators that have high dietary overlap with smaller

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mesopredators can suppress the subordinate species through prey competition, although a high degree of overlap does not necessarily indicate that competition is occurring (e.g., staple prey are abundantly available to both species). Competition is more likely to occur when a shared resource is in limited supply (Begon et al. 1996).

Another mechanism by which top-order predators can suppress the abundances of mesopredators is through direct killing (Berger and Gese 2007; Ritchie and Johnson 2009). Instances of intraguild predation tend to increase with high levels of dietary overlap, particularly when the larger species is 2–5 times larger than the victim species (Donadio and Buskirk 2006). Species that are subject to aggression and lethal interactions with a more dominant competitor often develop avoidance behaviors that influence their abundance and distribution (Fedriani et al. 2000; Lindström et al. 1995). Both exploitive and interference competition can occur among sympatric carnivores that preferentially select the same prey in greater proportion than their availability in the environment. When a limited resource is staple prey for both species, the dominant predator might outcompete its subordinate or aggressive encounters might occur, or both (Donadio and Buskirk 2006; Glen et al. 2007).

Both of Australia's largest terrestrial predators, the dingo (*Canis lupus dingo*; average mass of 16 kg) and the smaller introduced red fox (*Vulpes vulpes*; average mass of 4.6 kg) have been viewed historically as threats to pastoral enterprises. Predation by foxes also has been identified as a major threat to native fauna with masses $<$10 kg (Kinnear et al. 2002). To reduce their impacts dingo and fox populations have long been controlled through exclusion fencing, trapping, poison-baiting, and shooting (Fleming et al. 2001; Saunders and McLeod 2007). However, the mesopredator release hypothesis (MRH) and a growing body of data suggest that programs to control dingoes can be detrimental for conservation of biodiversity. This is because dingoes appear to suppress fox abundances across vast areas and thus benefit species that are vulnerable to predation by foxes (Johnson and VanDerWal 2009; Letnic et al. 2011).

Consistent with the MRH, macroecological studies have shown that the presence of dingoes is linked to the persistence of native rodents and ground-dwelling marsupials. Conversely, the ranges of rodents and marsupials declined where they overlapped little with dingoes (Johnson et al. 2007; Smith and Quin 1996). Similarly, field studies have demonstrated positive correlations between dingoes and native fauna threatened by foxes and negative relationships between threatened fauna and foxes (Letnic et al. 2009a, 2009b; Southgate et al. 2007; Wallach et al. 2009). These and other studies have prompted discussion of the maintenance or restoration of dingo populations, with the purpose of harnessing their fox-suppressive effects (Dickman et al. 2009). However, this idea is controversial because of the adverse impacts that dingoes have on livestock production and ambiguity as to whether the dingo is a native Australian species (Letnic et al. 2009a).

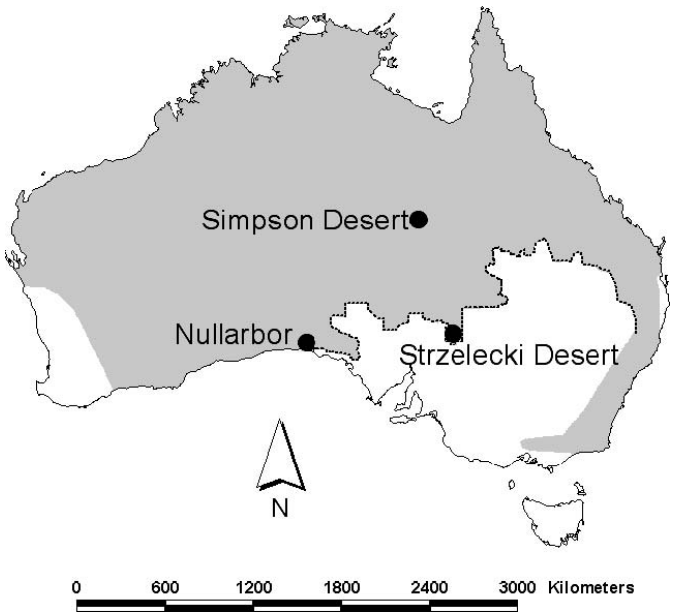


Fig. 1.—Map of the arid-zone study areas showing the locations of scat collection. The dashed line represents the dingo-barrier fence. Dingoes are rare in white areas on the map and common elsewhere.

The mechanism by which dingo–fox interactions might benefit conservation of biodiversity and ecological restoration is not clearly understood. Direct observations and fox remains found in digestive tracts and scats of dingoes indicate that dingoes occasionally prey on foxes (Glen et al. 2010; Marsack and Campbell 1990; Mitchell and Banks 2005). Additionally, foxes in the semiarid zone have been deterred from prey nests, warrens, and fox-feeding stations by the presence of dingo feces (O'Neill 2002), and foxes avoided bait stations visited by dingoes in southeastern Australia (Mitchell and Banks 2005). Such avoidance behavior by foxes could change the foraging patterns of foxes and, in turn, limit encounters between foxes and their prey, thereby increasing prey survival (Glen et al. 2007).

Dingoes also are likely to compete with foxes for food resources, particularly in times of drought when resources are scarce (Corbett 1995; Glen et al. 2007). Evidence for this form of competition is provided by studies showing high (65–94%) dietary overlap between sympatric dingoes and foxes (Glen and Dickman 2008; Mitchell and Banks 2005; Paltridge 2002; Pavey et al. 2008). Prey differentiation was noted in these studies, with foxes tending to consume smaller prey and dingoes consuming larger prey.

An understanding of the interactions between dingoes and foxes is required to evaluate the potential to incorporate the fox-suppressive effects of dingoes into conservation programs. We investigated the mechanisms by which a top-order predator might suppress the abundance of a sympatric mesopredator and benefit prey species at 3 widely separated sites in arid Australia (Fig. 1). On the basis of previous studies (Glen and Dickman 2008; Mitchell and Banks 2005; Paltridge 2002; Pavey et al. 2008) and similarities in the dentition of these 2 canids (Corbett 1995; MacDonald 1977), we predicted

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that substantial dietary overlap between dingoes and foxes would occur at all 3 study sites. We explored the potential for exploitative competition to occur between sympatric dingoes and foxes through analyses of diet and prey selectivity of these canids. Furthermore, in keeping with the concept of prey-scaling according to predator size (Sinclair et al. 2003) and the predictions of the MRH, we anticipated that larger prey ($\geq$1,000 g) would be more prominent in dingo diets and smaller prey ($<$100 g) would be more prominent in fox diets (Ritchie and Johnson 2009).

Materials and Methods

Study area.—The Simpson Desert study area spanned 2 private conservation reserves, Ethabuka and Cravens Peak, and 1 cattle grazing property, Carlo, located in southeastern Queensland (23°46′S, 138°28′E; 23°16′S, 138°17′E; and 23°29′S, 138°32′E, respectively; Fig. 1). The arid climate of this hot desert is characterized by a distinctive wet season between December and March with mean monthly rainfall ranging between 38 and 63 mm during these months; the nearest weather station (Boulia) has a mean annual rainfall of 302 mm (Bureau of Meteorology 2009). Mean daily maximum temperatures range from 33°C to 38°C in the summer and mean low temperatures range from 8°C to 18°C in the winter (Bureau of Meteorology 2009). The dominant landforms were sand dunes 8–10 m in height that are oriented in a north-northwest–south-southeast direction. Vegetation was hummock grassland dominated by *Triodia basedowii*, and the scattered trees found in swales were typically *Acacia cambagei* (Letnic and Dickman 2006). Water sources at this site included permanent springs and subartesian bores.

The study site in the Strzelecki Desert region was located north of the dingo-barrier fence in South Australia (30°75′S, 140°47′E; Fig. 1). The fence, which is 2 m high and $>$5,000 km long, is designed to exclude dingoes from sheep-grazing lands to the south; dingoes are common in areas north of the fence (Fleming et al. 2001). Cattle grazing occurred at the study site, and artificial bores and dams provided permanent surface water supplies. The dominant landforms were sand dunes 3–8 m in height that run northeast–southwest. The nearest weather station (Tibooburra) has a mean annual rainfall of 284 mm (Bureau of Meteorology 2009). Mean high and low temperatures range from 18°C to 36°C and 6°C to 22°C, respectively (Bureau of Meteorology 2009). Dune crests supported scattered trees and shrubs, including *Callitris glaucophylla*, *Casuarina pauper*, *Acacia ligulata*, and *Dodonaea viscosa*, with a sparse perennial understory. Vegetation in the swales between dunes was primarily ephemeral forbs, short-grasses, and shrubs.

The study site in the Nullarbor region was located in Wahgunyah National Park and was located west of the dingo-barrier fence where dingoes are common (31°45′S, 131°52′E; Fig. 1). The site was situated on coastal sand dunes in semiarid mallee heathland. The overstory consisted of *Eucalyptus gracilis* and *E. oleosa*; middle-story vegetation included *Melaleuca lanceolata* spp., *Geijera linearifolia*, and *Exocarpos aphyllus*. *Atriplex vesicaria* and *Rhagodia crassifolia* typified understory vegetation, and *Carpobrotus rossii* provided ground cover. The nearest weather station (Nullarbor) has mean maximum temperatures ranging from 18°C to 28°C and mean minimum temperatures ranging from 5°C to 16°C; mean annual rainfall is 302 mm (Bureau of Meteorology 2009). No livestock grazing occurred at the Nullarbor study site, and natural water sources were scarce; no artificial water sources were present. Although all 3 sites (with the exclusion of private reserves at the Simpson Desert site) are subject to sporadic predator reduction efforts—for example, intermittent poison-baiting using meat baits impregnated with sodium fluoroacetate (1080) or opportunistic shooting, or both—dingoes were common in all of the study areas (Letnic et al. 2009a; Letnic and Koch 2010).

Scat analysis.—Scats were collected in March and November 2007 (Strzelecki Desert), March–April 2008 (Nullarbor), and September–October 2008 (Simpson Desert). At each location scat samples were collected along unimproved roads, at watering points (springs and bores), and in swales and on dune tops. Samples were identified as those of dingoes or foxes based on size, smell, shape, and color (Triggs 1996). One or more fecal pellets deposited in the same spot were assessed to be a single scat. Scats were placed in plastic or paper bags and labeled with the location and date of collection. Scats were judged to be $<$2 months old based on observed characteristics, including color, smell, apparent moisture content, and level of deterioration (Paltridge 2002).

We sterilized samples via autoclave at 121°C for 20 min, or oven-dried them overnight at 100°C, and then washed them individually in nylon bags in a commercial washer. After washing, only indigestible fragments of prey remained (hair, teeth, bones, skin, scales, feathers, and exoskeletons). Using reference bone, teeth, and hair samples from species known or expected to be found within the study area and a source for identifying Australian mammalian hair (Triggs and Brunner 2002), we identified prey to the most specific, accurate taxonomic level possible. We examined hairs using whole mounts, cross sections, and scale casts under 10× and 40× microscopes as described in Triggs and Brunner (2002). When possible, we classified mammals and reptiles to the species level; we classified insects and birds to the class level.

Prey abundance assessments.—At all 3 sites coarse measures of prey abundance were conducted concurrently with scat collection. At the Strzelecki and Nullarbor sites we made estimates of the abundance of large- (kangaroo and livestock) and medium-sized (rabbit) mammals using 3 or 4 nocturnal spotlight transects (7–20 km long) at each site. Because of the sparse vegetation and understory in the Australian arid zone, spotlight surveys have been used previously in this region to estimate abundance of medium- and large-sized mammals (Letnic and Koch 2010; Read and Bowen 2001). In the Simpson Desert spotlighting was conducted using 4 transects ranging from 3 to 13 km in length. At all sites a 50-watt spotlight was used while we sat

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on the roof of a 4-wheel-drive vehicle moving at 15 km/h and counted large- and medium-sized mammals. Assuming observer visibility extended to 100 m on either side of the transect, we calculated indexes of abundance for large- and medium-sized mammals as mean number of animals sighted per hectare of spotlight survey.

We estimated small mammal and reptile abundances at the Strzelecki and Nullarbor sites on seven or eight 1-ha trapping grids composed of 6 pitfall traps (diameter = 150 mm, depth = 600 mm) equipped with a 10-m-long drift fence (height = 30 mm) and 25 box traps baited with peanut butter, oats, and cane syrup. Grids were at least 1 km apart and were checked for 4 consecutive mornings. In the Simpson Desert we assessed reptile and small mammal abundance using eight 1-ha trapping grids composed of 36 pitfall traps (diameter = 160 mm, depth = 600 mm) equipped with a 5-m-long drift fence. Box traps were not used at the Simpson Desert site, because they were found to be less effective (C. R. Dickman, University of Sydney, pers. comm.). Grids in the Simpson Desert were at minimum 1 km apart and were checked for 1–3 consecutive mornings. We calculated indexes of reptile and small mammal abundance at each site as the mean number of animals captured per hectare. We handled all animals in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Data analysis.—We classified prey items into the following categories: small, medium, or large mammals; birds; reptiles; insects; vegetation; other; or unknown. To ensure that we analyzed an adequate number of scats for each predator at each site we plotted the cumulative diversity of prey items identified in the sample against the number of scats dissected. We calculated the Brillouin index of diversity (Brillouin 1956) using the following equation:

$$\mathrm{H} = \frac{\ln N! - \sum \ln n_i!}{N},$$

where H is diversity, N is total number of individual prey recorded, and n_i is the number of individual prey items in the ith category. We used the Brillouin index of diversity instead of more common diversity indexes such as the Shannon index because prey items are sampled nonrandomly (Pielou 1975).

For the purposes of comparison with previous studies we report percent frequency of occurrence in this study (i.e., the number of scats for 1 predator species containing particular food items expressed as a percentage of the overall number scats for that species). Using the density of prey and the percent frequency occurrence of prey categories in the predators' diet, we calculated Ivlev's prey selectivity index (Ivlev 1961):

$$\mathrm{E} = \frac{r - p}{r + p},$$

where r is the proportion of the prey category in the predator's diet and p is the proportion of the availability of the prey category in the study area. Dietary selectivity index values range from −1 to +1. Index values near +1 indicate that the prey category is selected by the predator in much greater proportion than it is available in the habitat. Conversely, index values near −1 indicate that the prey category is selected much less than its abundance in the study area. Prey with index values near 0 are consumed in proportion to their availability. We calculated dietary overlap between foxes and dingoes using Pianka's index (Pianka and Pianka 1976):

$$\mathrm{DO} = \frac{\sum \mathrm{P}_{ij}\mathrm{P}_{ik}}{\sqrt{\sum \mathrm{P}_{ij}{}^2 \sum \mathrm{P}_{ik}{}^2}},$$

where P_{ij} is the proportion of prey category i in the diet of predator j and P_{ik} is the proportion of prey category i in the diet of predator k. Dietary overlap values range from 0 to 1, with 0 indicating no overlap and 1 indicating complete overlap.

Finally, it is common to compare prey of different predators according to size classes (Glen and Dickman 2008; Mitchell and Banks 2005; Paltridge 2002). In keeping with Paltridge (2002) and Letnic et al. (2009b), we denoted size classes as small for prey weighing <100 g, medium for those weighing 100–999 g, and large for prey weighing >999 g. We calculated the percentage of prey items taken by foxes and dingoes in each size class. We compared presence–absence data for each prey category using nonmetric multidimensional scaling (nMDS) plots based on Bray–Curtis similarity matrixes for each site. We then used analysis of similarities (ANOSIM), a nonparametric test that uses permutations to calculate significance between groups, to determine if the diets of dingoes and foxes differed significantly at each study site (Clarke 1993). The test statistic was the global R, which can range from −1 to +1, with a value close to −1 indicating that the variation within groups is higher than the variation between groups and a value close to +1 indicating that the variation between groups is higher than the variation within groups (Clarke 1993). If a significant result ($P < 0.05$) was obtained using ANOSIM, we used SIMPER to determine which prey categories contributed to differences in the predators' diets (Clarke 1993). We used PRIMER 5 for Windows (version 5.2.4) for all analyses (Clarke and Gorley 2001).

Results

We analyzed a total of 393 scats. Simpson Desert samples included 78 fox and 52 dingo scats; Strzelecki Desert samples included 31 fox and 146 dingo scats; and 52 fox and 34 dingo scats were analyzed from the Nullarbor region. The cumulative diversity, H(k), of prey items in the diet of each predator reached an asymptote at a sample size below the number of scats analyzed (Fig. 2), indicating that the sample sizes were sufficient. A combined total of 43 prey types were identified (Table 1).

Simpson Desert.—In the Simpson Desert 23 of a total of 34 food types were identified in both dingo and fox scats (Table 1). Pianka's index of dietary overlap was 0.849, and nMDS indicated minimal separation in the diets of dingoes and foxes (Fig. 3a). The diets of dingoes and foxes differed

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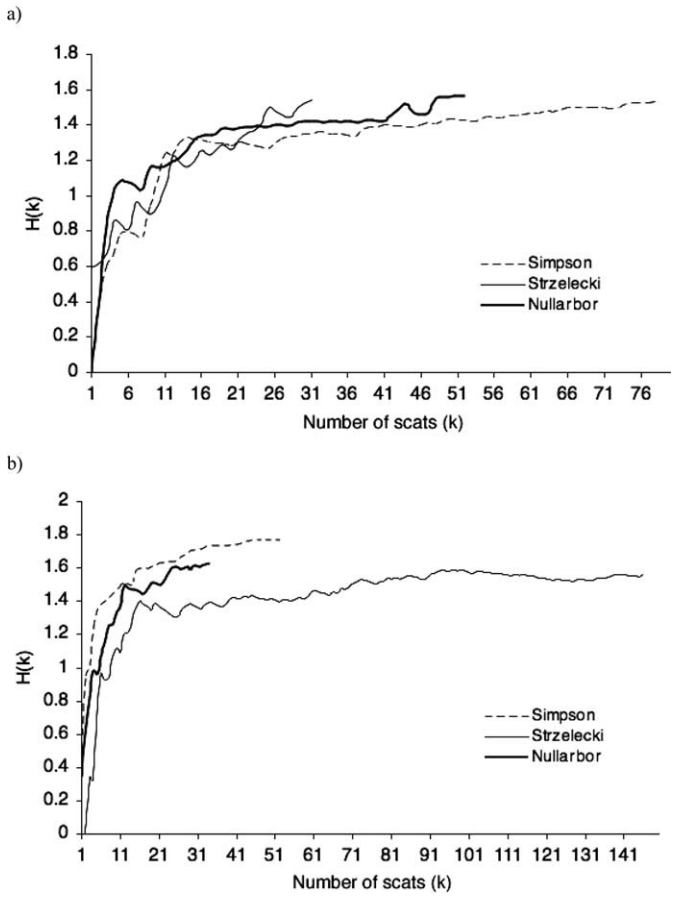


Fig. 2.—Cumulative diversity, H(k), of a) fox and b) dingo prey items with increasing sample size (k) for each study site.

significantly (global $R = 0.233$, $P = 0.001$). SIMPER analysis revealed that dingo and fox diets diverged in the prey categories of small mammals, insects, and large mammals, with the former 2 occurring more in fox diets and the latter comprising more dingo diets (Table 2a). Each predator consumed substantially more native rodents than dasyurids (Table 1). Native rodents were the dominant prey item of foxes and were consumed more than twice as often by foxes as by dingoes. Dasyurids were consumed less frequently by foxes than by dingoes. Foxes consumed more reptiles, and dingoes consumed more vegetation (Table 2a). Birds occurred nearly equally in the diets of both predators.

Large mammals in dingo and fox diets were primarily red kangaroos (*Macropus rufus*) and infrequently, feral camels (*Camelus dromedarius*). Medium-sized mammalian prey were few and included 2 occurrences of rabbit (*Oryctolagus cuniculus*) and 1 occurrence of echidna (*Tachyglossus aculeatus*) found in dingo scats. One unidentified medium-sized prey item was found in a fox scat. Fox remains were found in 4 dingo scats. Feral cat (*Felis catus*) and dingo hair appeared in 2 fox scats.

Reptiles and small mammals were the most abundant potential prey available in the Simpson Desert, followed by large and medium mammals (Table 3a). Dingoes and foxes consumed medium and large mammals disproportionately more than their abundance in the Simpson Desert (Table 3a). Foxes selected small mammals in greater numbers than their abundance, but dingoes consumed small mammals in proportion to their availability. Reptiles were represented in fox diets in proportion to their abundance and were selected slightly less in relation to their availability by dingoes.

Strzelecki Desert.—In the Strzelecki Desert 12 of 18 food types were found in both predators' scats (Table 1). Dietary overlap was high (0.970), but a statistically significant difference was found between the diets of the 2 predators (Fig. 3b; global $R = 0.129$, $P = 0.01$). SIMPER analysis identified that this difference resulted from the greater presence of medium mammals and reptiles in dingo diets and livestock in fox diets (Table 2b). Medium mammals (mainly rabbits) appeared in 73% of dingo scats but only 52% of fox scats. Livestock (*Bos* sp. or *Ovis aries*, or both) occurred in 16% and 12% of fox and dingo scats, respectively. Dingoes consumed more reptiles (primarily species of Agamidae) and insects, and foxes consumed more vegetation (Table 1). Both dingoes and foxes consumed red kangaroos; evidence of fallow deer (*Dama dama*) was found in 1 fox scat. Small mammals were few in either predator's diet and consisted of unidentified rodents and house mice (*Mus musculus*). Birds also were rare in predator scats, and 1 dingo scat contained feral cat remains (Table 1).

Small mammals were the most abundant prey at the Strzelecki site, followed by reptiles, medium mammals, livestock, and large mammals (Table 3b). Both dingoes and foxes showed a preference for large and medium mammals and livestock and consumed these items in greater proportions than their abundances in the environment (Table 3b). Small mammals had low selectivity indexes for both predators despite the high relative abundance of this prey category. Dingoes consumed reptiles in proportion to their abundance in the environment, but foxes selected this prey item disproportionately less than its abundance in the study area.

Nullarbor region.—In the Nullarbor region dingoes and foxes shared 11 of 20 food items (Table 1). Extensive dietary overlap occurred as indicated by Pianka's index (0.957) and the nMDS plot (Fig. 3c). We found no significant difference between the diets of the 2 predator species (global $R = 0.01$, $P = 0.301$). Sixty-five percent of dingo scats had medium mammal remains (primarily rabbits), and 48% of fox scats contained rabbits. Insects occurred in 50% of fox scats and 38% of dingo scats, and reptiles, such as skinks and snakes, occurred in 37% of fox scats and 29% of dingo scats (Table 1). Dingoes consumed more birds than did foxes (12% and 6% of scats, respectively). Only dingoes consumed macropods (*Macropus fuliginosus*), feral cats, and fish or crustaceans in the Nullarbor region; all of these prey items were rare in dingo scats. Large mammalian prey found in fox scats included 1 instance of feral goat (*Capra hircus*). Small mammals were uncommon in the diets of either predator; those that were found were rodents and *Sminthopsis* sp.

Reptiles were the most abundant prey item in the Nullarbor region, followed by small, large, and medium-sized mammals

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Table 1.—Percent frequency of occurrence of prey categories (based on presence–absence) and items in the diets of dingoes and foxes in the Simpson Desert, Strzelecki Desert, and Nullarbor region.

Prey item	Simpson Desert		Strzelecki Desert		Nullarbor region	
	Dingo	Fox	Dingo	Fox	Dingo	Fox
Small mammals	53.8	85.9	2.7	6.5	14.7	17.3
Dasyuridae, unidentified	3.8	1.3	—	—	—	—
Dasycercus cristicauda, mulgara	—	1.3	—	—	—	—
Sminthopsis spp.	9.6	3.8	—	—	2.9	1.9
Sminthopsis macroura, striped-face dunnart	7.7	3.8	—	—	—	—
Sminthopsis youngsoni, lesser hairy-footed dunnart	3.8	1.3	—	—	—	—
Sminthopsis crassicaudata, fat-tailed dunnart	1.9	—	—	—	—	—
Ningaui ridei, ningaui	3.8	2.6	—	—	—	—
Muridae, unidentified rodents	15.4	14.1	0.7	3.2	5.9	3.8
Muridae, unidentified native rodents	13.5	17.9	—	—	—	—
Leggadina forresti, Forrest's mouse	5.8	14.1	—	—	—	—
Mus musculus, house mouse	26.9	25.6	2.1	3.2	5.9	7.7
Notomys alexis, spinifex hopping-mouse	9.6	23.1	—	—	—	—
Notomys cervinus, fawn hopping-mouse	1.9	—	—	—	—	—
Notomys mitchellii, Mitchell's hopping-mouse	—	—	—	—	—	3.8
Pseudomys desertor, desert mouse	3.8	9.0	—	—	—	—
Pseudomys hermannsburgensis, sandy inland mouse	36.5	55.1	—	—	—	—
Medium-sized mammals	11.5	3.8	72.6	51.6	64.7	48.1
Mammalia (medium), unidentified	—	1.3	—	3.2	2.9	—
Oryctolagus cuniculus, rabbit	3.8	—	71.2	48.4	58.8	48.1
Tachyglossus aculeatus, echidna	1.9	—	0.7	—	—	—
Vulpes vulpes, fox	7.7	—	—	—	—	—
Canis lupus familiaris, dog	—	1.3	—	—	—	—
Felis catus, cat	—	1.3	1.4	—	2.9	—
Large mammals	48.0	3.8	14.4	12.9	5.9	1.9
Macropus rufus, red kangaroo	44.2	3.8	14.4	9.7	—	—
Macropus fuliginosis, western grey kangaroo	—	—	—	—	5.9	—
Capra hircus, feral goat	—	—	—	—	—	1.9
Camelus dromedarius, feral camel	7.7	—	—	—	—	—
Dama dama, fallow deer	—	—	—	3.2	—	—
Reptiles	38.5	48.7	21.9	16.1	29.4	36.5
Reptilia, unidentified reptiles	9.6	14.1	—	—	2.9	3.8
Agamidae, unidentified dragon	9.6	12.8	18.5	9.7	—	5.8
Pogona vitticeps, inland bearded dragon	1.9	3.8	5.5	—	—	—
Varanidae, unidentified lizard	1.9	10.3	—	—	2.9	—
Varanus gouldii, goanna	3.8	3.8	0.7	3.2	—	1.9
Moloch horridus, thorny devil	—	1.3	—	—	—	—
Tiliqua occipitalis, blue-tongued lizard	—	—	—	—	2.9	1.9
Serpentia, unidentified snakes	1.9	1.3	0.7	3.2	5.9	5.8
Scincidae, unidentified skinks	13.5	17.9	0.7	3.2	14.7	17.3
Birds	25.0	21.8	4.8	3.2	11.8	5.8
Aves, unidentified birds	25.0	21.8	4.8	3.2	11.8	5.8
Arthropods	46.2	69.2	16.4	6.5	38.2	50.0
Insecta, unidentified insects	46.2	69.2	16.4	6.5	38.2	50.0
Vegetation	51.9	25.6	7.5	16.1	20.6	28.8
Unidentified vegetation	51.9	25.6	7.5	16.1	20.6	28.8
Other	—	—	12.3	16.1	5.9	—
Livestock (*Bos* sp.)	—	—	11.6	16.1	—	—
Livestock (*Ovis aries*, sheep)	—	—	0.7	—	—	—
Fish or crustacean	—	—	—	—	5.9	—
Unknown	1.9	—	—	—	—	—
Unidentified items	1.9	—	—	—	—	—

(Table 3c). Both dingoes and foxes showed a preference for large and medium mammals, despite their low abundance relative to other prey (Table 3c). Small mammals also were selected in greater numbers than their abundance by both predators. Reptiles were underrepresented in both predators' diets in relation to their availability.

Discussion

This study is a limited-duration profile of the overlap in arid-zone predator diets. Because scats were collected during a few months of a single 12-month period, seasonal variations in prey abundance and thus predator diets cannot be detected in

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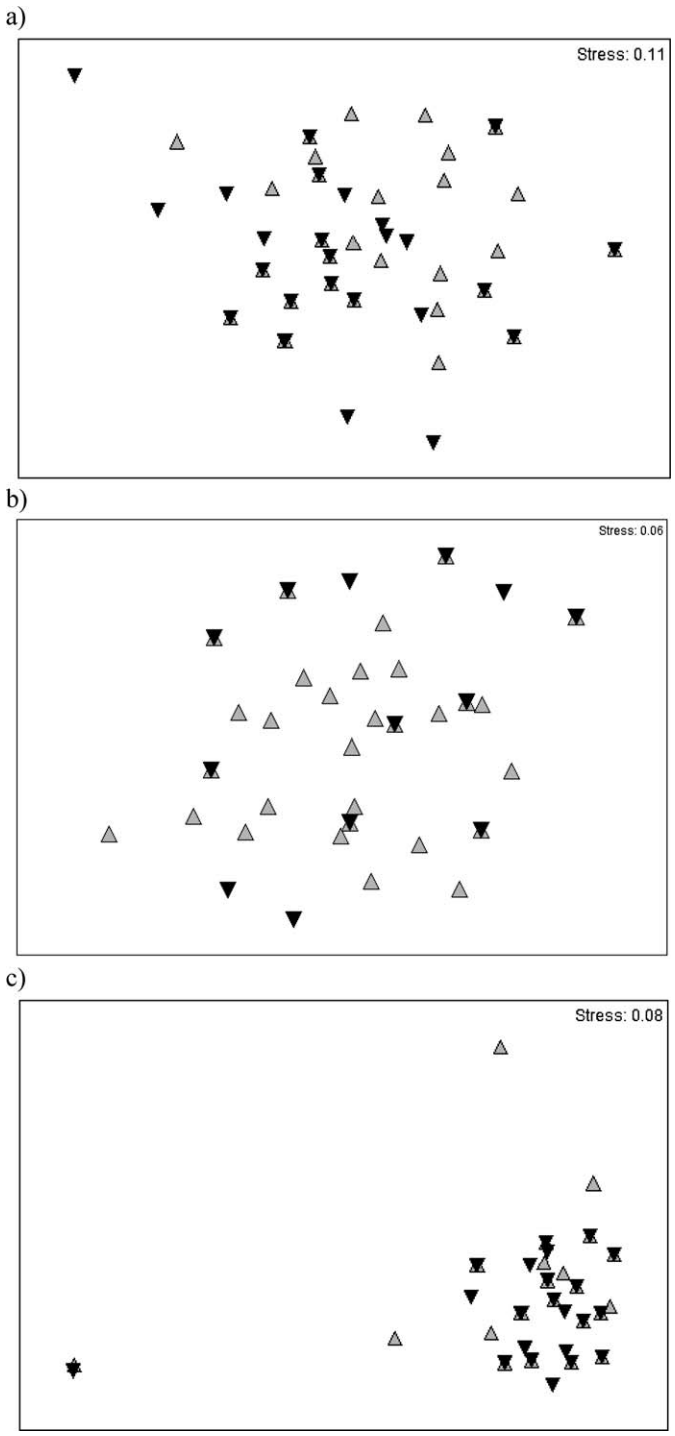


Fig. 3.—Ordination plot of nonmetric multidimensional scaling analyses (nMDS) showing the dietary overlap of foxes (▼) and dingoes (▲) in the a) Simpson Desert, b) Strzelecki Desert, and c) Nullarbor region. Stress is a measure of goodness of fit between rank-order of observed distances and those predicted from dissimilarities. Values <0.2 indicate that the nMDS plot is a good representation of dissimilarities (Quinn and Keough 2002).

our analysis. For instance, Catling (1988) showed that predator (fox and cat) diets responded to the breeding season of staple prey (e.g., rabbits). Furthermore, the availability of prey and predator abundance fluctuates in response to temporal variation in rainfall (Letnic and Dickman 2006; Letnic et al. 2005). Over the course of a 7-year study Corbett and Newsome (1987) found that dingoes in central arid Australia consumed primarily irruptive small and medium-sized prey after periods of rainfall but shifted to larger prey as drought conditions returned. Additionally, Pavey et al. (2008) identified variations in the dietary overlap of dingoes and foxes, depending on the stage of an irruptive rodent outbreak. Because of the relatively short duration of our study, long-term trends in prey abundance were not detectable. Similarly, it is conceivable that the differences in predator control conducted at each site could have influenced our results by altering the relative abundances of predator species and hence their prey preferences (Roberts et al. 2006). Assessments of prey abundance did not include birds and insects, and our analyses indicated that only the latter contributed to the difference between the canid diets at the Simpson Desert site. Furthermore, our trapping techniques might have been less effective in capturing larger reptiles. Although the high dietary overlap observed suggests that these prey species were comparably available to both dingoes and foxes (Mitchell and Banks 2005), we were unable to assess prey preferences for birds and insects, and prey selectivity for reptiles could be undervalued.

Despite these limitations, our findings offer insight into the potential for dietary competition and predatory interactions between sympatric dingoes and foxes in arid Australia. The extent of dietary overlap found in each arid study area (DO = 0.849–0.970) was greater than that reported for the Tanami Desert (DO = 0.63—Paltridge 2002) but was consistent with findings from a previous study from the Simpson Desert (DO = 0.93—Pavey et al. 2008) and studies conducted in mesic forest regions (DO = 0.91–0.94—Glen and Dickman 2008; Mitchell and Banks 2005). The extensive dietary overlap between dingoes and foxes suggests that considerable potential for dietary competition existed at each study site. If this high dietary overlap results in competition for food resources, it could explain the suppressive effect that dingoes have on fox abundances (Johnson and VanDerWal 2009; Letnic et al. 2011).

The similar prey preferences of foxes and dingoes also could contribute to dietary competition and aggressive interference. At all 3 sites dingoes and foxes selected large and medium mammals in greater proportion than their abundance in the environment. This disproportionately high consumption of the same prey conceivably could result in exploitive competition between the predators. The possibility of exploitive competition is even more likely in the Strzelecki and Nullarbor regions where rabbits, the most frequently consumed prey of dingoes and foxes, were consumed by both predators in greater proportion than their abundance. However, demonstrating that dingoes suppress fox abundance through exploitative competition would require manipulating the abundances of dingoes or the availability of food resources for foxes and observing the ensuing numerical and dietary responses of foxes. Such experiments would be challenging to

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Table 2.—The result of SIMPER analysis of predator diets in the a) Simpson Desert and b) Strzelecki Desert. Average similarity values show the mean similarity between the contents of each scat for dingoes and foxes. Percent contribution indicates the average contributions that individual prey categories make to dissimilarity between diets of the 2 predators. Livestock consists of *Bos* sp. and *Ovis aries*.

Predator species	Average similarity	Prey category	Average dissimilarity	Percent contribution	Cumulative percent
a) Simpson Desert					
Dingo	40.53	Small mammal	10.77	17.66	17.66
Fox	57.23	Insect	10.65	17.47	35.13
		Large mammal	10.54	17.29	52.41
		Vegetation	10.10	16.58	68.99
		Reptile	9.36	15.36	84.35
		Bird	6.47	10.61	94.96
b) Strzelecki Desert					
Dingo	44.22	Medium mammal	19.58	29.61	29.61
Fox	25.76	Reptile	10.05	15.20	44.80
		Livestock	9.81	14.83	59.63
		Vegetation	8.28	12.52	72.15
		Large mammal	8.09	12.23	84.37
		Insect	5.56	8.41	92.79

conduct because of the extensive home ranges of these species, and hence the large areas required (Fleming et al. 2001; Saunders and McLeod 2007), and logistical difficulties posed by the availability of few techniques that are capable of effectively manipulating the abundances of dingoes but not foxes.

Donadio and Buskirk (2006) argued that carnivores that have a high dietary overlap are likely to have more frequent encounters as they seek similar prey. These competitive encounters can result in interspecific aggression or killing over the contested resource. Furthermore, Donadio and Buskirk (2006) noted that interspecific killings are most likely to occur when an intermediate body-size difference exists between predators (e.g., the larger predator is 2–5 times bigger than the victim species) because at intermediate body-size differences, the larger predator is likely to perceive the smaller species as sizeable enough to be a competitor but small enough to defeat with minimal risk (Donadio and Buskirk 2006). Dingoes are, on average, 3.5 times larger than foxes, which when coupled with the observed high dietary overlap and similar prey selectivity, conceivably could lead to aggressive encounters between the 2 species. If encounters between dingoes and foxes result in fox mortality, intraguild killing could explain the suppressive effect that dingoes have on the abundance of foxes (Johnson and VanDerWal 2009; Letnic et al. 2011). The idea that dingoes suppress fox abundance by direct killing also is supported by the occurrence of fox remains in 4 dingo scats from the Simpson Desert and previous observations of dingoes killing foxes and the presence of fox remains in dingo scats (Glen et al. 2010; Letnic and Dworjanyn, in press; Letnic and Koch 2010; Marsack and Campbell 1990; Mitchell and Banks 2005).

Table 3.—Mean prey abundance and prey selectivity (E) at the a) Simpson, b) Strzelecki, and c) Nullarbor study sites. Prey abundance is reported as captures per hectare of reptiles and small mammals or spotlighted sightings per hectare of medium mammals, native large mammals, and livestock (*Bos* sp. and *Ovis aries*). *SE*s are in parentheses. NA = not applicable.

Prey category	Prey abundance	E (Dingo)	E (Fox)
a) Simpson			
Reptile	4.375 (0.668)	−0.194	−0.079
Small mammal	3.267 (0.796)	0.116	0.337
Medium mammal	0.006 (0.004)	0.986	0.960
Large mammal	0.016 (0.012)	0.991	0.896
Livestock	0	NA	NA
b) Strzelecki			
Reptile	6.440 (1.060)	0.005	−0.148
Small mammal	23.000 (1.670)	−0.933	−0.845
Medium mammal	0.184 (0.012)	0.983	0.976
Large mammal	0.008 (0.001)	0.996	0.996
Livestock	0.044 (0.008)	0.976	0.985
c) Nullarbor			
Reptile	1.000 (0.320)	−0.291	−0.189
Small mammal	0.850 (0.398)	0.674	0.716
Medium mammal	0.008 (0.009)	0.999	0.999
Large mammal	0.011 (0.019)	0.988	0.962
Livestock	0	NA	NA

Consistent with previous studies, our results showed that when rabbits are present they are an important dietary item for both dingoes and foxes (Catling 1988; Corbett and Newsome 1987). Furthermore, when rabbits are absent or rare, both predators increase their consumption of reptiles and invertebrates (Paltridge 2002), and in the case of dingoes, large prey such as livestock and kangaroos (Corbett 1995). In the Simpson Desert, where rabbits were absent, small rodents (<50 g) served as staple prey, particularly for foxes, for which the frequency of occurrence of native rodents was more than twice as high as that in dingo scats. Hence, the relatively low dietary overlap observed in the Simpson Desert could be due to the rarity of rabbits (Letnic and Dickman 2006), which were selected for by both dingoes and foxes at the other sites in this study. Other studies have shown that dietary overlap also could depend on temporal trends in prey abundances and hence predator diets. For example, Pavey et al. (2008) found that both dingoes and foxes had broader dietary niches during

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periods of low rodent abundance and higher dietary overlap during rodent outbreaks when both species preyed heavily on abundant rodents. However, our results support the notion that the presence of rabbits increases dietary overlap between dingoes and foxes, despite this prey item's relatively lower abundance. At the Strzelecki and Nullarbor sites overlap between the predators' diets was highest, despite rabbits being substantially less abundant than other prey items, particularly small mammals. The strong preference of both predators for rabbits when they are present in the landscape might reflect the relatively high energy rewards provided by rabbits in comparison to smaller prey such as rodents and lizards (Paltridge 2002), and in the case of dingoes, the relatively low abundances of large prey (Letnic et al. 2009b).

In the Simpson Desert dingo and fox diets were highly dissimilar with regard to the relative frequency of occurrence of small and large mammals. Camels were found in dingo feces, but because of their large size (400–600 kg), camels likely were not killed by dingoes. Rather, camel remains in dingo feces were likely the result of dingoes consuming carrion or preying on camel calves. Dingoes in the Strzelecki Desert and Nullarbor region also consumed more large mammals than did foxes. Because foxes are predominately solitary foragers (MacDonald 1977) and are less capable of individually subduing large prey, large fox prey in the Strzelecki Desert (cattle) most likely was consumed as carrion. The greater incidence of large mammals in dingo diets and small mammals in fox diets was consistent with the findings of previous studies that have found a tendency for foxes to consume smaller prey than dingoes (Letnic et al. 2009b; Marsack and Campbell 1990; Mitchell and Banks 2005; Paltridge 2002).

The predilection of foxes for smaller prey than what dingoes selected is consistent with the prediction made under the MRH that mesopredators are likely to have greater per capita impact on small prey than sympatric top-order predators (Ritchie and Johnson 2009). It also follows from the MRH that top-order predators can be expected to alleviate the predatory impact of mesopredators on small prey by suppressing the abundance or altering the behavior of mesopredators, or both (Ritchie and Johnson 2009). These predictions are borne out in the arid regions of Australia where an inverse relationship exists between the abundances of dingoes and foxes (Letnic et al. 2011; Newsome et al. 2001) and positive relationships exist between the presence of dingoes and the persistence and abundances of native rodents and ground-dwelling marsupials (Johnson et al. 2007; Letnic et al. 2009a, 2009b). These patterns, consistent with the predictions of the MRH, suggest that dingoes have the potential to be used as a mechanism to mitigate the predatory impacts of foxes on native fauna (Dickman et al. 2009; Letnic et al. 2011).

In conclusion, our results showed that sympatric dingoes and foxes have extensive dietary overlap, similar overrepresentation according to abundance of preferential prey in their diets, and that fox remains were present in the diet of dingoes. These findings are consistent with the notion that dingoes have the potential to suppress fox abundance through both dietary competition and intraguild predation. Although considerable dietary overlap was found between dingoes and foxes, dingoes tended to consume larger prey and foxes showed a preference for smaller prey. These findings are consistent with the MRH and support the notion that small prey benefit from the suppressive effect of dingoes on foxes. We recommend that future research seeks to manipulate dingo populations to provide a better understanding of their effects on the abundance, diet, and behavior of foxes. Studies of this nature will assist in evaluating the utility of incorporating the trophic effects of top-order predators into programs for the conservation of biodiversity.

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