

Do wild dogs exclude foxes? Evidence for competition from dietary and spatial overlaps

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Abstract The management of wild canids (wild dogs/dingoes and foxes) presents a conservation dilemma for land managers across Australia. These canids are predators of wildlife and domestic stock but dingoes are considered native and anecdotal reports suggest that they may suppress foxes such that dingo/dog conservation may have a net benefit to wildlife. This study examines dietary and spatial interactions between wild dogs and foxes in the Greater Blue Mountains region of NSW to address the possibility of suppression through competitive exclusion by dogs on foxes. Predator diets were compared using faecal analysis as well as an analysis of 19 dietary studies from similar forest habitats in eastern Australia. Spatial relationships were examined using data from an extensive canid control programme. Diets of wild dogs and foxes showed a high degree of overlap in species taken, indicating potential for competition. But there was also evidence of resource partitioning with the size and arboreality of mammalian prey differing between the two predators. Wild dogs and foxes responded to different landscape-scale variation in the physical environment, but there was no clear evidence of large-scale differences in their distribution. At the fine scale there was a negative association between these predators that indicated possible temporal avoidance or localized habitat shifts. Therefore, there is evidence for dietary competition and fine-scale exclusion, but no support for landscape-scale exclusion of foxes by wild dogs in the Blue Mountains.

Key words: *Canis lupus dingo*, *Canis lupus familiaris*, dingo, feral predator, fox, mesopredator release, predator:prey, *Vulpes vulpes*, wild dog.

INTRODUCTION

This study examines the potential for competitive interactions between the two wild canids of Australia, the wild dog (including dingoes *Canis lupus dingo*, feral dogs *Canis lupus familiaris* and their hybrids) and the red fox (*Vulpes vulpes*). The management of these species presents a considerable conservation dilemma for land managers across Australia. Due to the losses that these canids inflict on the livestock industry (Saunders *et al.* 1995; Fleming *et al.* 2001) there is pressure and expectation by rural communities that predator impact be minimized. In addition, there is a strong perception that these predators have a negative impact on native mammals, thereby amplifying pressure for predator control. The *Rural Lands Protection Act 1989* specifies that pest animals must be controlled on Crown lands, with wild dogs and foxes declared pests throughout New South Wales (NPWS 2001). The dingo, however, is considered to be a native animal (e.g. in NSW) requiring conservation, and considered

as a threatened species due to threats from hybridization (Corbett 1995; Wilton 2001). Thus, in NSW for example, the Department of Environment and Conservation is responsible for controlling wild dog and fox numbers in the reserve system whilst simultaneously conserving dingoes as a native species (NPWS 2001) despite uncertainties over their hybridization status (Corbett 1995; Wilton 2001).

The ecological roles of dingoes and foxes as top predators have also been part of the management debate. Increasingly, popular opinion proposes that the maintenance of dingo populations has a net benefit to wildlife by way of their supposed negative impacts on foxes (Smith & Quin 1996; Hobbs 2001; Newsome 2001; Daniels & Corbett 2003). Competition theory predicts that two competing species can coexist in a stable environment via some degree of resource separation (Gause 1934). If there is little or no separation, they occupy the same ecological niche and one competing species will eliminate or exclude the other (Hardin 1960; Begon *et al.* 1996). For interactions involving different-sized predators, this theory has been further developed in the mesopredator release hypothesis (Soulé *et al.* 1988; Sovada *et al.* 1995), whereby the disappearance of large apex predators such as dingoes (10–25 kg) may lead to the increase of smaller competing carnivores such as foxes (5–8 kg)

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and cats (*Felis catus* 3–6 kg) (see also Fedriani *et al.* 2000). Support for this comes from North America where in areas that have seen a decline in the coyote (*Canis latrans*), red fox numbers have increased (Linhart & Robinson 1972; Goodrich & Buskirk 1995; Crooks & Soulé 1999). This is an intuitively attractive theory to land managers and has influenced decisions regarding the control of canids in Australia (Hobbs 2001). This is despite a lack of clear understanding about dingo/fox interactions, and despite the fact that the nature of any benefits from dingo conservation have not been considered in detail (Newsome 2001).

Wild dogs and foxes use a wide range of prey, and are generally thought to have a degree of dietary niche overlap, most likely for medium-sized prey, although this overlap has not been formally quantified. Both predators are large cursorial hunters of mainly mammals, and are typically solitary predators in forest environments (Saunders *et al.* 1995). Dietary overlap will indicate a potential for interspecific competition, and if the considered resource is in short supply, dietary niche overlap is an essential condition of competition (Pianka 1981; Giller 1984). For example, in arid Australia fox abundance declines during drought due to declines in prey availability while competition with dingoes for use of watering points and carcasses is thought to intensify (Corbett 1995; Fleming *et al.* 2001).

Overlap in space use or similar habitats by wild dogs and foxes may also indicate potential competition. There are anecdotal accounts that where wild dogs are in high abundance foxes are rare (Jarman 1986; Newsome *et al.* 1997). This may be due to interspecific competition (interference or exclusion competition) or predator avoidance, as foxes have been found in the diets of wild dogs (Newsome *et al.* 1983; Marsack & Campbell 1990; McKay 1994). These anecdotal accounts have led to the popular belief that wild dogs suppress the abundance and distribution of foxes. However, there have been few attempts to quantify this apparent inverse relationship (Fleming *et al.* 2001), and other factors may have a greater influence on fox distribution. For example, in eastern NSW foxes are rare or absent from some eucalypt forests, and as the distance from freehold land increases the abundance of foxes decreases (Catling & Burt 1995).

An extensive poison baiting programme aimed at controlling wild dogs in the Greater Blue Mountains region provided a unique opportunity to explore the dietary and spatial aspect of wild dog/fox interactions over a large spatial scale. This programme involved repeated visits over 6 years to more than 300 permanent bait stations along 200 km of fire trails in four National Parks in that region (Gardens of Stone, Blue Mountains, Kanangra-Boyd and Abercrombie River). Baiting occurred biannually, in autumn and spring, to coincide with the breeding and dispersal of predators,

and provided data on bait takes and visitation rates for analysis of wild dog and fox spatial relationships.

In this article, three predictions of the hypothesis that wild dogs and foxes compete in the Greater Blue Mountains are examined (i) that high dietary overlap is likely between predators; (ii) that at the landscape scale, wild dogs and foxes show a negative spatial relationship; and (iii) that in areas where these canids coexist there is a negative spatial association at the fine scale. These predictions were tested by comparing the diets of wild dogs and foxes using analysis of predator scats from the Blue Mountains region. An analysis of previous dietary studies from eastern Australia was carried out to reveal broader trends of dietary niche overlap. Abundances of wild dogs and foxes were compared and the presence or absence of each species related to different abiotic landscape features using generalized linear models (GLM) and generalized additive models (GAM) of GIS data. Wild dog presence was also examined to establish whether this lessened the probability of fox presence at a particular location using the baiting data.

METHODS

Study area

The study was conducted in Blue Mountains and Kanangra-Boyd National Parks (NP), which have a combined area of 317 094 ha, and Gardens of Stone and Abercrombie River NPs, which together form the Greater Blue Mountains region (Fig. 1). This region is located 100–200 km west of Sydney (33°07'–34°20'S, 149°20'–150°40'E). The topography of the area is rugged with elevations ranging from 500 m to 1400 m. It contains a wide variety of vegetation types, including dry sclerophyll forests and woodlands, heath, moist forests and swamps. Winters are cool (daily average 0–8°C) and summers mild to warm (daily average 10–25°C) with an average annual rainfall of 1000 mm.

Diet overlap

For both dogs and foxes a minimum of 25 scats were collected from fire trails (mean distance covered $8.8 \text{ km} \pm 1.5$) at each of 10 sites which were separated by at least 5 km and were spread along access routes throughout the study area. Collections were carried out between late April and September 2002. During these cooler months canids are likely to rely on mammalian prey due to the limited occurrence of fruit and insects (Brunner *et al.* 1975). Scats could normally be distinguished between dog and fox by shape, size,

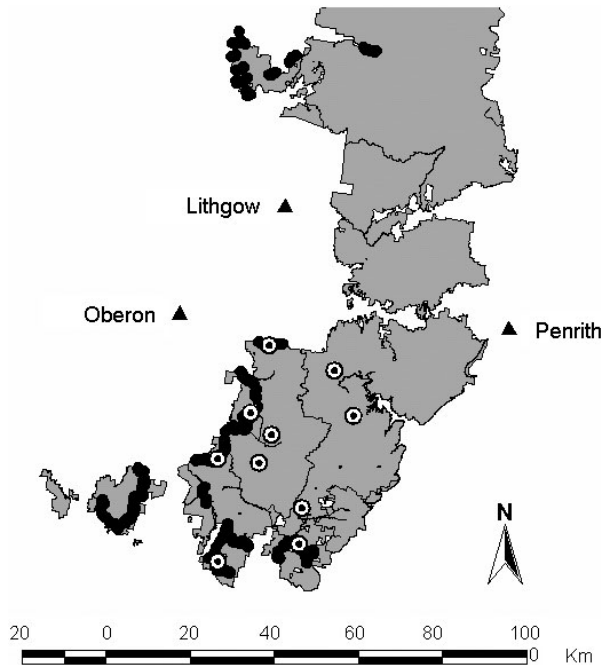


Fig. 1. Greater Blue Mountains region study area [shaded area National Parks and Wildlife Service (NPWS) estate]. (⊙) Scat collection sites; (●) NPWS bait station sites; (▲) Town.

odour and texture (Triggs 1996) but the 5% that could not be identified were excluded.

Scats were oven-dried at 90°C for 24 h to kill viable parasites (Brunner & Wallis 1986; Brunner *et al.* 2002). Prey remains were sorted macroscopically into bone fragments, mammalian hair, feathers, invertebrate remains and vegetation. Bone fragments were identified by comparison to reference skeletons and bone keys (Triggs 1996). Hairs were identified from microscopic analysis using a combination of cross-section, whole mount and cuticle scale impression techniques (Brunner & Coman 1974; Triggs 1996; Brunner *et al.* 2002). Non-mammalian remains were classified as birds, reptiles, invertebrates, fruit or vegetation.

For each site, dietary data were converted to percentage occurrence of food items, defined as the proportion of scats in a sample that contain a particular food item (Reynolds & Aebischer 1991). Niche breadth (B_A) was calculated for dog and fox data to compare their utilization of prey species. Levins' standardized formula was used to compare the proportion of prey species exploited by each canid (Hurlbert 1978; Krebs 1989):

$$B_A = \frac{(1 / \sum p_i^2) - 1}{n - 1}$$

where p_i = proportion of occurrence of each prey species in canid diet; n = number of prey species in canid

diet; B_A ranges from 0 to 1 (Bryce *et al.* 2002). This measure gives more weight to commonly eaten species and less to rarely consumed prey (Krebs 1989).

Niche overlap (O_{jk}), was estimated using Pianka's adaptation of MacArthur and Levins' formula (Pianka 1973; Krebs 1989):

$$O_{jk} = \frac{\sum n p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where j and k are the two canids being compared; O_{jk} ranges from 0 to 1 where 0 = no overlap and 1 = complete overlap (Bryce *et al.* 2002). Separate χ^2 -tests were used to examine differences between dogs and foxes in overall prey, mammal prey size and ground dwelling or predominantly arboreal prey species. Distinct mammal prey size categories could not be determined according to the Body Mass Difference Index (e.g. Jones & Barmuta 1998). Instead, three categories were used to differentiate mammal prey size (small < 0.75 kg, medium 0.75–10 kg, large > 10 kg).

Multi-dimensional scaling (MDS), one-way analysis of similarity (ANOSIM) and similarity percentages (SIMPER) were used to examine differences in diet between predators, using scat collection sites as replicates. Bray-Curtis dissimilarity matrices on untransformed data were used in the MDS as these provide the best determination of differences between data sets and give less weight to rarely occurring species (Krebs 1989; Clarke & Warwick 1994).

To assess broader trends in dietary niche overlap between predators, dog/fox diets were compared from 19 previous studies conducted in similar habitats to the eucalypt woodland/forest of the Blue Mountains region. The studies selected were from eastern Australia where common prey species such as swamp wallaby (*Wallabia bicolor*), possums, antechinus and rabbit (*Oryctolagus cuniculus*) were recorded in canid diets. Predominantly rural studies, where sheep and cattle dominated the diets, were excluded. Niche breadth and niche overlap were calculated using the same method as the diet analysis described above. Analysis of variance (ANOVA), SIMPER, ANOSIM and MDS were used to determine any difference between the diet of dogs and foxes in similar habitats on a large scale using studies as replicates.

Space use

Canid baiting was undertaken by National Parks and Wildlife Service (NPWS) biannually from 1996 to 2001 where wild dog and fox visitation was recorded at approximately 300 bait stations spaced a minimum of 500 m apart at 12 sites close to the forest/farmland interface of the study area (Fig. 1). Percentage bait-take by dogs and foxes was determined for each bait station used in more than five baiting periods (maxi-

mum 12). The identity of animals removing baits was established by tracks left in the sand of the bait station. Fine-scale associations between predators was then examined by comparing bait-take by foxes at stations that either had or had not recorded dog during the same session, using a χ^2 -test.

To obtain a coarse scale indication of habitat use at landscape level, bait station data from all years were pooled and converted to a presence or absence for each species at each bait-station location. Presence or absence was then compared with ArcView GIS layers (100 m grid cell size) of abiotic environmental variables using GLM and GAM in S-PLUS (Ferrier *et al.* 2002). The variables were latitude, longitude, predicted annual rainfall, predicted average temperature, distance to cleared land, and distance to water. Final models were chosen using stepwise model selection criteria based on lowest Akaike Information Criteria (AIC) values using the STEPAIC function in S-PLUS 6. Analysis of deviance tested for variables in the GAM that were significantly different from those in the GLM, and also whether there was any difference between the final GLM and GAM models (Hastie & Tibshirani 1990). The presence or absence of dogs was included in the fox model to determine if they had any influence on fox distribution. Model validation using new data was beyond the scope of this project. Therefore, the predictive robustness of the model was tested by comparing observed presence and absence of foxes with the predicted probabilities of occurrence produced by the model (Ferrier *et al.* 2002).

RESULTS

Dietary overlap

In total, 264 dog and 257 fox scats were analysed and identifiable dietary remains were found in 97% of the scats. Dog scats contained 26 mammalian prey species, as well as birds, invertebrates and reptiles, however, most were minor contributors to the diet (Table 1) but swamp wallaby (30.4%), common ring-tail possum (*Pseudocheirus peregrinus*) (16.6%) and birds (9.5%) were the most common items. Fox hairs were also found in a few dog scats (0.8%). Fox scats contained 21 mammalian prey species, birds and invertebrates, with major contributors to the diet common ringtail possum (18.8%), swamp wallaby (17.6%), rabbit (10%) and invertebrates (9.2%).

The dietary niche breadth of foxes ($B_A = 0.39$) was broader than dogs ($B_A = 0.30$) but niche overlap was high ($O_{jk} = 0.91$). In spite of this extensive overlap, the frequency of occurrence of different species in the diet of dogs and foxes differed significantly ($\chi^2_{30} = 53.02$, $P = 0.006$), particularly when grouping mammalian



Fig. 2. Multi-dimensional scaling of dietary information from 19 wild dog and fox diet studies in woodland/open forest habitats of south-eastern Australia. (▲) Dog; (△) Fox.

prey by size ($\chi^2_2 = 13.70$, $P = 0.001$). Dogs ate more large mammals than medium and small mammals whereas foxes utilized all sizes evenly. Dogs ate significantly more ground dwelling mammals (70% of mammals eaten) than arboreal species ($\chi^2_1 = 48.71$, $P < 0.001$), while for foxes the difference was not significant.

Analysis of the 19 other canid diet studies revealed the niche breadth of dogs ($B_A = 0.34$) was very similar to that of foxes ($B_A = 0.31$), and this pattern was not statistically different from the 2002 Blue Mountains data ($\chi^2_1 = 0.01$, $P = 0.923$). However, niche overlap from previous data was lower ($O_{jk} = 0.69$) than the Blue Mountains data. Overall dog diet was characterized by macropods, possums, wombats (*Vombatus ursinus*) and rabbits, while foxes ate more rabbits, possums, swamp wallabies, rodents and dasyurids (Table 2). Summary diet information derived from the 19 studies used to examine the similarity between dog and fox diet (as summarized in Table 2) can be found at <http://www.bees.unsw.edu.au/banks/publications/Mitchell&Banks-appendix1.htm>. Multi-dimensional scaling (Fig. 2) and ANOSIM confirmed the difference between the prey selection of the two predators (global $R = 0.32$, $P = 0.001$). Two-way ANOVA (using arcsine transformed percentage occurrence in studies as replicates) showed an interaction between predators and prey size ($F_{2,64} = 31.28$, $P < 0.001$), with dogs having more large- and medium-sized mammals in their diet with few small prey, while foxes had more medium and small mammals than large prey (Fig. 3). Also, both dogs and foxes ate more ground dwelling prey than arboreal species but there was a difference in their

Table 1. Frequency of occurrence of prey items found in dog and fox scats from the Blue Mountains in 2002

		Percentage of scats containing prey item		
	Prey	Dog	Fox	Total
Small (<0.75 kg)				
Dasyurids	Brown antechinus	8.7	6	7.4
	Dusky antechinus	2.4	1.2	1.8
	Common dunnart	0.8	1.6	1.2
Rodents	New-Holland mouse	0	0.4	0.2
	Bush rat	4.3	3.2	3.8
	Swamp rat	0.8	2	1.4
	Brown rat [†]	0	0.4	0.2
Petauroideas	Eastern pygmy possum	2	1.6	1.8
	Feathertail glider	0.4	0	0.2
	Sugar glider	4	6.4	5.2
	Squirrel glider	0.4	2	1.2
	Yellow-bellied glider	1.6	4.8	3.2
	Greater glider	3.6	6.4	5
Medium (0.75–10 kg)				
Petauroideas	Common ringtail possum	16.6	18.8	17.7
	Common brushtail possum	4.7	6.4	5.6
Monotremes	Platypus	0.4	0	0.2
	Echidna	3.2	2	2.6
Dasyurids	Spotted-tailed quoll	0.8	0	0.4
Lagomorphs	European rabbit [†]	4.7	10	7.4
Canids	Fox [†]	0.8	0	0.4
Large (>10 kg)				
Vombatiforms	Common wombat	2.4	0.8	1.6
Macropods	Swamp wallaby	30.4	17.6	24.1
	Eastern grey kangaroo	6.3	6.4	6.4
	Red-necked wallaby	6.7	3.2	5
	Walleroo	1.6	0	0.8
	Feral pig [†]	4	5.2	4.6
Ungulates	Feral goat [†]	0.8	0	0.4
	Dog [†]	0.4	0	0.2
Canids	Bird	9.5	7.2	8.3
	Reptile	0.4	0	0.2
	Invertebrate	5.9	9.2	7.6
Total prey items		325	307	632
Total scats analysed		253	250	503

[†]Introduced species; [‡]Dog could be native (dingo) or introduced (wild dog).

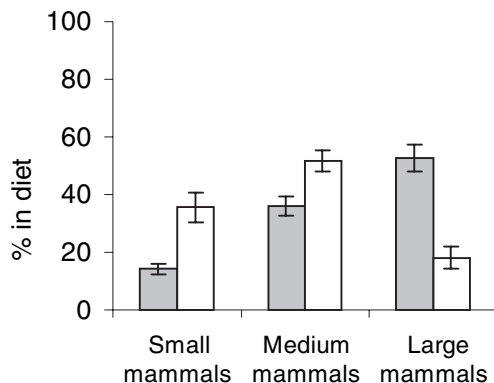


Fig. 3. Frequency of occurrence (mean \pm SE) of small, medium and large mammalian prey species found in (■) wild dog and (□) fox studies from woodland/open forest habitats of south-eastern Australia.

proportional consumption of each prey type ($F_{1,64} = 8.35$, $P = 0.005$) (Fig. 4).

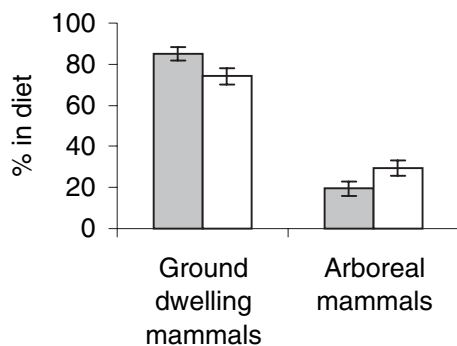
Space use

There were 2222 cases where bait was taken from more than 300 bait stations monitored between 1996 and 2001. Foxes were identified in 46.72% of cases, dogs in 14.94% while pigs (*Sus scrofa*), cats and unidentified species made up 34.52% of cases. Bait takes recorded as unknown may be due to disturbance such as rain and wind, or multiple species investigation of the bait station (B. D. Mitchell, pers. obs. 2003). Visitation was highly patchy at both the local and regional scale. There was a significant negative association between bait stations used by dogs and foxes

Table 2. Mean percentage of scats containing of different-sized mammalian prey determined from 19 studies diet of wild dogs (D) and foxes (F) in south-east Australia from woodland/open forest habitats

Prey		Mean % occurrence		SE	
		D	F	D	F
Small (<0.75 kg)					
Dasyurids	Antechinus spp.	3.1	10.8	1.0	2.8
	Dunnart spp.	0.1	0.8	0.0	0.5
Rodents	House mouse/new-Holland mouse	0.6	1.6	0.2	0.6
	Bush rat/broad-toothed rat	4.6	11.5	1.2	2.1
	Swamp rat/eastern chestnut mouse	1.4	2.4	0.5	1.6
	Black rat	1.8	2.6	1.3	1.4
	Unidentified rat spp.	1.1	0.9	0.6	0.4
Petauridids	Feathertail glider/eastern pygmy possum	0.1	0.4	0.0	0.2
	Sugar glider/squirrel glider	0.4	1.0	0.3	0.3
	Yellow-bellied glider	0.5	0.5	0.2	0.2
Medium (0.75–10 kg)					
Petauridids	Greater glider	1.6	1.7	0.5	0.6
	Ringtail possum	7.8	14.1	2.4	3.9
	Brushtail possum species	6.9	9.9	2.2	1.6
Perameles/potoroos	Bandicoots/potoroos	6.0	6.8	1.6	2.3
Monotremes	Echidna	3.6	0.6	0.8	0.2
Dasyurids	Spotted-tailed quoll	0.1	0.1	0.0	0.1
Lagomorphs	Rabbit/hare	9.0	15.9	1.6	3.7
Felids	Cat	0.1	0.0	0.0	0.0
Canids	Fox	0.2	1.7	0.1	0.6
Large (>10 kg)					
Phascolarctids	Koala	0.2	0.2	0.1	0.2
Vombatiforms	Common wombat	11.0	1.3	3.6	0.4
Macropods	Swamp wallaby	24.9	9.2	3.8	2.3
	Eastern grey kangaroo	3.2	2.0	0.8	0.8
	Red-necked wallaby	4.9	0.9	1.3	0.6
	Other macropods	6.0	0.4	2.0	0.3
Ungulates	Feral pig	0.5	0.2	0.3	0.2
	Livestock (cow, sheep, horse)	1.8	2.1	0.8	1.2
Canids	Dog	0.2	0.7	0.1	0.4
Niche breadth (B) [†]		0.34	0.31		
Niche overlap (O) [†]		0.69			

[†]Niche breadth and overlap were not calculated from means (original study data was used).

**Fig. 4.** Frequency of occurrence (mean \pm SE) of ground dwelling and arboreal mammalian prey species found in (■) wild dog and (□) fox studies from woodland/open forest habitats of south-eastern Australia.

(logistic regression $\chi^2_1 = 24.32$, $P < 0.001$) across all times and bait stations such that the occurrence of a bait-take by a dog at an individual bait station lessened the chance of a fox take at the same bait station. Similarly, a regression of proportional visitation by dogs and foxes to individual bait stations at any time showed a weak but significant negative association ($F_{1,250} = 15.95$, $P < 0.001$, $R^2 = 0.06$).

The stepwise GLM for fox presence/absence produced a model with five of the eight environmental variables from the null model explaining 14.46% of the variation. A GAM on the fox GLM provided a better fit and explained more than twice the deviance, however, the only variable that was significantly different from the linear fit as a partial predictor was latitude. As additive models are non-predictive, even though the plots allow general assessment, the final

model used for predicting fox activity was the GLM equation:

$$\begin{aligned} \text{Fox presence/absence} = & 6.07988e^{-05} \text{Longitude} \\ & - 2.400234e^{-05} \text{Latitude} - 1.276307e^{-02} \text{Rainfall} \\ & + 4.797247e^{-04} \text{Cleared land} - 6.989496e^{-02} \text{Temperature} \\ & + 157.3886 \end{aligned}$$

Thus, there was an increased chance of fox occurrence in the south-eastern areas of the study area that had lower average temperature and annual rainfall, and were further from cleared land. Dog presence/absence was added to the final model and the deviance was reduced, however, this model was no better than the final model. The predictive accuracy of the model was not strong given that both foxes and wild dogs were found across the whole study area. The fox distribution model was reasonably good at predicting presence, but not absence (Fig. 5a). There was little agreement between the predicted and observed results of this model and it tended to make all or nothing predictions (Fig. 5b). Coarse scale associations were therefore tested further using the density of scats km^{-1} of each predator on scat collection transects as an index of abundance (Banks 2000) with the density of fox scats having a strong positive association with dog scats ($F_{1,9} = 92.721$, $P < 0.001$, $R^2 = 0.921$). We conducted a similar analysis using arc-sine transformed proportional bait-take of transects as indices of activity (Banks 2000) (rather than individual bait stations) in a general linear model of the effects of site, year and dog activity, analysing the two seasons separately. Sites marginally differed in fox activity in spring ($F_{8,40} = 1.90$, $P = 0.08$) and autumn ($F_{8,31} = 2.06$, $P = 0.07$) but there was no association between fox activity and dog activity (spring $F_{1,40} = 2.59$ $P = 0.12$; autumn $F_{1,31} = 0.02$ $P = 0.88$), thus providing additional support for the findings of the stepwise GLM that there was no negative relationship between dog and fox presences at the larger scale.

DISCUSSION

Dietary analysis of wild dogs and foxes in the greater Blue Mountains region showed an almost complete overlap of dietary niche, with fox niche slightly broader than dog niche. Overall, predator scats contained material from 28 mammal species, and birds, invertebrates and reptiles, although two prey species dominated the diet of both predators, the swamp wallaby and ringtail possum. Such overlap suggests that similar sorts of prey were available to each predator and competition theory predicts some degree of resource partitioning is needed to allow them to coexist, unless prey availability is not limiting (Schoener 1986). An assessment of prey abundance was beyond the scope of this study, but the size and type of mam-

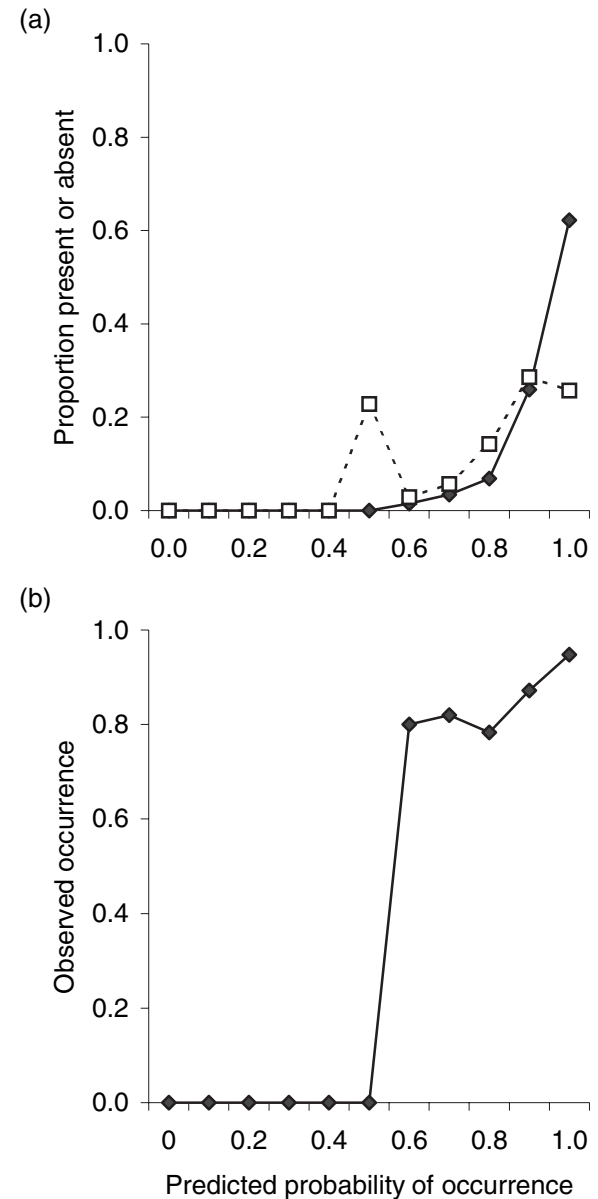


Fig. 5. The predictive accuracy of the fox generalized linear model: (a) discrimination capacity; (b) calibration. (—◆—) fox present; (---□---) fox absent.

malian prey differed between the two predators. Dogs took more large-sized mammalian prey, such as swamp wallaby and eastern grey kangaroo (*Macropus giganteus*), whereas foxes consumed more medium-sized prey, such as ringtail possum and rabbit. These data supported the prediction of possible dietary competition, and dogs and foxes may be avoiding intense dietary resource competition via differential prey selection.

The analysis of previous studies of canid diets from similar habitats in various areas of south-eastern Australia revealed a similar, but stronger trend for dietary differences than the Blue Mountains study that

suggested resource partitioning in woodland/forest habitats in eastern Australia. Niche overlap was smaller and multivariate analysis revealed distinct differences between the two predators based on prey size and mobility. Dogs utilized large- to medium-sized prey with few small prey, while foxes took more medium and small prey than large prey.

Dietary differences may also reflect relative hunting abilities rather than competition processes alone. Dogs are two to four times larger than foxes and thus likely to be able to take larger prey (Rosenzweig 1966; Gittleman 1985; Jones & Barmuta 1998). Dogs can also live in social groups, facilitating cooperative hunting to tackle larger prey such as kangaroos, wallabies, wombats and pigs (Corbett 1998), whereas foxes are obligate solitary foragers (MacDonald 1977). Thus, the larger or more difficult prey in fox scats may have been scavenged as carrion (for instance from the remains of wild dog kills). In that case, dogs may facilitate the coexistence of foxes. However, foxes have been observed harassing juveniles (Banks *et al.* 2000) and adults (Hornsby 1982) of large macropods, and fox predation limits recruitment in eastern grey kangaroos, indicating that foxes can catch their own large prey (Banks *et al.* 2000). Unfortunately, hair analysis did not enable differentiation between young and adult prey to confirm whether large prey were being taken. Similarly, it is unlikely that smaller prey were mostly inaccessible to dogs. Wild dogs have the ability to hunt small prey, such as rodents and rabbits, and these food items are sometimes found in high proportions in their diet (Newsome *et al.* 1983; Triggs *et al.* 1984; Robertshaw & Harden 1985).

If resource partitioning via competition is occurring, and because foxes can catch their own large prey, competition theory predicts that in the absence of dogs or other larger predators, the diet of foxes would include more large prey. There are no studies available in Australia where fox diets have been examined in the absence of wild dogs. However, outside Australia, foxes show little evidence of including large prey in their diet and continue to take predominantly small- and medium-sized prey when there are no sympatric larger members of the Carnivora (MacDonald 1977; Doncaster *et al.* 1990; Reynolds & Aebischer 1991; Lindström 1994; Cavallini & Volpi 1996). But large prey were not highly available in these studies and the only way to determine if resource partitioning by prey size is occurring as a result of competition would be through a wild dog removal experiment.

There was no clear evidence of large-scale differences in the distribution of foxes and wild dogs. Most importantly, the presence or absence of wild dogs was not a strong, significant predictive variable of fox occurrence at the landscape scale. This is in contrast to the second prediction of the competitive exclusion hypothesis. Habitat use by wild dogs in Australia is

generally poorly known outside arid and semiarid areas (Fleming *et al.* 2001). In the Fortescue River region in north-western Australia, dingoes centre their activity in riverine habitats (Thomson 1992), presumably because water is an essential resource in limited supply, and the riverine areas had the highest prey abundance (Thomson 1992). Dingoes from arid central Australia showed no preference for either mulga or open habitat that contained similar abundances of mammal prey species (Edwards *et al.* 2002). In south-eastern Australia, where rainfall is greater, dingoes shifted areas of activity in accordance with abundance of prey (Newsome *et al.* 1983). Similarly, dingoes moved to waterholes to take advantage of increased kangaroo abundance in the arid zone (Corbett & Newsome 1987). Thus, prey abundance and the availability of water are likely to be strong determinants of dog presence. However, water is not likely to be a limiting resource in the Blue Mountains with adequate annual rainfall and many creeks and rivers interlacing the region.

Habitat use by foxes in eastern Australia is better known than that for dogs. Catling and Burt (1995) in particular suggested that foxes were habitat generalists but were rarely found far away from freehold land or land that had been severely disturbed (see also Kurki *et al.* 1998). Conversely, in the Greater Blue Mountains there was a positive, though weak, relationship between fox occurrence and the distance from cleared land. Others have also suggested that the fox is probably more abundant in fragmented environments due to the mosaic of food, cover and den sites available (Saunders *et al.* 1995). Even though foxes will move through dense vegetation in the absence of roads and trails (Meek & Saunders 2000), these thoroughfares are thought to provide an easy way into forests for foxes (Andrews 1990; Bennett 1990). As a result, the surveys from this study, all conducted on roads except one, may overstate activity in forest areas, especially as a single fox can visit many bait stations. Notably, the model explained little of the variance of canid presence/absence and highlights the difficulty in finding landscape scale surrogates for variables that are important for determining species distributions. It is unlikely that foxes are responding directly to the variables selected as significant predictors, but rather that these variables are surrogates for something else important to them (Ferrier *et al.* 2002).

At the finer scale of individual bait stations, there was a negative association between wild dogs and foxes. Foxes had a lower likelihood of visiting bait stations that were also visited by dogs during a baiting event. Similarly, visitation rates by foxes and dogs to the same bait stations showed a significant negative relationship. These results support the third prediction of possible exclusion at the fine scale. Wild dogs and foxes coexist on a large scale in other areas of eastern

Australia (Robertshaw & Harden 1985; Newsome & Catling 1992; Catling & Burt 1994, 1995; Fleming 1996), and the examination of coarse scale associations showed no large exclusion. Thus, the finer scale avoidance may have occurred via temporal avoidance or localized habitat shifts. Corbett (1995) observed that during drought, foxes avoided dingoes at shared resources such as watering points and carcasses. There is a similar relationship between sympatric coyotes and red foxes in North America, where foxes can be chased and killed by coyotes, and hence often avoid the larger canid (Harrison *et al.* 1989; Theberge & Wedeles 1989). In spite of this, coyotes will tolerate foxes in their territories and at a carcass (Gese *et al.* 1996). However, fine scale avoidance may also be generated by predator avoidance behaviours, but the strength of predation by dogs on foxes is not known. Regardless of the mechanism of avoidance, it is unclear whether the fine scale avoidance would produce the dietary differences detected in this study as the key prey species taken by both predators have wide distributions and are unlikely to differ markedly on small scales. For example, swamp wallabies are habitat generalists (Troy & Coulson 1993) and, therefore, it is unlikely that the presence of dogs would restrict the access of foxes to areas of swamp wallaby abundance.

In summary, we found evidence of high dietary niche overlap by wild dogs and foxes, but there is good evidence of niche partitioning based on prey size that would alleviate strong competition. We also found fine scale negative association between dogs and foxes, but not coarse scale as previously thought. However, the only way to clearly demonstrate the existence of competition between wild dogs and foxes, and measure its effects, would be to conduct wild dog removal experiments (Connell 1983; Schoener 1983). If interspecific competition or intraguild predation is a factor influencing fox abundance and fine scale spatial utilization, fox numbers should increase after wild dog removal, thus supporting the mesopredator release hypothesis. Analysis of the home ranges of wild dogs and foxes in this area would also be valuable. It could be that wild dogs and foxes in the Blue Mountains are similar to coyotes and foxes in North America, where fox territories tend to be on the periphery or outside those of coyotes, and where the territories of coyotes are determined by the abundance of preferred prey (Harrison *et al.* 1989; Theberge & Wedeles 1989).

There are two important caveats on these conclusions about spatial interactions. First, the predator population studied was highly managed, undergoing biannual poison control. Baiting affects resident and transient animals alike and by removing individuals from the population there are probably few or no established animals. As such, it is possible that stronger exclusion would be observed in areas without disruptive control programmes. Second, the study area is

one of relatively high productivity and in areas of high resource availability wild dogs may tolerate foxes due to the abundance of prey, water and cover. However, in resource poor areas, such as the arid zone of Australia, competitive exclusion effects may be stronger, to the detriment of fox abundance. There is some support for this theory from arid zone studies (Thomson 1992; Corbett 1995), and it may be these areas that are better suited for exclusion experiments.

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