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Interference competition at the landscape level: the effect of free-ranging dogs on a native mesocarnivore

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Summary

1. Free-ranging domestic dogs are the world's most common carnivore and can negatively interact with native wildlife at multiple levels. Yet the intraguild competitive effects of dogs on the distribution and habitat use of native carnivores are poorly known, especially in areas of conservation concern.

2. We examined the spatial distribution of sympatric populations of radiocollared Indian foxes and free-ranging dogs to determine if Indian foxes alter their habitat use in the presence of dogs. We tested the effects of landcover type, primary prey abundance (rodents) and the presence of dogs as predictors of Indian fox spatial distribution in a threatened grassland habitat in central India.

3. By counting rodent burrows, we determined that the relative abundance of rodents was higher in fallow land and agricultural land compared to natural grasslands. From radiotelemetry data, we determined that the presence of dogs was closely linked to human-modified habitats, such as agricultural land and human settlements.

4. Top ranked models, based on Akaike's Information Criterion corrected for small sample size, indicated that the negative effects of the presence of dogs and agricultural land, and the positive effects of the presence of grassland and fallow land habitats were the strongest predictors of Indian fox spatial distribution. Thus, the use of the landscape by Indian foxes was determined not only by habitat type, but also by the presence of a mid-sized carnivore, the dog.

5. *Synthesis and applications*. Our results show that the presence of domestic dogs on the periphery of natural habitats can interfere with the spatial distribution of a sympatric carnivore. Vaccination and sterilization programmes, aimed at reducing population sizes and pathogen prevalence, do not restrict the free-ranging behaviour of dogs. Therefore, in areas of conservation value, control of free-ranging dogs would be required to fully mitigate the deleterious effects of dogs on native carnivores and other wildlife.

Key-words: *Canis familaris*, carnivore conservation, Indian fox, intraguild competition, population control, spatial segregation, subsidised predator, *Vulpes bengalensis*

Introduction

The introduction of generalist predators by humans has had negative impacts on native species around the world (Macdonald & Sillero-Zubiri 2004; Salo *et al*. 2007). In particular, domestic cats *Felis catus* Linnaeus and dogs *Canis familiaris* Linnaeus have had destructive effects on a broad range of native species (e.g. Dickman 1996; Atkinson 2006). Most studies examining the impacts of introduced predators have focused primarily on their direct predatory effects (Short, Kinnear & Robley 2002; Woods, Mcdonald & Harris 2003), and their role in pathogen transmission (Cleaveland *et al*. 2000; Funk *et al*. 2001; Fiorello, Noss & Deem 2006). However, evidence suggests that intraguild competition between introduced and native carnivores can also be deleterious (Dickman 1996; Glen & Dickman 2005; Vanak & Gompper 2009b).

Dogs are among the world's most common carnivores, and have been introduced throughout the world as an ubiquitous commensal of humans. In much of their range, dogs are free-ranging, irrespective of their ownership status (Wandeler *et al*. 1993). In rural areas, and areas that border nature reserves, free-ranging dogs interact with wildlife at multiple levels, including as predators, prey, and pathogen reservoirs (Butler, du Toit & Bingham 2004; Fiorello *et al*. 2004; Whiteman *et al*. 2007; Srbek-Araujo & Chiarello 2008; Lacerda, Tomas & Marinho-Filho 2009; Vanak & Gompper 2009b). However, dogs,

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as mid-sized canids, can also exert a top-down influence on smaller carnivores through interference competition, which at its extreme is manifested as intraguild predation (Glen & Dickman 2005; Mitchell & Banks 2005; Vanak & Gompper 2009b).

Intraguild interference competition has been shown as an important driver of community structure and composition across a wide range of taxa (Case & Gilpin 1974; Creel, Spong & Creel 2001; Grether *et al*. 2009). The dynamics of interference competition are particularly well documented among native species in the Carnivora family Canidae (Cypher & Spencer 1998; Creel, Spong & Creel 2001; Nelson *et al*. 2007; Ritchie & Johnson 2009). In the absence of a competitor or predator species, small carnivores should be distributed based on habitat quality and preferred food availability (van der Meer & Ens 1997; Roemer, Gompper & Van Valkenburgh 2009). However, small carnivores are often the subordinate intraguild competitor in most communities with intact carnivore guilds (Prugh *et al*. 2009; Roemer, Gompper & Van Valkenburgh 2009) and thus, are potentially subject to top-down effects that mediate their ability to use preferred habitat (Ritchie & Johnson 2009). Whether smaller carnivores exhibit the same kinds of avoidance tactics against dogs as they would against other intraguild competitors has not been closely examined (Vanak & Gompper 2009b), but is plausible given that dogs are an important source of mortality for many species of mesocarnivore (Harris 1981; Vanak 2008; Vanak & Gompper 2009b).

Some recent examples have demonstrated that sympatric carnivores alter their behaviour to avoid competition from dogs. In Australia, Mitchell & Banks (2005) found that red foxes *Vulpes vulpes* Linnaeus avoided bait stations that were previously visited by dingoes even though they overlapped spatially at the landscape level. This result, in combination with the fact that dingoes may kill foxes, is reflected in an inverse relationship between dingo and red fox activity patterns (Mitchell & Banks 2005). Such observations are not limited to Australia: in southern Chile, chilla foxes *Lycalopex griseus* Gray avoided scent stations previously visited by dogs (Silva-Rodríguez, Ortega-Solís & Jiménez, 2009).

These general patterns of intraguild interactions are also expected even when dogs are not the top-predator in the ecosystem (Vanak & Gompper 2009b) as is the case in India, where dogs share the landscape with wolves *Canis lupus* Linnaeus and other large carnivores. Smaller carnivores, such as the Indian fox *Vulpes bengalensis* Shaw, might be expected to exhibit similar tactics against dogs as they would against other intraguild competitors, especially since dogs are also known to kill (without consuming) foxes (Vanak 2008). Indian foxes also avoid rich food sources and show a vigilance-foraging tradeoff in the presence of dogs (Vanak, Thaker & Gompper 2009). When exposed to a live dog at experimentally provisioned food trays, Indian foxes reduced consumption by 70% and displayed increased vigilance behaviour, similar to behavioural changes seen when red foxes were experimentally exposed to golden jackals *Canis aureus* (Scheinin *et al*. 2006). Whether such direct avoidance of dogs by foxes at the local scale extends to avoidance of prey-rich habitats at the landscape level has yet to be robustly addressed for any native mesocarnivore. This is important as dogs are ubiquitous in rural areas world-wide, and therefore may have large-scale effects on native carnivores, especially when they occur at high densities near or within protected areas.

In this study, we examined the landscape level interactions between free-ranging dogs and the Indian fox, a common mesocarnivore of the Indian plains (Gompper & Vanak 2006). The Indian fox is a grassland specialist (Vanak & Gompper 2010) and an opportunistic omnivore that depends mainly on wild-caught food such as small mammals, invertebrates and seasonally available fruits (Vanak & Gompper 2009a). We expected that the presence of dogs in the landscape would be an important predictor of the spatial distribution of Indian foxes. If dogs did not exert competitive dominance, we expected the spatial distribution of foxes to be primarily determined by habitat preference and prey abundance.

Materials and methods

The study was conducted in and around a portion of the Great Indian Bustard Sanctuary (GIBS) in central India (17° 49′ 40″ N and 75° 51′35″ E). The study area consisted of six protected grassland patches

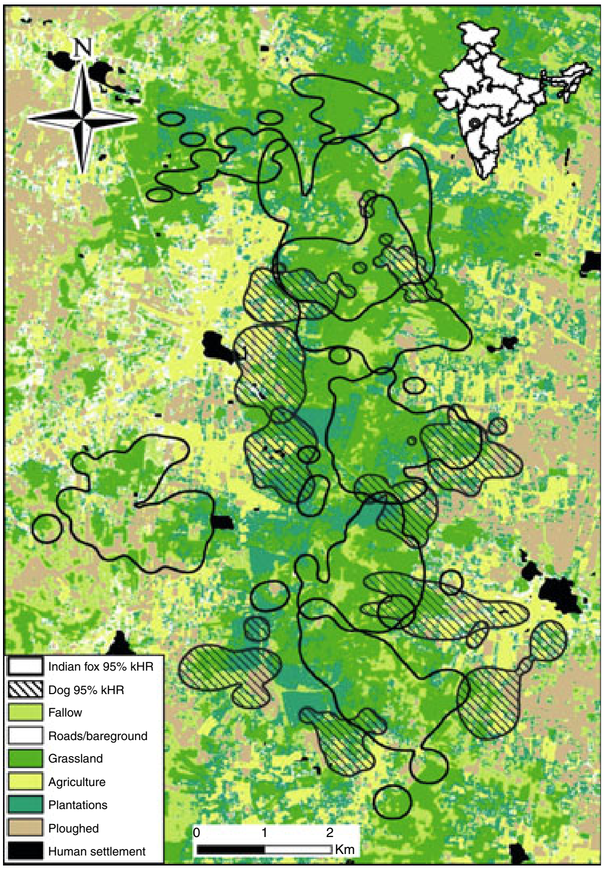

Fig. 1. Map of part of the study area in Maharashtra, India. The 95% kernel home-ranges of Indian foxes and dogs illustrate the spatial separation between the species on the landscape. For clarity, we have only plotted home-ranges of simultaneously-tracked foxes (n = 8) and dogs (n = 11). (Please refer to the online article for the colour version of this figure).

(*c.* 6 km^2) within a matrix of sugarcane fields, seasonal crops, communal grazing lands, and forestry plantations that collectively totalled *c.* 130 km^2 (Fig. 1; see below). The study area also includes several villages with a combined human population of *c.* 50 000, largely dependent on agro-pastoralism. We derived a habitat map of the study area from a 5·8 m resolution LISS IV multispectral imagery (IRS P6, National Remote Sensing Agency, Hyderabad, India), categorized to the following eight landcover/landuse categories: (i) grasslands (25·6% of area), included protected grasslands and public grazing lands; (ii) fallow land (16·5%), included areas that had not been actively ploughed for 2–3 years and had early successional vegetation; (iii) plantation (15·5%), included protected forestry plantations of native and exotic species; (iv) agriculture (14·7%), included standing crops of maize, groundnut and other pulses; (v) ploughed land (20·9%), included freshly ploughed or cleared land; (vi) bare soil (5·6%), included areas of compacted soil due to high human use; (vii) permanent human settlements (1·1%); and (viii) water bodies (0·1%). This region experiences a wet season from July to October during which 95% of the precipitation occurs (temperature range = 16–32 °C, mean annual precipitation = 600 mm), a cool-dry season from November to February (temperature range = 6–37 °C) and a hot-dry season from March to June (temperature range = 18–47 °C). Aside from dogs and foxes, other carnivores inhabiting the study area include the grey wolf (the home-range of one wolf pack overlapped the study area; Habib 2007), golden jackal, jungle cat *Felis chaus* Schreber, and grey mongoose *Herpestes edwardsi* Geoffroy. However, unlike foxes and dogs, these species are uncommon and rarely encountered (A. T. Vanak, pers. obs.).

Dogs are common in the study area, occurring at densities ranging from 24 dogs km^{-2} in farmlands to as high as 113 dogs km^{-2} in the villages (A. T. Vanak, unpublished data). Free-ranging dogs in this area are mixed breed mongrels, and adults weigh *c.* 17 kg ± 3·1 SD (n = 74; A. T. Vanak, unpublished data). These dogs can be generally categorized as: (i) herding dogs that accompany grazing livestock into grassland habitat during the day; (ii) farm dogs that are free to roam between farmlands and natural grasslands; or (iii) village dogs that are restricted to the human settlements (A. T. Vanak, unpublished data). Ownership of dogs in this area is dependent on the above categories, with herding dogs (1–2/household) most closely associated with one household, farm dogs (3–8/household) being loosely associated with farms and their buildings and structures, and village dogs being un-owned and dependent on communal resources. There are no truly feral dogs (*sensu* Vanak & Gompper 2009b) in the study area, although dogs from all of the above categories may occasionally be seen in packs of 2–8 individuals. Dogs in the study area are mainly dependent on human-derived food, with only 11% of their diet (based on relative occurrence, RO) comprising of wild-caught foods (Vanak & Gompper 2009a). Dogs in this area are not subject to any external population control measures, nor do they receive vaccinations for rabies or other canine diseases (A. T. Vanak, unpublished data).

Indian foxes are a common carnivore in the natural grassland habitats of the GIBS. At the landscape level, Indian foxes select for native grasslands, forestry plantations and fallow land over human-dominated habitats such as agricultural land and human settlements (Vanak & Gompper 2010). The presence of native grasslands is the dominant predictor of habitat selection at the home-range scale across all seasons (Vanak & Gompper 2010). The diet of foxes at the study site is comprised principally of wild-caught foods, including invertebrates (33% RO), rodents (20% RO), and fruits of *Zizyphus* spp. (18·5% RO). Unlike dogs, Indian foxes do not consume human-derived food in the study area, do not scavenge from large-mammal carcasses, and include only a small amount of agricultural produce in their diet (Vanak & Gompper 2009a).

CAPTURE AND HANDLING

Details of the capture and handling protocols of Indian foxes are given in Vanak (2008) and Vanak & Gompper (2010). Although all dogs in the region are free-ranging to some degree, we targeted dogs on farms bordering fox habitat for radiocollaring, under the assumption that these animals are most likely to range into wild habitat. Most dogs were handled after obtaining permission from their owners, although some were captured using box traps, throw-nets, or by chemical immobilization using a blow-pipe. Dogs were also occasionally caught in padded foot-hold traps meant to capture foxes. After physically restraining the captured animals, we immobilized them with a xylazine hydrochloride and ketamine hydrochloride regime when necessary (A.V. Belsare & A. T. Vanak, unpublished data). Animals were ear-tagged and fitted with a VHF radiotransmitter (foxes: model M1930, weight *c.* 35 g, dogs: model M2510B, weight *c.* 350 g, Advanced Telemetry Systems, Isanti, MN, USA;) following which they were released at the capture site. Handling procedures were approved by the Institutional Animal Care and Use Committee of the University of Missouri (protocols 4262 and 4265).

RADIOTELEMETRY AND ANALYSIS OF SPATIAL DISTRIBUTION

Radio-locations of foxes and dogs were obtained by homing in on animals or by triangulating from fixed and mobile null-peak telemetry stations from three or more locations. To minimize error due to animal movements, we collected all triangulation data for each non-stationary animal by obtaining simultaneous fixes from at least three stations or within a 3 min interval. Locations were collected every 28 (±2) h to provide an approximately equal number of temporally and spatially independent locations (Mean Swihart and Slade index = 0·51 ± 0·06 SE for all animals) in every part of the day (Garton *et al.* 2001). We conducted a telemetry accuracy assessment to estimate the precision of directional azimuths (Withey, Bloxton & Marzluff 2001) by obtaining location estimates once a month during tracking sessions for 5–7 test transmitters. We obtained 76 location estimates from 246 azimuths and estimated the precision of telemetry bearings to be 2·43° (±0·47 SE).

To determine patterns of spatial distribution of foxes and dogs we calculated 95% kernel home-ranges for all individuals with ≥30 locations (Seaman *et al.* 1999). These locations were evenly spaced over the duration of the study. We pooled locations across seasons as there were no differences in landscape-level habitat selection between seasons for either foxes (Vanak & Gompper 2010) or dogs (A. T. Vanak, unpublished data). We calculated fox and dog utilization distributions (UD) using a fixed kernel estimator with bandwidth selected by the 'plug-in' method using the KDE function in Matlab (The Mathworks Inc, Natick, MA, USA; Beardah & Baxter, 1995). We fitted a minimum convex polygon to the outer boundaries of all 95% kernel home-ranges to designate the intensive study area (130·4 km^2; Vanak & Gompper 2010). To determine the effect of food resources (rodent abundance), landcover category, and the presence of dogs on the distribution of foxes at the landscape scale, we pooled data across all individual foxes for our analysis. Indian foxes form pairs and defend territories (Vanak & Gompper 2010) but we expect the effects of food resources, landcover, and the presence of dogs to outweigh the potential effects of conspecifics.

ESTIMATING RODENT RELATIVE ABUNDANCE

To determine rodent abundance on the landscape, we first enumerated rodent burrows as an index of relative abundance. We assumed that burrow counts reflect actual rodent abundance in different habitats on the landscape as found by Home (2005) in a similar dry habitat in western India. In Home's (2005) study, active burrow counts of the Indian desert jird *Merriones hurrianae* Jordon were highly correlated ($r^2 = 0{\cdot}98$) with density estimates. Although the Indian desert jird does not occur in our study area, similar burrowing species (e.g. Indian gerbil *Tatera indica* Hardwicke) are found and are mainstays in the diet of the Indian fox (Vanak & Gompper 2009a).

We overlaid a 1×1 km grid on a map of the study area and randomly selected 45 sample grids representing 30% of the intensive study area. Within each grid we walked a 1600×2 m strip-width transect and counted active rodent burrows (those showing signs of recent use). We did not differentiate between ploughed land and agriculture, and pooled the two categories during sampling. Bare-soil landcover occupied a small proportion of the total area and was highly patchily distributed. We assigned a zero value to all bare-soil patches because we did not find any rodent burrows in any of the patches that were encountered. We did not sample in human settlements for logistic reasons, and assigned zero value to this landcover type, assuming that rodent species of interest (Vanak & Gompper 2009a) were unlikely to be found in human settlements. Because of the difficulty in gaining access to plantations on private lands, we were unable to sample four of the 45 transects. We used a one-way analysis of variance (ANOVA) and Fisher's Least Significant Difference assessments (LSD) to test for differences in relative rodent abundance between the landcover categories (Table 1).

We created a GIS layer of rodent relative abundance by assigning to each 5·8 m pixel a randomly generated value within one standard deviation of the mean rodent density estimate for each landcover category. We repeated this exercise 1000 times and averaged the values for each pixel to obtain a single surface. The resultant raster image was re-sampled to a 30 m resolution (the minimum bandwidth value for fox UD estimates) using a bilinear function to smooth the estimate for each pixel. Thus, by incorporating the variance in the estimate of rodent abundance, we created an index of food resources that is independent of the underlying landcover map.

Table 1. Estimates of relative rodent abundance and parameter estimates of dog presence in the different landcover categories in and around the Great Indian Bustard Sanctuary, India. These values were used as inputs to generate a landscape of rodent abundance and dog presence respectively

Landcover type	Rodent burrows (ha) ± SE	*n* (rodent transects)	Dog parameter estimates† ± SE
Grassland	23·5 ± 4·3	26	−0·021 ± 0·09*
Fallow	55·8 ± 9·9	7	−0·272 ± 0·12
Agriculture‡	39·6 ± 5·1	19	0·295 ± 0·10*
Ploughed‡	39·6 ± 5·1	19	−0·896 ± 0·12*
Plantation	8·9 ± 4·3	4	0·291 ± 0·10
Bare ground	0	0	0·210 ± 0·15*
Human settlement	0	0	0·340 ± 0·05*

†Water was used as a reference variable for deriving parameter estimates for dog presence on the landscape.
‡Ploughed land and agriculture were pooled while sampling for rodent abundance.
*Significant at $P < 0{\cdot}05$.

MAPPING DOG PRESENCE ON THE LANDSCAPE

It was not logistically feasible to collect distribution data for all dogs in the study area, so we created an index of dog presence based on radiotelemetry locations ($n = 998$ points). We used logistic regression analysis to determine landcover categories that best predicted the presence of dogs by comparing landcover attributes of point locations of dogs to an equal number of paired random points generated within the intensive study area (Hosmer & Lemeshow 2000). Significant parameter coefficients from the logistic regression analysis of only those landcover categories that had a positive effect on dog distribution (Table 1) were used to develop a spatial surface describing presence of dogs (similar to Johnson *et al.* 2002). We constructed this surface by first generating a Euclidean distance raster for each selected landcover category. We then weighted each 30 m pixel by multiplying the Euclidean distance with the inverse of the coefficient from the logistic regression for that cover type. Finally, we averaged these weighted distances for each pixel across all landcover categories to produce one surface representing the overall weighted proximity to areas with high probability of dog occurrence. The greater the value at any given pixel, the lower the risk of encountering a dog at that pixel. Although this index assumes that dogs were evenly distributed across each landcover type, we believe this assumption is valid because the intensive study area of 130 km^2 includes five villages of similar human densities, land-use practices and dog populations (Fig. 1).

MODELLING PRESENCE OF FOXES AS A FUNCTION OF HABITAT, DOGS AND RODENTS

We compared attributes of the covariates at fox point locations ($n = 1841$ points) to an equal number of randomly generated points in the intensive study area. For each point location, we determined the landcover type, rodent relative abundance (square root transformed), and probability of dog encounter (log transformed) on the landscape. We used a logistic regression analysis to compare attributes at each point location to random sites. We tested the data for multicollinearity and excluded human habitation as a variable because its minimum tolerance was $< 0{\cdot}001$. All other variables had a tolerance range between 0·58 and 0·93. All statistical analyses were conducted in SPSS 15·0 (SPSS Inc., Chicago, IL, USA).

We used an information-theoretic approach to develop *a priori* models that best explained the distribution of Indian foxes on the landscape. We developed a global model that included relative abundance of rodents, index of dog-dominated habitats and landcover variables that are considered as important predictors of Indian fox habitat use (Vanak & Gompper 2010), and assessed the goodness-of-fit of this model using the omnibus test of model coefficients (Burnham & Anderson 2002). Using variables derived from the global model, we developed seven sets of candidate sub-global models (Appendix S1, Supporting Information). These candidate models reflect specific hypotheses about the relationship between the variables and the presence of Indian foxes.

We used Akaike's Information Criterion corrected for small sample size (AIC_c) to assess model weights (w_i) and ranked candidate models using ΔAIC_c (Burnham & Anderson 2002). To account for model selection uncertainty we averaged the estimates of the coefficients of main effect variables in each model with $\Delta AIC_c \leq 2$ (Burnham & Anderson 2002). We determined the magnitude of the effect of each predictor variable on the response variable with the odds ratio (Hosmer & Lemeshow 2000).

Results

We radiocollared 35 Indian foxes (from 40 individuals captured) and 25 dogs (from 80 individuals captured) between November 2005 and April 2007. We obtained sufficient telemetry data to calculate home-ranges and UD for 32 foxes (mean number of locations = 76·9 ± 7·8 SE) between April 2006 and May 2007 and for 24 dogs (mean number of locations = 58·6 ± 9·7 SE) from November 2005 to April 2007. The home-range estimates for all these animals reached an asymptote after approximately 40 locations. Mean Indian fox 95% kernel home-range size was 2·39 km^2 (± 0·31 SE; Fig. 1) and mean dog home-range size was 0·45 km^2 (± 0·11 SE; Fig. 1).

Rodent abundance varied by landcover category (ANOVA $F_{3,\ 55}$ = 4·819, P = 0·005), with fallow land having higher densities of burrows than grassland (LSD P = 0·004) and plantations (LSD P = 0·002). Similarly, agricultural land had higher rodent abundance than grassland (LSD P = 0·018) and plantations (LSD P = 0·008; Table 1). We found burrows of gerbils in both human-modified habitat as well as natural habitat.

Logistic regression analysis of habitat use by dogs indicated selection of human-modified habitat, with human settlements, agricultural land and bare-ground having a significant positive effect and grasslands and ploughed land having a significant negative effect (Table 1). The resultant distance-based weighted index provided us with a robust measure of probability of occurrence for dogs based on the landcover category.

MODEL SELECTION

The best fit model among the candidate models (ω_i = 0·676) supported the hypothesis that both habitat parameters as well as the presence of dogs influenced the spatial distribution of Indian foxes (Table 2). The next best supported model (ΔAIC_c = 1·472; ω_i = 0·324) included some habitat parameters and the presence of dogs and rodents. All other models had a ΔAIC_c > 25 and therefore provided little support (Burnham & Anderson 2002). Model-averaged parameter coefficients for the top two models showed a negative effect of agricultural land (β = −1·46 ± 0·26 SE) and positive effects of distance to dog-dominated habitats (β = 1·75 ± 0·08 SE), grassland (β = 2·90 ± 0·15 SE), fallow land (β = 1·85 ± 0·18 SE), plantations (β = 0·001 ± 0·001 SE) and the abundance of rodents (β = 0·034 ± 0·047 SE) on the probability of fox occurrence. The odds ratio estimates indicated that dogs, grassland, agricultural land and fallow land had the strongest effects on fox spatial distribution (Fig. 2). The odds of an area being used by foxes increased by 8·1 and 3·4 times for grassland and fallow land habitat respectively, and increased by 5·7 times for every unit increase in distance from dog-associated habitat. Foxes avoided agricultural land, with the odds of an area being used by foxes decreasing by 4·35 times (odds ratio = 0·23). Other variables in the model such

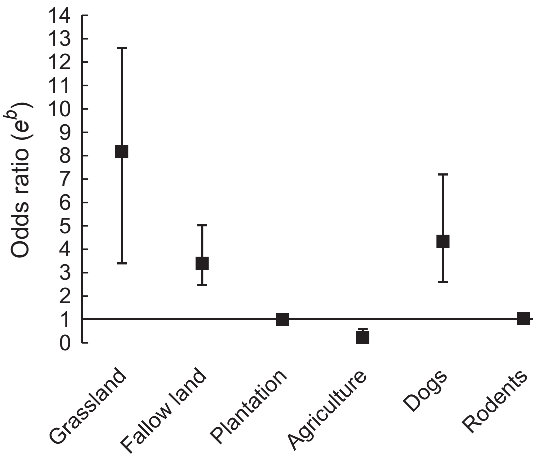

Fig. 2. Odds ratios and 95% confidence intervals from the highest-ranked models predicting the probability of occurrence of the Indian fox. Parameters include landcover category (grassland, fallow land, plantation and agriculture), distance to dog-dominated habitats, and rodent abundance. Odds ratios < 1 indicate negative effect on occurrence while > 1 indicates a positive effect on occurrence.

Table 2. Models ranked by Akaike's Information Criterion values corrected for small sample size (AIC_c) that best explain the spatial distribution of the Indian fox. Columns include the number of parameters (K), AIC_c value, distance from the lowest AIC_c (ΔAIC_c), and Akaike's model weight (ω_i)

Model	AIC_c	K†	ΔAIC_c	ω_i
8) Grs + fllw + plnt + agri + plgh + dog	2456·59	8	0	0·676
13) Grs + fllw + plnt + agri + plgh + dog + rdnts	2458·07	9	1·472	0·324
7) Fllw + grass + plnt + dog	2482·34	6	25·742	0·000
14) Global	2529·65	10	73·058	0·000
11) Grs + dog + rdnts	3070·54	5	613·947	0·000
12) Grs + agri + dog + rdnts	3072·32	6	615·723	0·000
9) Grs + agri + dog	3110·91	5	654·315	0·000
10) Dog + rdnts	3216·38	4	759·787	0·000
5) Dog	3278·27	3	821·677	0·000
4) Grs + fllw + plnt + agri + plgh + soil	3376·07	8	919·475	0·000
3) Grs + fllw + plnt + agri + plgh	3405·36	7	948·769	0·000
2) Grs + fllw + Plnt	3524·7	5	1068·11	0·000
1) Grs	4377·15	3	1920·56	0·000
6) Rdnts	5077·07	3	2620·48	0·000

†Number of parameters (K) includes intercept β_0 and residual variance σ^2

Grs, grassland; Plnt, plantations; Agri, agriculture; Plgh, ploughed land; Fllw, fallow land; Soil, bare soil; Rdnts, relative abundance of rodents; Dog, distance to dog-dominated habitat types.

as plantations, and abundance of rodents were poor predictors as the confidence intervals of the odds ratio included 1·00.

Discussion

The avoidance of habitat occupied by competitors is a strong indicator of the effects of interference competition. Our results support the hypothesis that dogs negatively influence the spatial distribution of Indian foxes at the landscape level and may exclude them from accessing high-quality foraging habitat. Similar patterns of spatial segregation have been indirectly measured between dogs and chilla foxes (Silva-Rodríguez, Ortega-Solís & Jiménez, 2009) and have been observed in other canids (e.g. coyotes and red foxes; Sargeant, Allen & Hastings 1987; Harrison, Bissonette & Sherburne 1989). The observed segregation between dogs and Indian foxes could be a function of differences in habitat preference or prey selection rather than competitive exclusion (Todd, Keith & Fischer 1985; Gosselink *et al.* 2003). Indian foxes prefer grasslands over human-modified habitats (Vanak & Gompper 2010), whereas dogs select for agricultural fields and human settlements. However, the presence of Indian foxes was not explained by habitat alone, since models with only habitat parameters had no support among the top ranked models. Instead, candidate models with combined effects of landcover type, the presence of dogs, and rodent abundance were the best predictors of fox presence. Based on the parameter estimates from the top candidate models, grasslands and fallow land were the main positive influences on fox presence, whereas the presence of dogs and human-modified habitats, such as agricultural land, were the main negative influences (Fig. 2). This effect of dogs at the landscape level further supports the hypothesis that dogs are an interference competitor, especially since they are an important cause of Indian fox mortality (Vanak 2008) and are directly avoided by foxes at food sources (Vanak, Thaker & Gompper 2009).

The avoidance of habitats due to the presence of a competitor has been shown for several other carnivores (Creel, Spong & Creel 2001; St-Pierre, Ouellet & Crete 2006). For example, kit foxes *Vulpes macrotis* Merriam partition habitat, space and diet with larger coyotes (Nelson *et al.* 2007). This is understandable since not only do coyotes and kit foxes compete for similar prey, but coyotes are also one of the main intraguild predators of kit foxes, and are expected to displace foxes from the best foraging habitats. Thus, avoiding the risk of encountering coyotes is a greater influence on kit fox habitat selection than relative prey abundance (Nelson *et al.* 2007). However, unlike coyotes and kit foxes, Indian foxes and dogs in this study area do not compete for the same food resources, as foxes are dependent on rodents, invertebrates and native, uncultivated fruit, whereas dogs subsist on human-derived food (Vanak & Gompper 2009a). Despite this, Indian foxes avoid provisioned food in the presence of dogs (Vanak, Thaker & Gompper 2009). Thus, the presence of dogs may be precluding foxes from foraging in agricultural lands, where rodent abundances are higher than in natural areas (Table 1). The presence of dogs may also explain the low contribution of high-value foods such as agricultural and horticultural produce to the diet of Indian foxes (Vanak & Gompper 2009a). The putative avoidance of prey-rich areas that are inhabited by free-ranging dogs further supports the argument that dogs play the role of a mid-sized canid in intraguild interactions with smaller carnivores (Vanak & Gompper 2009b). This can result in risk aversion behaviour at the cost of lost foraging opportunities for the subordinate competitor (Vanak, Thaker & Gompper 2009).

MANAGEMENT OF DOG POPULATIONS

Dogs are among the world's most common carnivores (Wandeler *et al.* 1993) and are heavily subsidized by humans (Butler & du Toit 2002; Vanak & Gompper 2009a), which allows them to occur at high densities, even in rural areas with high conservation value. Dogs can exert intrusive edge effects in fragmented habitats (Whiteman *et al.* 2007; Lacerda, Tomas & Marinho-Filho 2009; Vanak & Gompper 2009b). For example, pathogen spill-over from dogs is a substantial threat to wild carnivore populations (Funk *et al.* 2001; Cleaveland *et al.* 2007). However, addressing pathogens alone (e.g. via a vaccination programme; Haydon *et al.* 2006; Cleaveland *et al.* 2007) will not fully mitigate the influence of dogs on wild carnivore populations because intraguild competition from dogs can also be detrimental. Our results indicate that the presence of dogs may be preventing sympatric carnivores from accessing prey-rich habitats. Such interference competition could result in lower population sizes, increasing the likelihood of local extirpation (Cypher *et al.* 2001; Macdonald & Sillero-Zubiri 2004) particularly in fragmented and human-dominated habitats.

Reducing dog populations via lethal control and animal birth control (ABC) programmes can potentially reduce contact rates between dogs and wild carnivores. However, countries such as India have among the highest populations of dogs in the world (*c.* 25 million; Menezes 2008), because ABC programmes are rarely carried out in rural areas. The lack of population control and the availability of food waste continue to result in very high densities of dogs in India. Furthermore, farmers and livestock herders depend on dogs to provide a deterrent against crop- and livestock-raiding wildlife [similar to Butler, du Toit & Bingham (2004) for Zimbabwe]. Therefore, controlling dog–wildlife interactions in rural areas, 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. However, neither vaccination nor sterilization alone will greatly reduce the presence of dogs in the landscape. In areas of conservation concern, control measures must also include the removal of un-owned dogs, restriction of free-ranging activity and a strong emphasis on responsible dog ownership. These management approaches must be implemented in a sustained and integrated manner for a long-term solution.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. *A priori* hypotheses and specific models to test the influence of habitat, primary prey, and competitor presence on the spatial distribution of the Indian fox in and around the Great Indian Bustard Sanctuary, India.

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