INTRAGUILD INTERACTIONS BETWEEN NATIVE AND DOMESTIC CARNIVORES IN CENTRAL INDIA

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by

ABI TAMIM VANAK

Dr. Matthew E. Gompper, Dissertation Supervisor

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

INTRAGUILD INTERACTIONS BETWEEN NATIVE AND DOMESTIC CARNIVORES IN CENTRAL INDIA

presented by Abi Tamim Vanak,

a candidate for the degree of Doctor of Philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

Matthew E. Gompper

Mark R. Ryan

Joshua J. Millspaugh

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Hong S. He

Mark R. Ellersieck

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INTRAGUILD INTERACTIONS BETWEEN NATIVE AND DOMESTIC CARNIVORES IN CENTRAL INDIA

Abi Tamim Vanak

Dr. Matthew E. Gompper, Dissertation Supervisor

ABSTRACT

I determined the various factors affecting the resource selection and spatial ecology of the Indian fox *Vulpes bengalensis*, a small canid endemic to the Indian subcontinent. Despite being widespread throughout India, and commonly occurring in many dry grassland habitats, little is known about the ecology of this species. I investigated habitat selection by the Indian fox in a grassland region in central India that represents a mix of natural and human-dominated habitats to discern if and how foxes respond to human encroachment on native habitats. I collected home range and habitat selection data on 32 radio-collared Indian foxes in the Great Indian Bustard Wildlife Sanctuary, Nannaj, Maharashtra over a one year period. Adult Indian fox 95% kernel density home-range sizes varied between sexes and among seasons. Males had consistently larger home-ranges than females across all seasons but there was no inter-seasonal variation. Females had smaller home-range sizes during the cool-dry season which is also the denning period, than during any other season. Compositional analysis of Indian fox selection of home-ranges at the landscape level showed heavy influence of the

presence of grasslands, plantations and fallow land. Indian foxes avoided human-modified habitat such as agricultural land and human settlements. The presence of grasslands was also the dominant predictor of Indian fox habitat selection across seasons within the home-range as determined by AIC ranked discrete-choice models. The results indicate that Indian foxes select for natural grasslands and avoid human-modified habitat.

The distribution, abundance and resource selection patterns of meso-carnivores such as the Indian fox are also heavily influenced by the effects of top-down intraguild competition with sympatric larger carnivores. Competitive dynamics among carnivores are asymmetric and interference competition and the associated occurrence of intraguild predation are unidirectional, with larger carnivores negatively influencing smaller carnivores. Competition can affect the subordinate competitor in several ways: by limiting spatial distributions resulting in scattered interspecies territories, constraining habitat selection, reducing prey encounter rates and food intake, or requiring increased hunting effort.

In my study area, the domestic dog *Canis familiaris,* is the most common mid-sized carnivore. As the world’s most common carnivore, dogs are known to interact with wildlife as predators, prey, competitors, and disease reservoirs or vectors. Despite these varied roles in the community, the interaction of dogs with sympatric carnivores is not well understood. Dogs have the potential to be exploitative, interference and apparent competitors with sympatric carnivores.

I examined competition for food between dogs and the Indian fox through dietary analysis. Dogs subsisted largely on human derived material from direct feeding, and scavenging on garbage, crop residue and livestock carcasses (83% relative occurrence). Wild caught foods constituted only 11% relative occurrence of dog diet. Indian foxes are omnivorous and included a wide variety of food types in their diet. The majority of Indian fox diet consisted of invertebrates (33% relative occurrence), rodents (20% relative occurrence) and fruits of *Zizyphus mauritiana* (18.5% relative occurrence). Indian foxes did not include any human derived material, nor did they scavenge from large mammal carcasses, and included only a small portion of agricultural produce in their diet. The diet of free-ranging dogs is typical of dogs from other parts of the world. However, the low contribution of human-derived food sources to the diet of Indian foxes was surprising since the species is a generalist carnivore. Although there was limited dietary overlap between dogs and foxes in this study, dogs may actually be preventing foxes from accessing agricultural lands and human associated foods by interference competition.

Dogs have the potential to be effective interference competitors, especially with medium and small-sized carnivores, and may fulfill the role of a mid-sized canid, especially in areas where the native large carnivore community is depauperate. I experimentally examined the behavioral responses of the Indian fox to the presence of dogs and dog odors. Since resource competition between dogs and foxes is low, it is unclear whether foxes perceive dogs as interference competitors. To test this I exposed foxes to neutral, live dog, and animal odor cues at food trays and recorded the amount of food eaten, time spent at food trays, and vigilance and non-vigilance behaviors. When dogs were visible, foxes continued to visit the food trays, but reduced the amount of time spent (by 83%) and food eaten (by 70%) at those trays. Foxes were 10 times more

vigilant during dog trials than during neutral and odor trials and also exhibited lower levels of non-vigilance behavior (resting, playing) when dogs were visible. In contrast, dog odors did not affect fox foraging and activity. These results show that vigilance/foraging tradeoffs due to interference competition can occur between native and domestic carnivores, despite low dietary overlap.

To avoid the effects of interference competition and intraguild predation, subordinate competitors such as the Indian fox can alter space use patterns which may result in a reduction of foraging opportunities. To determine if interference competition between dogs and foxes influences the space use patterns of foxes at a landscape level, I conducted a radio-telemetry study of 32 Indian foxes and 25 free-ranging dogs in and around the Great Indian Bustard Wildlife Sanctuary in central India. Using a logistic regression analysis in an information theoretic framework, I determined the effects of landcover type, primary prey abundance (rodents) and dog presence on the landscape on the space use of foxes. As expected, Indian foxes showed low overlap with dogs based on the volume of intersection index. Top AIC ranked models showed a positive influence of grasslands and a negative influence of agricultural land and dog presence. Rodent abundance only had a weak positive effect. This suggests that fox space use is determined not only by habitat type, but also influenced by the presence of a mid-sized carnivore, the dog.

These results suggest that the competitive intraguild dynamics that are seen among wild carnivores can also occur between wild and domestic carnivores, despite a seeming lack of competition for food and other resources. The role of dogs as intraguild competitors of wild carnivores has thus far been under-recognized. Dogs are among the

world’s most common carnivores and are heavily subsidized by humans. As a result, they can occur at high densities even in rural areas, where they tend to range freely into wild habitats. Therefore, dogs can pose threats to native carnivore communities, and extend the edge of anthropogenic disturbance well beyond the borders of human settlements.

CHAPTER 1: *Vulpes bengalensis*: THE INDIAN FOX

ABSTRACT

The Indian fox is a small canid, endemic to the Indian subcontinent. Although it is widespread, little is known about its ecology, behavior and population status. This chapter reviews the existing literature (up to 2006) on the Indian fox and is presented in the form of a Mammalian Species account which was published in 2006.

TAXONOMIC CLASSIFICATION

Vulpes bengalensis (Shaw, 1800)

Indian Fox

Canis bengalensis Shaw, 1800:330. Type locality "Bengal." Type "probably exported from Calcutta" (Pocock 1936); restricted to "the adjoining area of India [near Calcutta], south of the Ganges" (Pocock 1936:49).

Canis kokree Sykes, 1831:101. Type locality "Dukun, (Deccan), East Indies."

Canis (Vulpes) indicus Hodgson, 1833:237. Type locality not specified. Restricted to "India" (Pocock 1941:129).

Canis (*Vulpes*) *rufescens* Gray, 1833-4:plate 6. Type locality not specified. Restricted to "India" (Pocock 1936:49).

Canis chrysurus Gray, 1837:577. Type locality "India". Restricted to "Nepal" (Pocock 1936:49). Type specimen is apparently the same individual as the type of *V. xanthura* (skin is type of *chrysurus,* skull is type of *xanthura*; Pocock 1936).

Vulpes hodgsonii Gray, 1837:578. Type locality "North India, Nepal."

Vulpes xanthura Gray, 1838:68. Type locality not specified. Restricted to "Nepal" (Pocock 1936:49). Type specimen is same individual as type of *V. chrysurus*.

V[*ulpes*]. *bengalensis*: Gray, 1838:68. First use of current name combination.

Context and content

Order Carnivora, suborder Caniformia, family Canidae, subfamily Caninae, genus *Vulpes* (Wilson and Reeder 1993). *Vulpes bengalensis* is monotypic.

Diagnosis

Vulpes bengalensis (Fig. 1) is a small fox of the Indian subcontinent, where it overlaps primarily with *V. vulpes*. *V. bengalensis* can be distinguished from *V. vulpes* by the former species having a black tipped tail, grayish body pelage that lacks mixing of red hairs, brownish or rufous legs, ears that are the same color as nape or darker (but never with a black patch as in *V. vulpes*), and smudges of black hairs around upper part of muzzle in front of eyes (Johnsingh and Jhala 2004; Menon 2003; Pocock 1936, 1941; Prater 1980; Roberts 1997). Dorsal guard hairs of *V. bengalensis* can be differentiated from those of *Canis lupus*, *C. aureus*, *Cuon alpinus*, and *V. vulpes* in India by medullary index, scale structure, counts, and position (Chakraborty and De 2001). The size of Indian fox scats is approximately 25% smaller in diameter than those from sympatric carnivores such as golden jackal (*C. aureus*) and jungle cat (*Felis chaus*; Vanak 2003).

General characters

Vulpes bengalensis is a relatively small fox with an elongated muzzle, long pointed ears, and bushy tail ca. 50-60% length of head and body (Menon 2003; Roberts

1997). Dorsal pelage is grayish and paler ventrally; legs tend to be brownish or rufous. Tail is bushy with prominent black tip. Back of ears is dark brown with black margin. Rhinarium is naked and lips are black, with small black patches of hair on upper part of muzzle in front of eyes (Johnsingh and Jhala 2004; Menon 2003; Prater 1980; Roberts 1997). Extensive variation in coat color may occur between populations and seasonally within populations (Pocock 1936, 1941).

External measurements (in mm; mean and parenthetical range with *n*) of males and females, respectively, from the collections of the Bombay Natural History Museum are: length of head and body, 500 (390-575, 6), 472 (460-480, 3); length of tail, 289 (247-320, 5), 276 (245-312, 3); length of hind foot, 118 (110-125, 5), 114 (112-116, 3); length of ear, 71 (68-73, 4), 75 (72-79, 3; Johnsingh and Jhala 2004). Body masses for males and females are 2.7-3.6 kg and >1.8 kg, respectively (Johnsingh and Jhala 2004; Pocock 1936; Roberts 1997). In Nepal, external measurements (mean ± *SD*, in mm) of 3 males and 2 females, respectively, are: total length, 747.7 ± 30.3, 785.6 ± 32.5; length of tail, 277 ± 12.6, 292.7 ± 6.1; length of hind foot, 122.0 ± 1.3, 114.5 ± 4.7; length of ear, 77.2 ± 4.3, 76.2 ± 0.2 (Mitchell 1977). External measurements (mean ± *SD,* in mm) of 10 males and 7 females collected throughout India and Pakistan are: length of head and body, 526.2 ± 45.3, 514.5 ± 40.6; length of tail, 295.0 ± 24.2, 303.8 ± 28.5; length of hind foot, 116.3 ± 7.4, 115.6 ± 6.0 (*n* = 9 and 6, respectively; Pocock 1936).

Skull of *V. bengalensis* (Fig. 2) has a relatively short, broad muzzle; nasal bones are broad posteriorly. Width above P2 is ca. 1/3 length of palate, and height of upper canine is less than combined lengths of upper carnassial (P4) and M1; upper carnassial is smaller than M1 (Pocock 1936). Cranial measurements (mean ± *SD*, in mm) of adult males (*n* = 11) and adult females (*n* = 14, except where indicated), respectively, throughout India, Pakistan, and Nepal are: condylobasal length, 111.2 ± 7.4, 106.8 ± 4.1; zygomatic breadth, 64.0 ± 3.5, 59.6 ± 3.4; postorbital width, 20.0 ± 1.1, 19.6 ± 1.1; interorbital width, 21.3 ± 2.0, 19.6 ± 1.4; width of maxillary, 18.1 ± 1.4, 17.0 ± 1.1; length of maxillary tooth row, 50 ± 3.6, 48.1 ± 1.8 (*n* = 13 females); length of mandible, 85.0 ± 6.0, 81.6 ± 4.2 (*n* = 13 females); length of P4, 9.2 ± 0.6, 9.4 ± 0.5; length of m1, 11.0 ± 0.5, 10.7 ± 0.7 (*n* = 13 females; Pocock 1936). Greatest lengths of skull (in mm) for 2 adult females and 1 adult male from Field Museum of Natural History are 110.4, 110.7, and 115.8, respectively.

Distribution

Vulpes bengalensis is endemic to the Indian subcontinent (Fig. 3) from the Himalayan foothills and Terai of Nepal through southern India and from southern and eastern Pakistan to eastern India and southeastern Bangladesh (Chesemore 1970; Johnsingh and Jhala 2004; Khan 1984, 1985; Mitchell 1977; Roberts 1997; Sarker and Sarker 1984; Shrestha 1997). *V. bengalensis* has not been recorded from Afghanistan or Iran or from the Western Ghats, India (Johnsingh and Jhala 2004; Roberts 1997). Populations may be expanding into the Sundarbans, Bangladesh with decline of mangrove forests (Seidensticker 1987). *V. bengalensis* is rarely abundant within its range, and may be absent from many localities within its range (Vanak 2005).

Fossil record

Prototocyon (= *Sivacyon*-McKenna and Bell 1997) *curvipalatus*, the type comprised of an associated skull and mandible, was first described as *Canis* (= *Vulpes*) *curvipalatus* and is considered closely allied to *V. bengalensis* (Bose 1880). The remains were recovered from the early Pleistocene Upper Siwaliks horizon of the Siwalik Hills, India (Colbert 1935; Pilgrim 1932).

Form and function

Dental formula is i 3/3, c 1/1, p 4/4, m 2/3, total 42 (Johnsingh and Jhala 2004). Tongue has 3 pairs of papillae arranged in converging lines (Sonntag 1923). External brain anatomy of *V. bengalensis* has been described (Lyras and van der Geer 2003).

Dorsal guard hairs are 4-5 cm long and 60 μm in diameter at proximal region, with a gross appearance of black in distal region and yellow in proximal region (Koppikar and Sabnis 1976). Females have 3 pairs of mammae (Johnsingh and Jhala 2004; Pocock 1936, 1941).

Forefeet and hind feet have 4 toes with nonretractable claws, and pads of feet are naked (Pocock 1941; Roberts 1997). Measurements (mean ± *SD*, range, in cm) of 11 paw prints from southern India are: total length, 4.11 ± 0.18, 3.3-5.1; total width, 3.53 ± 0.14, 3.0-4.3; pad width, 1.91 ± 0.13, 1.2-2.5; pad length, 1.89 ± 0.1, 1.5-2.6; pad-toe gap, 0.79 ± 0.18, 0.3-2.3 (Vanak 2003). Mean diameter (± *SE*) of 55 Indian fox scats collected from the Rollapadu (Andhra Pradesh) and Ranebennur (Karnataka) Wildlife Sanctuaries is 14.25 ± 0.31 mm (Vanak 2003).

Ontogeny and reproduction

Indian foxes form pair bonds that extend beyond the reproductive period. In Gujarat, mating occurs December-January (Johnsingh and Jhala 2004); elsewhere, mating and parturition is timed to the monsoon season and availability of resources (Johnsingh 1978; Roberts 1997). In Nepal, a female collected in late December had 3 embryos (Mitchell 1977). Mating involves an extended copulatory tie, gestation lasts 50-53 days, and pups are generally born between January and May (Acharjyo and Misra 1976; Johnsingh 1978; Manakadan and Rahmani 2000; Prater 1980). Litter size is 2-4, and averaged 2.7 in Bhal, Gujarat (Johnsingh and Jhala 2004). Four neonates weighed 52-65 g and were 52-65 cm in total length; pups are born with eyes closed (Acharjyo and Misra 1976).

Nursing and post-natal care lasts several months. In Tamil Nadu, young are born in January, and nursing may extend through late April (Johnsingh 1978). In Pakistan, births occur July-August, coinciding with onset of southwest monsoon (Roberts 1997). In Andhra Pradesh, where den use is restricted to pup-rearing season, scats of pups were found at den sites in April-May; pups remained at den sites until beginning of monsoon after which dens were abandoned (Manakadan and Rahmani 2000). Both parents bring food to pups and guard den. Aggregations of Indian foxes at den sites have been reported when dispersal of grown individuals is delayed, although presence of helpers has not been observed (Johnsingh 1978; Johnsingh and Jhala 2004). Nursing by > 1 female has been observed, but relationships of these females to young and to each another were unclear (Johnsingh 1978). Play among pups is common for the first 3 months, and consists of vertical leaps, back-arching, foreleg stabs, submissive displays, and play solicitation; the adult male will occasionally play with young (Johnsingh 1978). In northwestern India, dispersal of young occurs during the onset of the monsoon season when resources are abundant (Johnsingh and Jhala 2004).

Ecology and behavior

Vulpes bengalensis prefers semi-arid flat to undulating terrain, and is relatively abundant in regions with low rainfall where vegetation is principally short grasslands or scrub, thorn, or dry deciduous forests. Indian foxes avoid dense forests, steep terrain, tall grasslands, and true deserts (Johnsingh and Jhala 2004; Macdonald and Sillero-Zubiri 2004; Prater 1980). In Nepal and northeastern India, *V. bengalensis* occurs up to 1350-1500 m (Johnson et al. 1980; Mitchell 1977; Pocock 1936). Indian foxes are relatively tolerant of habitat disturbance and can be found near agricultural fields, human habitations, and irrigation backs (Johnsingh 1978; Manakadan and Rahmani 2000; Prater 1980; Vanak 2003).

Vulpes bengalensis occurs at densities from 0.04-0.06 to 1.63 per km^2 and undergoes fluctuations in local abundance due to altered prey availability and outbreaks of disease (Awasthi et al. 1994; Johnsingh and Jhala 2004; Manakadan and Rahmani 2000). Densities of breeding pairs vary from 0.01 to 0.15 per km^2 as a function of rodent availability (Johnsingh and Jhala 2004). In the Kutch area of Gujarat, density of breeding pairs was 0.10/km^2 (Home 2005). Population densities are greatest in semi-arid grasslands of peninsular India; in Rollapadu (Andhra Pradesh) and Ranebennur (Karnataka) wildlife sanctuaries, the Indian fox is the most common carnivore and during some years direct sightings are a daily occurrence (Vanak 2005; Vanak and Gompper 2007). In Andhra Pradesh, density of Indian foxes in grazing lands tends to be lower than in adjacent protected areas (Manakadan and Rahmani 2000). The Indian fox is widely distributed in northern and southern highlands of Balochistan, Pakistan (densities of 0.02-0.03/km^2) with a more patchy distribution in central highlands and southern lowlands, and absence in northern highlands. Overall density in Balochistan is estimated at 0.008/km^2 with a province-wide population size of 557 individuals (Mian 2003a, 2003b). Analyses based on body and brain masses indicate that 71-94 km^2 is the minimum area necessary to support a population of *V. bengalensis* (Smallwood 1999).

The Indian fox is primarily crepuscular and nocturnal; although individuals may occasionally become active during cool periods of daylight, they generally spend the hotter daylight hours under cover or in dens (Johnsingh 1978; Vanak and Gompper 2007). Microhabitat use surveys and den site mapping in Andhra Pradesh suggest a preference for open habitats and lower grass height and avoidance of dense vegetation (Manakadan and Rahmani 2000; Vanak and Gompper 2007). *Vulpes bengalensis* is typically seen in pairs at dens or groups of dens (Manakadan and Rahmani 2000). Three types of den are used: simple, short dens with 2 openings used for brief rest periods, complex dens with multiple openings, and dens under rocks or rock crevices (Johnsingh 1978). Complex multi-entrance dens are most common, and can be used to survey Indian foxes (Johnsingh 1978; Vanak 2003). Several of the openings may lead to a central sleeping chamber 60-90 cm below ground (Prater 1980). In Tamil Nadu, 8 such dens had 6-23 openings each and were inhabited over extended periods (e.g., > 15 yrs; Johnsingh 1978). A den complex in Andhra Pradesh had 43 openings, and large complexes may cover 80 m^2 (Johnsingh and Jhala 2004; Manakadan and Rahmani 2000). All holes at a den complex are not used by foxes; 2-7 active holes per den is typical, with other holes sometimes being used by rodents or monitor lizards (*Varanus bengalensis;* Manakadan and Rahmani 2000).

Indian foxes have several vocalizations, including a chattering bark that consists of a sharp yelp repeated 3-4 times (Johnsingh and Jhala 2004; Mivart 1890; Prater 1980). Other calls include a growl, whimper, whine, and growl-bark (Johnsingh 1978).

The Indian fox is omnivorous and opportunistic (Home 2005; Johnsingh 1978; Johnsingh and Jhala 2004; Manakadan and Rahmani 2000; Roberts 1997; Vanak 2003). In southern Tamil Nadu, several vertebrate and invertebrate prey species were identified from fecal analyses, indicating a diet in this region of insects, ground-nesting birds, and small mammals (Johnsingh 1978). In Rollapadu, Andhra Pradesh, scat analyses identified rodents, leporids, monitor lizard, *Acoryphya* grasshoppers, and seeds of *Arachis hypogea*, *Cassia fistula,* and *Zizyphus mauritiana*. Scats from pups at Rollapadu contained primarily rodent fur (Manakadan and Rahmani 2000). Of 67 scats from adult foxes in Rollapadu, Andhra Pradesh, and Ranebennur, Karnataka, 85% contained remains of invertebrates, 46% mammals, 16% birds, and 4% reptiles (Vanak 2003). Remains of fruits and seeds (mainly *Z. mauritiana*) occurred in 33% of scats and 34% had undigested plant matter. Among all scats, 13% were composed of 1 food type, 46% of 2 food types, 28% of 3 food types, and 12% of 4 food types (Vanak 2003). Similar dietary patterns occurred in grassland and scrub habitat in the Kutch region of Gujarat, where across habitats and seasons, arthropods were the most important food items, followed by mammals (Home 2005). Arthropods occurred in 77% and 84% of scats collected in grassland and scrub habitats, respectively (Home 2005). Other prey items found in scats from grassland and scrub habitats, respectively, included mammals (46%, 53%), fruits (54%, 23%), reptiles (44%, 26%), and birds (6%, 2%); percent occurrence of fruits and reptiles in scats differed significantly between grassland and scrub, and occurrence of several other food types differed between habitats within particular seasons. Minimum number of scats required to analyze annual food habits of Indian foxes is ca. 100 (Home 2005). Other notable food items recorded in the diet of *V. bengalensis* are centipedes, land crabs, scorpions (*Palamneus*), shoots and pods of *Cicer arietum,* and fruits of *Azadirachta indica*, *Citrullus vulgaris*, *Ficus bengalensis, Mangifera indica*, *Melia azedarachta,* and *Syzigium cumini* (Johnsingh and Jhala 2004; Mivart 1890; Pocock 1941; Prakesh 1959, 1975; Prater 1980; Roberts 1997). Indian foxes may scavenge kills by wolves (*Canis lupus*; Jhala 1993). *Vulpes bengalensis* is a potential predator on eggs and chicks of the endangered great Indian bustard, *Ardeotis nigriceps*, although analyses of fox scats from Rollapadu Wildlife Sanctuary, Andhra Pradash did not detect presence of bustard remains (Manakadan and Rahmani 2000). Indian foxes may play a role in regulating rodent populations (Advani 1987).

Vulpes bengalensis and *V. vulpes* rarely overlap, or where overlap occurs, they avoid or replace each another (Pocock 1941; Prakash 1994; Roberts 1997). Agonistic interactions between *V. bengalensis* and the common mongoose (*Herpestes edwardsi*) were observed in Tamil Nadu (Johnsingh 1978). Wolves and jackals (*C. aureus*) usurp and enlarge fox dens (Johnsingh and Jhala 2004; Manakadan and Rahmani 2000), and once in Velavadar National Park, Gujarat, Indian fox and wolf pups simultaneously shared a den site (Johnsingh and Jhala 2004).

Lifespan in captivity is 6-8 years (Johnsingh and Jhala 2004). In the wild, disease and predation by larger carnivorous birds, mammals, and reptiles cause mortality (Manakadan and Rahmani 2000). In India, wolves, free-ranging domestic dogs (*C. familiaris*), and raptors have been reported to chase or kill *V. bengalensis* (Johnsingh and Jhala 2004; Manakadan and Rahmani 2000; Prater 1980). A study of wolf food habits in Gujarat found *V. bengalensis* in 2.3% (*n* = 601) of fecal samples (Jhala 1993). In some areas such as Tamil Nadu and Karnataka, India, anthropogenic mortality is high; humans, assisted by domestic dogs, kill Indian foxes for flesh, teeth, and pelts (Johnsingh 1978; Johnsingh and Jhala 2004; Manakadan and Rahmani 2000; Vanak 2003, 2005; Appendix I). When pursued, Indian foxes will twist, turn, and double back attempting to escape (Prater 1980).

In Rollapadu Wildlife Sanctuary, a population of ca. 40-50 foxes declined in 1 year to ca. 10 animals before recovering (Manakadan and Rahmani 2000; Vanak 2003). A similar decline occurred in areas of Gujarat (Johnsingh and Jhala 2004). Parasites reported for *V. bengalensis* include heartworm, *Dirofilaria immitis* (Rao and Acharjyo 1971, 1993), nematodes (*Subulura numidica*, *S. vulpis*; Khera 1954), Mallophaga biting lice (*Trichodectes canis*; Mitchell 1977), Anoplura sucking lice (*Linognathus setosus bhatii*; Dutta 1988), fleas (*Ctenocephalides felis felis*, *C. f. orientis*, and *Pulex irritans*; Mitchell 1977), and ticks (*Haemaphysalis heinrichi* and *H. bispinosa;* Hoogstraal and

Kim 1985; Mitchell 1977). Anoplura sucking lice (*L. vulpis*) collected from "*V. rüppellii bengalensis*" in Karachi, Pakistan (Cardozo-de-Almeida et al. 1999) were likely from *V. bengalensis.*

Genetics

Diploid chromosome number of *V. bengalensis* is 60 includes 10 metacentric and submetacentric autosomes, 48 acrocentric autosomes, a metacentric X, and an acrocentric Y chromosome (Ranjini 1966; Srivastava and Bhatnagar 1967; Wurster and Benirschke 1968). Microchromosomes occur (Bhatnagar 1973).

Conservation

Vulpes bengalensis was listed as Least Concern by IUCN Red List global rankings in 2004 (Johnsingh and Jhala 2004). In India, *V. bengalensis* is protected as a Schedule II species under the Indian Wildlife (Protection) Act of 1972 (as amended up to 2002; Anonymous 2002), and populations are declining in parts of the country, notably Karnataka and Tamil Nadu, due to loss of short grassland-scrub habitat to agriculture, industry, and development (Johnsingh and Jhala 2004). Numbers have declined in arid western India (Prakash 1994). Although widespread in its distribution, *V. bengalensis* may occur at high densities only in habitats such as the semi-arid grasslands of peninsular India which are highly endangered ecosystems and poorly represented in the protected area network of India; < 2% of potential Indian fox habitat falls within protected areas in southern India (Vanak *et al.* in press). Populations in Nepal have decreased (Shrestha 1997). In Bangladesh, although *V. bengalensis* is considered widely distributed and is a 1st schedule species under the Bangladesh Wildlife (Preservation) (Amendment) Act of 1974 and therefore open to hunting and shooting by an ordinary game hunting permit, viable populations may be uncommon or may no longer persist, and the species is considered Vulnerable (Khan 1984, 1985; IUCN Bangladesh 2000).

Remarks

Local vernacular names for *V. bengalensis* include: Lokeria, Lokri, Löm, Lomri, Lúmri (Hindi); Lokeria (Central India); Lukhariya (Bundelkund); Khekar, Khikir (Bihar); Khek-shiyal (Bengali); Kokri (Marathi); Kulla naree (Tamil); Hiyal (Assamese); Kodisilai (Oriya); Lamhui (Manipuri); Kuru naree (Malayalam); Khekri (Gond); Gunta nakka, Konka-nakka, Poti Nara (Telegu); Chandak-nari, Hakku-nari, Kanka nari, Kemp-nari, Konk, Konku-nari, Sanna nari (Kanarese), Lokdi (Gujarati and Kutchi); Fyauroo, Phauroo, Phiamro (Nepali); Khek shial (Bangladeshi; Johnsingh and Jhala 2004; Khan 1984; Menon 2003; Pocock 1941; Prater 1980; Vanak 2003).

Vulpes bengalensis is featured in many tales from ancient Jataka texts and Panchatantra (Macdonald and Sillero-Zubiri 2004). In some areas, vocalizations of Indian foxes are taken as omens (Prakash 1994). Capture and ceremonial release of *V. bengalensis* during the Sankaranti religious festival occurs in Karnataka (Vanak 2003).

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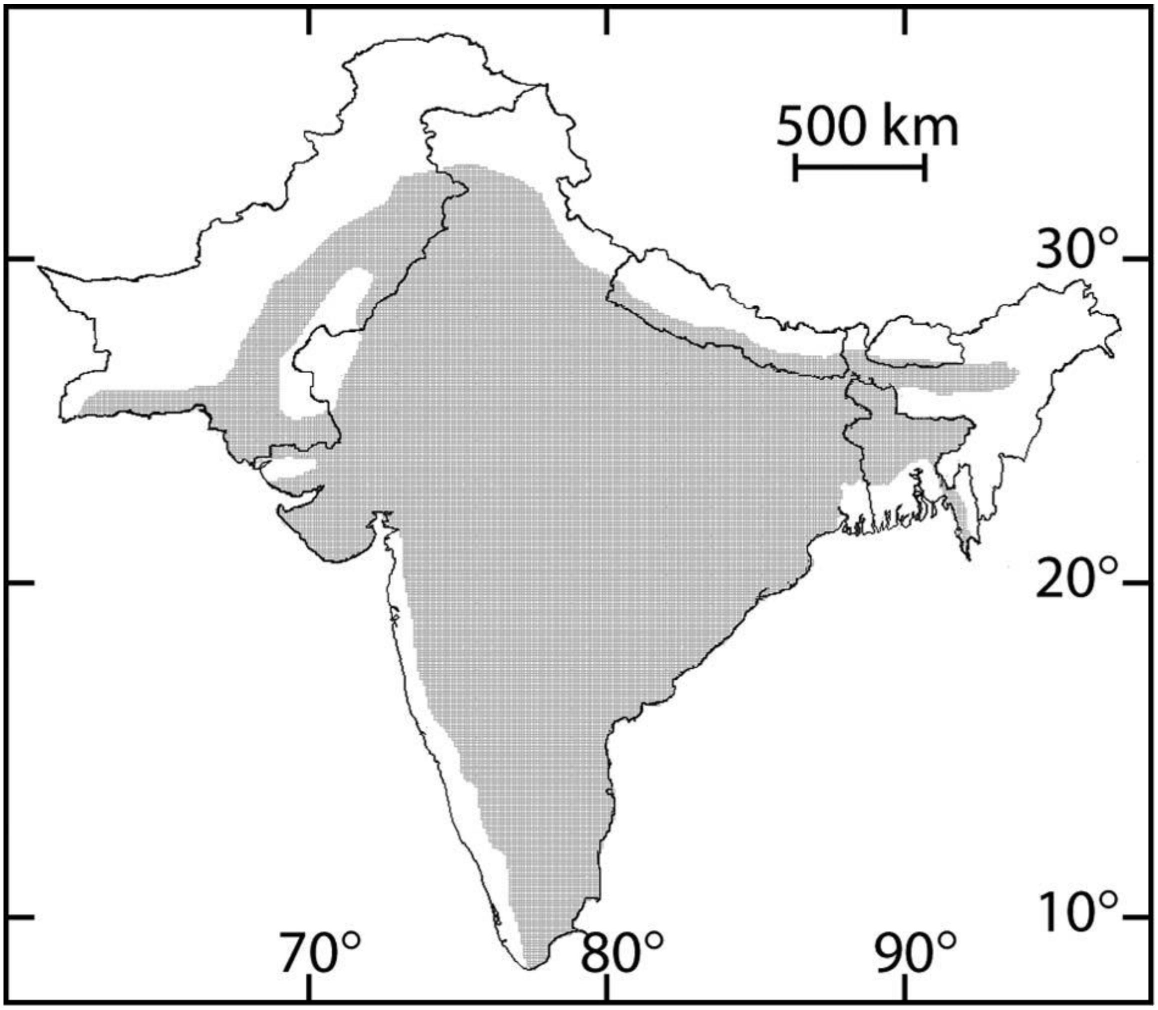
Figure 1. Adult female *Vulpes bengalensis,* Nanaj, Maharashtra, India, February 2006. Photograph by A. T. Vanak.

Figure 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of adult female *Vulpes bengalensis* (Field Museum of Natural History, Chicago, Illinois 83083). Greatest length of cranium is 110.7 mm.

Figure 3. Geographic distribution of *Vulpes bengalensis*.



Chapter 2: DOGS AS CARNIVORES:
THEIR ROLE AND FUNCTION IN INTRAGUILD COMPETITION

ABSTRACT

As the world's most common carnivore, dogs *Canis familiaris* are known to interact with wildlife as predators, prey, competitors, and disease reservoirs or vectors. Despite these varied roles in the community, the interaction of dogs with sympatric carnivores is not well understood. Here I review how domestic dogs have been classified in the literature, and illustrate how the location and ranging behavior of dogs are important factors in predicting their impact on wild prey and sympatric carnivores. I detail evidence of dogs as intraguild competitors with other wild sympatric carnivores in the context of exploitative, interference, and apparent competition. Dogs can have localized impacts on prey populations but, in general they are poor exploitative competitors of wild carnivores. Most dog populations are highly dependent on human derived food, and because of these subsidies, they can occur at high population densities. Thus at a population level, dogs could outcompete native carnivores, and especially so when prey is limited. Dogs have the potential to be effective interference competitors, especially with medium and small-sized carnivores, and may fulfill the role of a mid-sized canid, especially in areas where the native large carnivore community is depauperate. Dogs can also be ideal reservoirs of diseases, because most populations in rural areas of the world are free-ranging and unvaccinated. The transmission of diseases such as rabies and canine distemper virus from dogs to wild carnivores has resulted in severe population declines in several

endangered species of carnivores. Because dogs can be effective disease reservoirs, they can thus be viewed as disease-mediated apparent competitors, capable of inflicting large-scale population-wide declines in carnivores. Based on this information, I propose a conceptual model that uses dog population size and ranging patterns to predict the potential for dogs to be intraguild competitors. I ultimately discuss how these interactions between dogs and carnivores might influence native carnivore communities.

INTRODUCTION

Dogs *Canis familiaris* are the world's most common carnivore, introduced by humans to every continent. Throughout the world, most dogs engage in some form of free-ranging behavior irrespective of whether they are owned. In the course of this free-ranging activity, dogs interact with wildlife at multiple levels, including as predators (Kruuk and Snell 1981), prey (Edgaonkar and Chellam 2002), competitors (Butler et al. 2004), and disease reservoirs or vectors (Butler et al. 2004; Cleaveland et al. 2000; Fiorello et al. 2006; Funk et al. 2001). Despite this, the impact of dogs in natural environments has not been well documented and I know little about the nature and ecological impact of competitive interactions between dogs and sympatric carnivores.

Growing evidence documenting competitive dynamics between wild carnivores suggests that intraguild competition affects the persistence and abundance of carnivore populations and thus can have dramatic consequences for the structure of carnivore guilds (Karanth and Sunquist, 1995, Linnell and Strand, 2000, Creel et al., 2001, Caro and Stoner, 2003, Donadio and Buskirk, 2006). When sympatric carnivore populations compete for resources, this competition results in spatial patterns such as complete or partial exclusion of at least one species and scattered interspecies territories (Creel et al. 2001; Johnson et al. 1996). Larger carnivores suppress populations of other guild members by direct predation for food and through two forms of interspecific competition: 1) Exploitative competition, whereby asymmetric competitive abilities in obtaining limited resources explain patterns of species co-occurrence; and 2) Interference competition, whereby patterns of species co-occurrence result from direct interactions such as spatial exclusion, harassment, or at an extreme, direct mortality, known as intraguild predation (Case and Gilpin 1974; Laundré et al. 2001; Palomares and Caro 1999). Exploitative competition in carnivores has not been directly demonstrated, but can be inferred in cases where competitors such as lions *Panthera leo* and hyenas *Crocuta crocuta* kleptoparasitize cheetahs *Acinonyx jubatus* and African wild dogs *Lycaon pictus* resulting in appreciable hunting costs (Creel et al. 2001). On the other hand, interference competition and intraguild predation is a common occurrence among carnivores and there are several examples of these phenomena. For example, intraguild predation by lynx *Lynx pardinus* on mongooses *Herpestes ichneumon* and genets *Genetta genetta* results in clear interspecific habitat segregation in the Doñana National Park in south-western Spain (Palomares and Delibes 1994). In Africa, cheetahs have been observed to avoid lions, even though this may lead to using habitat with lower prey availability (Creel et al. 2001).

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

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

Classifying free-ranging dogs

Modern dogs evolved from the gray wolf *Canis lupus,* and current evidence suggests a single origin from Asia (Savolainen et al. 2002). The domestication process resulted in a reduction of body size and a change in the cranio-dental configuration (Clutton-Brock 1995; Coppinger and Schneider 1995). As a result of these morphological changes, dogs are capable of consuming and surviving on a wide range of food types, from scavenging human-derived garbage to killing mammalian prey that may be several times their body mass. However, the socio-ecology and diet of dogs varies with their dependence on humans and this in turn affects their competitive ability with wild carnivores. For example, MacDonald and Carr (1995) observed distinct differences in social organization of free-ranging dogs that lived in villages and those that occupied the more rural areas. Village dogs defended territories and were mostly solitary with some loose social grouping. On the other hand "sylvatic" dogs led a more "wolf-like" existence, often forming packs and occasionally roaming alone (Boitani et al. 1995). Although village dogs were entirely dependent on human-derived food, the free-ranging "sylvatic" dogs were more opportunistic and supplemented their diet with wild derived foods, even without cooperatively hunting like wolves (Boitani et al. 1995; MacDonald and Carr 1995).

Indeed, the dependence of dogs on human-derived materials (HDM), which I define as including scavenged human food refuse, crops, livestock, farmed animals, and human feces, as well as food derived from direct feeding of dogs, is typical for the vast majority of free-ranging dog populations for which diet has been studied. Although many studies have shown that dogs kill and feed on wildlife, these studies have been mainly prey-focused, examining the mortality of particular prey species as a function of dog predation (e.g. Lowry and McArthur 1978; Manor and Saltz 2004; Yanes and Suárez 1996). Such studies give an incomplete picture of dog foraging ecology. A reliance on HDM, even when wildlife is also killed and consumed, is more common (Atickem 2003, Vanak, Chapter 4; Butler and du Toit 2002; Butler et al. 2004). Given that several studies have, however, revealed the ability of dogs to subsist on a diet comprised solely of wildlife (Campos et al. 2007; Kruuk and Snell 1981; Triggs et al. 1984), the reliance on HDM may be a function of the opportunistic nature of dogs and learned behavior rather than more definitive ecological constraints.

The variance in diet of dogs may also be a function of location and the extent to which these dogs range freely. In much of the developed world, dogs are confined, remaining indoors or constrained to a proscribed outdoor area by the owner. However, dog populations often range freely in urbanized regions of both developed and less developed countries (Beck 1975; Daniels and Bekoff 1989; Oppenheimer and Oppenheimer 1975; Pal 2003). In rural areas of most of the world, much of a dog's daily activity involves unconfined movements, despite being owned or affiliated with specific human habitations. Several efforts have been made to categorize dogs and most authors agree that these categories are flexible and that dogs may fall into more than one category or switch categories (Boitani et al. 1995; Daniels and Bekoff 1989; Green and Gipson 1994; MacDonald and Carr 1995; Nesbitt 1975). I describe some of the most commonly used categorizations below:

1) Owned dogs: Dogs that are owned and restricted in movement to a proscribed outdoor or indoor area. Although the potential for these dogs to interact with wildlife is limited, they can nonetheless have an effect on wildlife when they accompany humans into natural areas or if their unvaccinated status enhances the disease reservoir competency of the broader dog population (Banks and Bryant 2007; Fiorello et al. 2006; Lenth et al. 2008).

2) Urban free-ranging dogs: Dogs that are not owned by humans, but are commensals, subsisting on garbage and other HDM as their primary food source (Beck 1975). They usually do not come into contact with wildlife, except in urban parks (Banks and Bryant 2007; Lenth et al. 2008).

3) Rural free-ranging dogs: Dogs that are owned or peripherally associated with human habitations, but are not confined to a proscribed outdoor area. These include (but are not limited to) "stray" dogs and owned farm dogs whose daily activity pattern may involve ranging that can bring them into contact with wildlife, especially when human habitations border wildlife reserves or other natural areas (Butler et al. 2004, Vanak, Chapter 4).

4) Village dogs: Unconfined dogs that are associated with human habitations in rural environments, but rarely leave the immediate vicinity of the village (MacDonald and Carr 1995, Vanak, Chapter 4).

5) Feral dogs: Dogs that are completely wild and independent of human derived food sources (Green and Gipson 1994; Nesbitt 1975).

6) Wild dogs: Dingoes, feral dogs and their hybrids in Australia that have a history of independence from humans and are no longer considered domesticated (Corbett 1995).

To determine how location and ranging play a role in the diet of dogs, I reviewed existing published (n = 20) and unpublished (n = 1) studies of dog ecology that included some description of the location, diet and ranging of a population of dogs. I categorized dog locations as: (1) urban, if they were in cities or suburbs with high human densities and had little or no contact with wildlife habitat, (2) rural, if the locations were in villages or farmland with low human densities and had moderate contact with wildlife habitat, or (3) wild, if the dogs lived in native habitats with no human contact. Ranging behavior was categorized as: (1) limited, if the dogs had home-ranges of <100 ha or were confined to particular neighborhoods or villages, (2) free-ranging, if the dogs had home-ranges of >100 ha or moved freely between villages and in the surrounding landscape, or (3) feral, if the dogs were free-ranging and avoided human association. Based on description and dietary analyses, I classified the diet of dogs as: (1) human-dependent, if the entire diet consisted of HDM, either from direct feeding or through scavenging of human refuse, (2) opportunistic, if the diet consisted mainly of HDM, but included some portion of wild caught food, and (3) wild, if the majority of the diet consisted of wild caught food.

I excluded fully confined dogs in any location as they pose no direct threat to wildlife. Although some authors describe urban populations of dogs as free-ranging or feral, these dogs have a limited range, often as small as 0.26 km^2 (Beck 1975). Adequate information on certain combination of categories was lacking (urban and free-ranging, urban and feral, wild and limited range), and I suspect that dog populations fitting these categories are absent or rare. Of the studies that were included in this review, all examples of urban dogs indicate that they have a limited range and have diets that are entirely human dependent (Fig. 1). As ranging of rural dogs increases, their diets become more opportunistic and less human dependent. For example, five out of eight feral dog populations are almost entirely dependent on wild caught food (Fig. 1). Thus, the diet of dogs is closely linked to their location and ranging behavior. As dogs range farther into wilderness areas, it is also more likely that they will encounter native carnivores and will interact with them as predators, prey and competitors.

Dogs as predators and prey of native carnivores

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

Dogs can also form an important prey item in the diets of several carnivores, especially those living in close proximity to humans. For instance, leopards *P. pardus*, lions and hyenas in Africa are known to regularly consume dogs. In Zimbabwe, Butler *et al.* (2004) reported 53% of all confirmed dog kills were by these carnivores. Wolves in Finland consumed almost all dogs that were killed, although food acquisition might not have been the primary motive for predation (Kojola et al. 2004). Coyotes *C. latrans* in urban and rural areas of North America regularly kill pet dogs (Grinder and Krausman 1998). In India, several studies have found dogs to be an important component of leopard diet (Edgaonkar and Chellam 2002; Mukherjee and Sharma 2001; Singh et al. 2007). High dog densities may even be responsible for increased leopard-human conflict in some areas if leopards come into greater contact with humans in the process of hunting dogs (Athreya 2006; Athreya et al. 2007).

Dogs as exploitative competitors

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

It is unclear whether dogs are effective competitors with carnivores for wild-caught food in most natural environments. There is little evidence in the literature that pressure from dog predation on wild prey is high enough to decrease prey availability for native large carnivores. Scott and Causey (1973) found no evidence of predation on deer by rural free ranging dogs. Similarly, Lowry and McArthur (1978) noted that dogs were responsible for only twelve deer deaths in the Couer d'Alene drainage, Idaho, USA in 1975. Although deer remains were found in 15.5% of 58 dog stomachs analyzed in south-eastern Quebec, it is not possible to determine how much of this may have been scavenged (Bergeron and Pierre 1981). However, several other studies have shown that dogs can have significant localized impacts that can lead to a decrease of some prey populations (e.g. Barnett and Rudd 1983, 1996; Genovesi and Dupre 2000; Iverson 1978; Kruuk and Snell 1981; Taborsky 1988). For example, dogs are one of the main contributors to a declining kid/female ratio in mountain gazelles *Gazella gazella* in Israel (Manor and Saltz 2004).

Despite the potential for negative impacts of dogs on prey communities, it is still unclear whether exploitative competition can occur between dogs and wild carnivores. For example, Atickem (2003) found low overlap between sympatric free-ranging dog and Ethiopian wolf *C. simiens* diet based on scat analysis and concluded that exploitative competition may not be an important interaction between these two species. Food habits of free-ranging dogs and Indian foxes *V. bengalensis* reveal a similar pattern, wherein dogs have low dietary overlap with foxes, since dogs were heavily dependent on human derived food and foxes consumed mainly wild caught food (Vanak, Chapter 4). Dietary studies of wolves at the same study site in India (Habib 2007) also indicate a lack of resource overlap with dogs.

The lack of dietary overlap between dogs and wild carnivores is not surprising because, with a few exceptions (Campos et al. 2007; Glen et al. 2006; Mitchell and Banks 2005), most dog diets are comprised principally of human derived food material (Atickem 2003; Butler and du Toit 2002; Green and Gipson 1994, Vanak, Chapter 4). Butler et al (2004) suggests this as a major reason that dogs may be ineffective competitors with wild carnivores. However, a caveat to this suggestion is that, because of human subsidies, free-ranging dogs can reach high population densities (Butler et al. 2004; Daniels and Bekoff 1989), and can therefore have a large numerical effect on native prey by keeping predation pressure constant on prey populations.

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

Furthermore, dogs scavenge, and thus may indirectly compete with native carnivores by reducing the carcass biomass available. Butler *et al.* (2004) observed free-ranging dogs on the periphery of a wildlife reserve in Zimbabwe and found that dogs dominated vultures at domestic and wild animal carcasses and were effective, although subordinate, competitors for carcasses with lions, leopards, spotted hyaenas, and side striped jackals *C. adustus* (Butler and du Toit 2002). This pattern of scavenging was also observed in western India, where livestock carcasses on the periphery of villages were dominated by dogs, and thus were less available for golden jackals, *C. aureus* (Aiyadurai and Jhala 2006).

Dogs as Interference competitors

Interference competition is manifested by direct interactions such as spatial exclusion, harassment, or at an extreme, mortality by intraguild predation (Holt and Polis 1997). In response to interference competition, the subordinate competitor uses one of two strategies to reduce encounters with dominant competitor(s): avoiding range overlap, or modifying range use to reduce interactions while still allowing for home range overlap. For example, red foxes avoid areas where coyotes are present (Fedriani et al. 2000; Gosselink et al. 2003), coyotes avoid wolf territories (Berger and Gese 2007; Crabtree and Sheldon 1999), and Arctic foxes, *Alopex lagopus,* avoid red fox territories (Elmhagen et al. 2002; Tannerfeldt et al. 2002). In these cases, interference competition results in non-overlapping territories, in favor of the dominant competitor.

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

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

These general patterns of intraguild interactions are also expected between free-ranging domestic dogs and native carnivores elsewhere in the world, even when dogs are not the top-predator in the ecosystem. To determine whether smaller carnivores also perceive dogs as competitors, Vanak (Chapter 6) exposed Indian foxes *V. bengalensis* to dogs at a rich food source and found that foxes reduced visitation rates by half, reduced consumption of food by over 70%, and increased vigilance behavior. Vanak (Chapter 4) also noted a lack of human-derived food in the diet of Indian foxes when compared to domestic dog diet, and speculated that the presence of dogs may prevent foxes from accessing these resources. The reactions of foxes to dogs were similar to those of red foxes to golden jackals described by Scheinin et al. (2006) and this strengthens the argument that dogs are perceived as intraguild predators by smaller carnivores (Vanak, Chapter 6). Such aversion of dogs is not limited to small carnivores as dogs also deter wolves from accessing garbage dumps in Italy, simply by their presence in larger numbers (Boitani and Ciucci 1995).

Although direct interactions between dogs and carnivores are only rarely observed, even the temporary presence of dogs can affect wild carnivore activity and landscape use. Recent studies have shown avoidance or change in activity patterns by carnivores in multi-use recreation areas used by humans with dogs (George and Crooks 2006; Lenth et al. 2008; Reed and Merenlender 2008). These studies compared measures of carnivore presence in areas without recreation trails to areas with trails that were used by humans and companion dogs. George and Crooks (2006) reported that the probability of detecting bobcat *F. rufus* decreased with increasing human activity (due to dog walkers), and that bobcat displayed temporal displacement in areas used by hikers, bikers and domestic dogs. A more direct relationship between bobcat use of habitat and dog presence was shown by Lenth et al. (2008) who found lower bobcat detections in wildlife areas where dogs were allowed to roam freely. However, the same study also showed that red fox detections were higher in areas used by dogs, which the authors suggest may be due to the generalist nature of the red fox and its propensity to tolerate human presence for access to anthropogenic resources.

The most extreme form of interference competition is the killing of the subordinate competitor, the phenomenon known as intraguild predation. Intraguild predation can be categorized into cases where the killed species is consumed and cases where the killed animal is not eaten (Palomares and Caro 1999). It is theoretically more intriguing when the subordinate species is not consumed after intraguild predation (Amarasekare 2002; Palomares and Caro 1999), as this suggests that the dominant species is merely reducing numbers of the putative competitor. Interference competition without consumption has been well documented among mammalian Carnivora (Donadio and Buskirk 2006; Palomares and Caro 1999). Reasons for this form of intraguild predation are not clear but it has been suggested that removing the subordinate species reduces resource competition (Roemer et al. in press).

Dogs have been reported to suffer from intraguild predation without consumption by larger carnivores. Dogs are killed by wolves (Boitani and Zimen 1979; Fritts et al.

1989; Habib 2007; Jethva and Jhala 2004; Jhala 1993; Kojola et al. 2004; Naughton-Treves et al. 2003; Pulliainen 1993; Zimen and Boitani 1979), coyotes (Bider and Weil 1984; Howell 1982; Timm et al. 2004), mountain lions *Puma concolor*, and bears *Ursus* spp. (Goldenberg 2008 and other popular press in North America; Lott 2002). In most cases these dogs may be free-ranging or confined pets which are attacked in the vicinity of human habitation, or they may be hunting or companion dogs that are attacked in wild habitats (Kojola and Kuittinen 2002).

Conversely, I know less about the extent of dogs killing wild carnivores without consumption as these cases have only been reported anecdotally. Trained dogs have been used to hunt red foxes in the UK, Europe and elsewhere since the 16th century (Itzkowitz 1977; Orendi 2004), but the killing of foxes, jackals and other carnivores by free-ranging dogs in the wild is only occasionally reported. For example, Pils and Martin (1974), reported an attack on a red fox den in Wisconsin, USA by “three free-roaming mongrel dogs” which resulted in the death of a lactating female. Dogs have killed kit foxes, (Ralls and White 1995) and were also suspected to be a source of mortality for the Indian fox in central India (Vanak 2007). Three feral dogs were observed killing a coyote in Kansas, USA (Kamler et al. 2003) and farm dogs, were responsible for killing 20 of 77 eastern spotted skunks *Spilogale putorius* that were found dead (Crabb 1948). Perhaps one of the more famous anecdotal reports of dogs killing carnivores led to the rediscovery of the black-footed ferret *Mustela nigripes* in Wyoming, USA, when a farm dog brought in a dead ferret (Miller et al. 1996). In most of the above cases the dogs did not consume their quarry.

Dogs as apparent competitors

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

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

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

Conservation practitioners have attempted, with mixed success, to mitigate some of these effects by vaccination programs aimed at the reservoir (dogs) or the susceptible hosts (wild carnivores). For example, mass vaccination of dogs around the Serengeti-Mara Ecosystem against rabies was sufficient to control rabies in dogs (Cleaveland et al. 2007). However, vaccination of African wild dogs against rabies in the Serengeti failed for various debatable reasons (Burrows et al. 1995; Cleaveland et al. 2007; Woodroffe et al. 2004) and the population went locally extinct (Woodroffe 2001). On the other hand, a low coverage, less invasive, reactive vaccination program met with greater success in reducing the occurrence of rabies in Ethiopian wolves in the Bale Mountains National Park in Ethiopia (Haydon et al. 2006; Randall et al. 2006). The above examples clearly illustrate how dogs can harbor shared parasites that sometimes result in widespread epidemics and population declines in species of conservation concern, thus displaying patterns similar to those expected under a framework of apparent competition. These case studies also reiterate the importance of dogs as an integral part of diverse ecosystems and how it is becoming increasingly important to incorporate the role of dogs in the management and conservation of native carnivore populations.

CONCEPTUAL MODELS OF DOG RISK TO CARNIVORES

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

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

Interference competition: Dogs are potentially interference competitors, especially for mid-sized and small carnivores. I predict that the ranging behavior of dogs may have a greater effect on their ability to be interference competitors than the size of the population. Even at low population densities, wide ranging dogs can be effective interference competitors (Fig. 2b), because ultimately interference competition is manifested in interactions between individuals. However, as population size increases, there is an additive effect with ranging behavior on the competitive risk posed by dogs, as larger numbers of wide ranging dogs can collectively compete with a larger section of the carnivore community, especially small/mid-sized carnivores which make up the bulk of the carnivore community (Roemer et al. in press).

Apparent competition: Parasite mediated apparent competition is perhaps the largest threat that sympatric carnivores may face from dogs. While exploitative and interference competition affects individuals, the effects of apparent competition due to shared parasites can be felt at the population level because initial parasite transmission from dogs to native carnivores can be amplified by subsequent intraspecific transmission in native carnivore populations. Dogs can be excellent apparent competitors, particularly when they occur at high population densities (Fig. 2c). Because a minimum threshold level is required for parasite vectors to be effective, low densities of dogs are unlikely to have a large effect, irrespective of their ranging behavior. However, once the minimum threshold population level for pathogen reservoir status (enzootic status) is achieved, then ranging behavior becomes more important. An unvaccinated wide ranging dog that is part of an infected population has an increased chance of coming into contact with carnivores or of leaving infective materials in the environment.

CONCLUSIONS AND FUTURE RESEARCH

Dogs, by virtue of their close association with humans, are found in every continent (except Antarctica). Although they may differ morphologically from wolves due to the domestication process, they still retain characteristics that make them a potentially important member of the carnivore guild. Dogs are also generally subsidized by humans wherever they exist and are therefore insulated from food scarcity. They are also shielded from intraguild feedback mechanisms (such as intense predation by larger carnivores) by safe refuges in human habitations. These direct and indirect subsidies can result in high-density populations of free-ranging dogs even in rural areas where native carnivore communities are relatively intact. For example, Butler and Bingham (2000) report a population of at least 1.36 million dogs in Zimbabwe's communal lands, with an annual growth rate of 6.5%. Even in developed countries such as the USA, dog populations can be locally abundant (431 dogs/ km^2 in rural areas of Nevada: Daniels and Bekoff 1989). The combined effect of large population sizes and free-ranging behavior creates problematic scenarios for conservation practitioners when these enhanced dog populations influence species of conservation concern.

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

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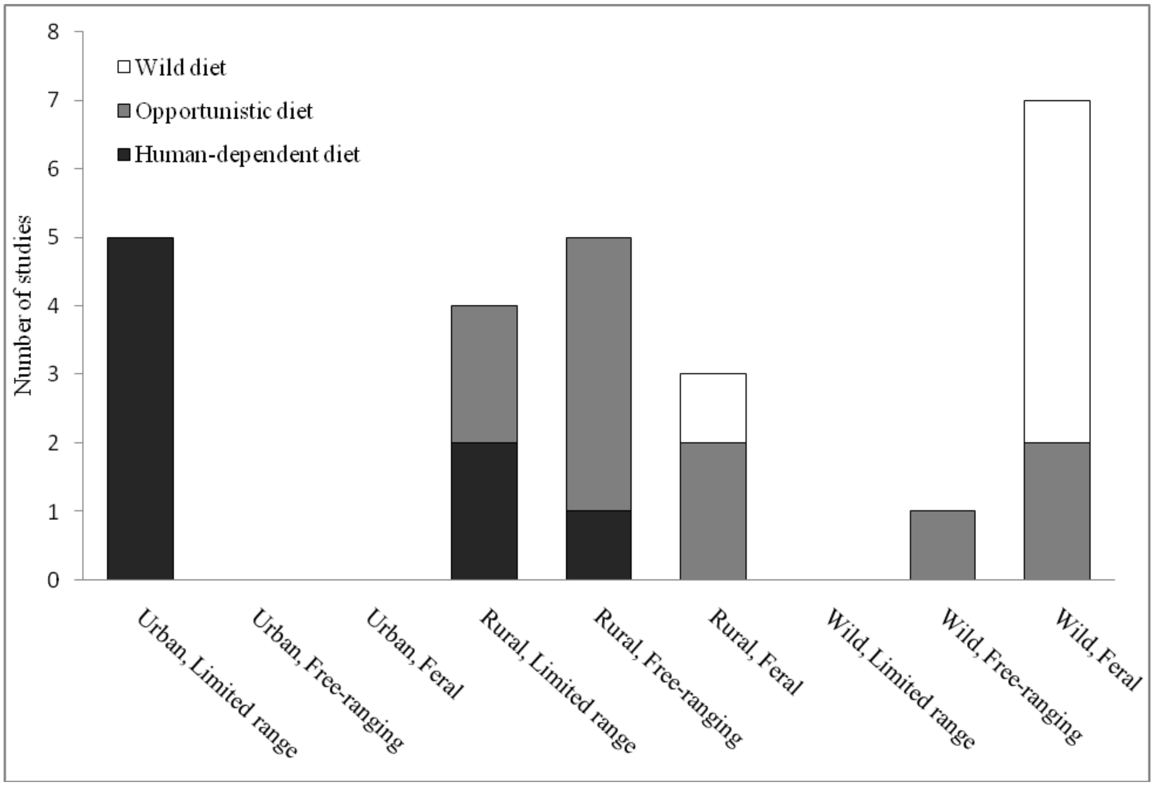
Figure 1: Summary of studies (n=21) that report the location (urban, rural, wild) ranging behavior (limited, free-ranging, feral) and diet (human-dependent, opportunistic, wild) of domestic dogs.

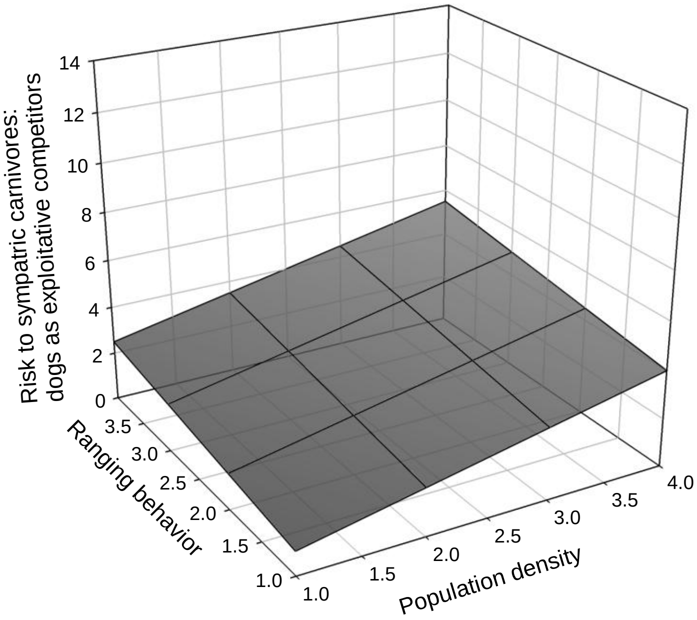


List of sources

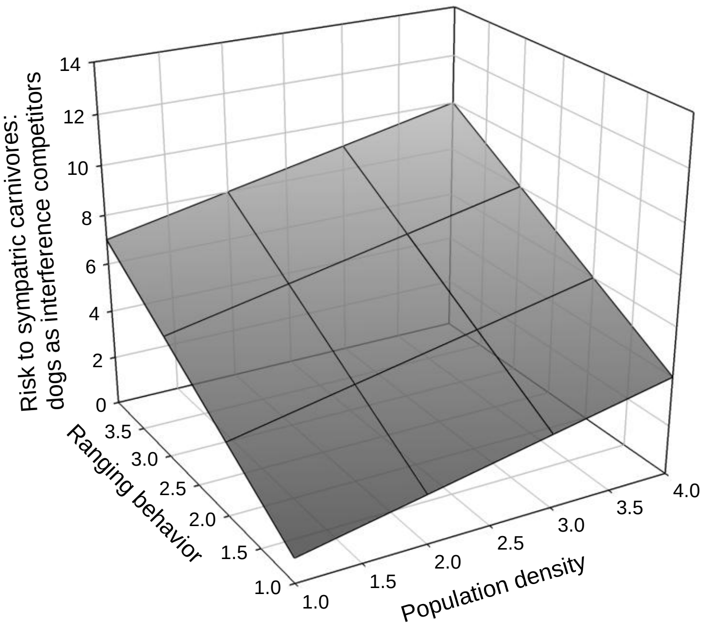
Urban, Limited range: Daniels 1983; Daniels and Bekoff 1989; Fox 1975; Oppenheimer and Oppenheimer 1975; Rubin and Beck 1982; *Rural, Limited range:* Berman and Dunbar 1983; Daniels and Bekoff 1989; MacDonald and Carr 1995; Meek 1999; *Rural, Free-ranging:* Atickem 2003; Butler and du Toit 2002; MacDonald and Carr 1995; Manor and Saltz 2004, Vanak, Chapter 4; Meek 1999; *Rural, Feral:* Campos et al. 2007; Gipson and Sealander 1976; Kamler et al. 2004; *Wild, Free-ranging:* Daniels and Bekoff 1989; *Wild, Feral*: Boitani et al. 1995; Glen et al. 2006; Kruuk and Snell 1981; Mitchell and Banks 2005; Scott and Causey 1973; Taborsky 1988; Yanes and Suárez 1996.

Figure 2: Conceptual model of the effect of domestic dog population density and ranging behavior on the competitive risk dogs may pose to sympatric native carnivores with respect to (a) exploitative, (b) interference, and (c) apparent competition.

A)



B)



Risk to sympatric carnivores: dogs as interference competitors
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Ranging behavior
1.0
1.5
2.0
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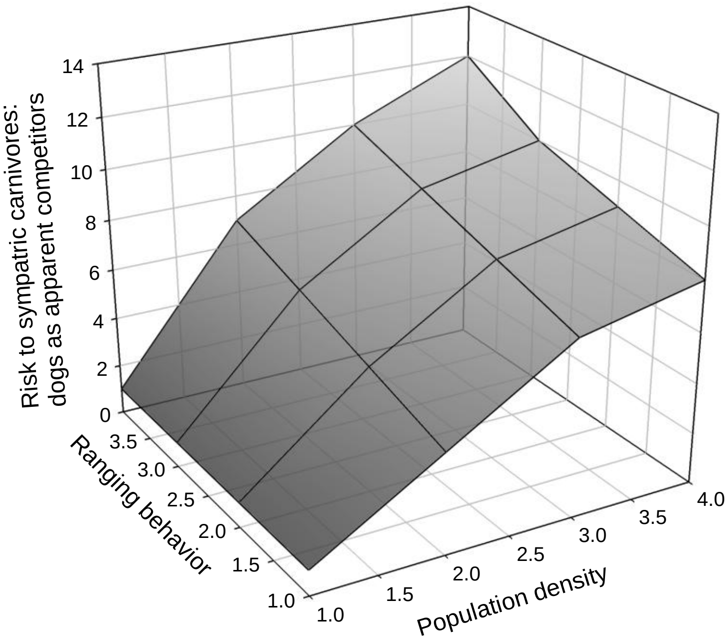
3.0
3.5
Population density
1.0
1.5
2.0
2.5
3.0
3.5
4.0

C)



Risk to sympatric carnivores: dogs as apparent competitors
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2
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6
8
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12
14
Ranging behavior
1.0
1.5
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2.5
3.0
3.5
Population density
1.0
1.5
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Chapter 3: SPATIAL ECOLOGY OF THE INDIAN FOX IN A DRY GRASSLAND ECOSYSTEM IN CENTRAL INDIA

ABSTRACT

The Indian fox *Vulpes bengalensis* is reportedly one of the most common carnivores in the rare and declining grassland plains of the Indian subcontinent. Yet little information is available on the habitat ecology of this species. I investigated habitat selection by the Indian fox in a grassland region in central India that represents a mix of natural and human-dominated habitats to discern if and how foxes respond to human encroachment on native habitats. I collected home range and habitat selection data on 32 radio-collared Indian foxes in the Great Indian Bustard Sanctuary, Nannaj, Maharashtra over a one year period. Adult Indian fox 95% kernel density home-range sizes varied between sexes and among seasons. Males had consistently larger home-ranges than females across all seasons but there was no inter-seasonal variation. Females had smaller home-range sizes during the cool-dry season which is also the denning period, than during any other season. Compositional analysis of Indian fox selection of home-ranges at the landscape level showed heavy influence of the presence of grasslands, plantations and fallow land. Indian foxes avoided human modified habitat such as agricultural land and human settlements. The presence of grasslands was also the dominant predictor of Indian fox habitat selection within the home-range as determined by discrete-choice analysis. The results indicate that Indian foxes select for natural grasslands and avoid human-modified habitat. Semi-arid short grasslands are among the most endangered habitats in India and are poorly represented in the protected area network. Indian foxes occur at highest

densities in grassland habitats and thus may be an indicator species for the effects of habitat loss on obligate grassland species.

INTRODUCTION

The Indian fox *Vulpes bengalensis* is an endemic canid of the Indian subcontinent. The species is widespread, ranging from the foothills of the Himalayas in the north to the southern tip of the Indian peninsula, and from Sindh Province of Pakistan east to Bangladesh (Gompper and Vanak 2006; Johnsingh and Jhala 2004). However, little is known about the ecology of the Indian fox. The Indian fox is primarily reported from semi-arid, flat, or undulating terrain in biogeographic zones 3, 4 and 6 of India, which are typically drier biomes characterised by low rainfall and scrub, thorn, or dry deciduous forests, or short grasslands (Rodgers et al. 2000). Although the species is considered to be common, it is encountered at highest frequencies only in protected semi-arid short grasslands and dry scrub areas (Manakadan and Rahmani 2000; Vanak 2005; Vanak and Gompper 2007). Even though these habitats are among the most endangered in India (Rahmani 1989; Singh et al. 2006), and are subject to constant human encroachment, they are rarely the focus of conservation attention. A gap analysis of Indian fox conservation in southern India indicated that less than 2% of these dry biomes are covered under existing protected areas (Vanak et al. in press).

Large contiguous native grassland habitats are now rare or non-existent in India, having been extensively converted to agricultural or industrial purposes or heavily degraded due to grazing pressure (Rahmani 1989; Singh et al. 2006). Conservation efforts or management of such grassland habitats are hampered by a lack of information on the habitat ecology and the spatial use of animals found in human dominated landscapes. Indian foxes represent an example of this lack of information. Based on anecdotal observations, Indian foxes have been described as being generally tolerant of human disturbance and are reportedly found near agricultural fields and human habitations (Johnsingh 1978a; Prater 1980). However, a survey in southern India reported that Indian foxes are more commonly seen in protected grassland habitats than disturbed agricultural landscapes (Vanak 2005). Other species of foxes also vary in their tolerance of human-modified habitats. For example, the kit fox *V. macrotis,* which is similar in body size to the Indian fox, not only tolerates human-altered habitats in California, USA, (Zoellick et al. 2002) but also thrives in one urban area (Cypher and Frost 1999). Conversely, the swift fox *V. velox* prefers continuous native prairies, only marginally uses dry-land agricultural fields, and completely avoids irrigated agricultural lands in Texas, USA (Kamler et al. 2003). The variation in tolerance to human-altered habitats by these fox species is likely a function of the degree of habitat choice specialization, as kit foxes appear to be habitat generalists (Frost 2005) whereas swift foxes are considered to be habitat specialists (Kamler et al. 2003).

To determine whether Indian foxes are tolerant of human-altered landscapes, I examine their home-range selection and habitat use in a fragmented landscape in central India. This area is typical of much of the central Indian plateau, with a mix of native and human altered grassland habitats. It is also home to several endangered species such as the Indian bustard *Ardeotis nigriceps*, Indian grey wolf *Canis lupus pallipes*, and blackbuck *Antilope cervicapra.* Indian foxes are the most common native carnivore in some protected grassland regions (Vanak and Gompper 2007), but I do not know how their habitat selection is affected by human encroachment into native grasslands. Based on recent surveys (Vanak 2005; Vanak and Gompper 2007) I predict that Indian foxes may be more similar to swift foxes in that they will select for native grasslands over disturbed or human-modified habitats.

STUDY AREA AND METHODS

This study was conducted in and around the Great Indian Bustard Sanctuary (GIBS) at Nannaj, Maharashtra, in central India (17° 49’ 40” N and 75° 51’35” E). The sanctuary consists of six protected grassland patches (6 km^2 of 8,496 km^2 GIBS) within a matrix of sugarcane fields, seasonal crops, communal grazing lands, and forestry plantations (Figure 1). The study area is bordered by several villages with a combined human population of approximately 50,000 that is largely dependent on agro-pastoralism (http://solapur.gov.in/htmldocs/dgraphy.htm accessed on 11/Jun/08). This region experiences a wet season from Jul–Oct during which 95% of the precipitation occurs (Temp. range = 16-32 °C, mean annual precipitation = 600mm), a cool-dry from Nov–Feb (Temp. range = 6-37 °C) and a hot-dry season from Mar–Jun (Temp. range =18-47 °C).

The study area consists of a matrix of landuse types: protected grassland, grazing land, ploughed land, agricultural land with standing crops, fallow land, and forestry plantations. The agricultural land and vineyards typically radiate outward from the settlements, gradually taper to fallow lands and then merge with the grassland. The fallow land, grazing land and protected grassland form an intricate complex, the borders of which are not easily discernable in some areas. The focal grassland and fallow complex on which this study occurred is about 17 km long and approximately 3 km wide

(Fig 1.). Interspersed in this swath of habitat are forestry plantations of drought resistant varieties of *Acacia spp.*, *Azadirachta indica*, *Eucalyptus* hybrid and *Glyricidia sepium*. There are also some patches of natural scrub vegetation, consisting of *Zizyphus mauritiana*, *Acacia leucophlea, A. nilotica* and other trees and shrubs characteristic of the Type 6 Tropical Thorn Forest (Champion and Seth 1968). The grassland flora is dominated by *Aristida* spp., *Heterpogon* spp., *Chrysopogon* spp., *Cymbopogon* spp. and *Dicanthium* spp. Besides the Indian fox, other mammal species that inhabit this area are the Indian wolf, blackbuck, golden jackal *C. aureus*, jungle cat *Felis chaus*, and black-naped hare *Lepus nigricollis.*

Capture and Handling

To determine home-range and habitat selection of Indian foxes, I conducted a radio-telemetry study from April 2006 to August 2007. All captures of foxes were conducted in the presence of a wildlife veterinarian. I captured Indian foxes using padded Victor Soft-catch # 1 leg-hold traps at sites pre-baited and monitored for 4-5 days prior to deployment. A radio-transmitter was attached to each trap so that it emitted a signal when the trap was triggered. All foxes were anesthetized with a combination of xylazine hydrochloride and ketamine hydrochloride (Belsare and Vanak in prep) and were ear-tagged with self-piercing monel ear tags (Hasco Tag Company, Dayton KY, USA). I weighed each fox to the nearest 20 g on a digital scale and measured their body dimensions. I estimated age based on body size and tooth wear. Each captured fox was fitted with a 20g ATS model M1930 radio transmitter (149-151 Mhz; Advanced

Telemetry Systems, Isanti, MN, USA) which is <2% of body weight (mean = 2.47 kg, ± 0.06 SE, n = 35). All foxes were kept in a cloth bag until they were fully recovered from the effects of anesthesia (Mean = 37 mins, range = 20 - 59 mins) following which they were released at the capture site.

Radio Telemetry and home-range analysis

Radio-locations of foxes 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, I collected all triangulation data for each non-stationary animal by obtaining simultaneous fixes from at least three stations or within a 2 minute interval. Locations were collected every 28 hr to provide an independent and approximately equal number of locations in every part of the day (Garton et al. 2001).

I conducted a telemetry accuracy assessment to estimate the precision of directional azimuths (White et al. 1990; Withey et al. 2001) by obtaining location estimates for 5-7 test transmitters once a month during tracking sessions. Test transmitters were either placed 15 cm above ground or were fitted to tethered domestic dogs in the study area. In this way I obtained 76 location estimates from 246 azimuths and estimated the precision of telemetry bearings to be 2.43° (±0.47SE). I estimated each location from the azimuths using Lenth's maximum likelihood estimator in program LOAS 4.03 (Ecological Software Solutions LLC, Hegymagas, Hungary).

To calculate home-ranges of the individual foxes, only those animals with ≥30 locations for at least one season were used to estimate utilization distributions (UD), which minimizes potential bias in home-range estimation due to small sample sizes (Kernohan et al. 2001; Seaman et al. 1999). I calculated the utilization distributions using fixed kernel estimators using the KDE function in Matlab (The Mathworks Inc, Natick, MA USA; Beardah and Baxter 1995). Kernel size or bandwidth was selected using the "plug-in" method (Gitzen et al. 2006; Wand and Jones 1995). I excluded the outer 5% of the interpolated UD estimate using Hawth's tools in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA, USA) to reduce potential bias in home-range estimates resulting from extremely low use areas on the tails of the UD. I used two-way Analysis of Variance (ANOVA) to contrast seasonal and gender home-range sizes and unpaired t-tests to compare annual home-range size between sexes.

I estimated overlap of space use and site fidelity within and between sexes and seasons by calculating the Volume of Intersection (VI) index (Fieberg and Kochanny 2005; Kernohan et al. 2001). This index measures the degree of overlap between individual UDs as:

$$VI = \iint \min[\hat{f}_1(x,y), \hat{f}_2(x,y)]dxdy$$

where $\hat{f}_1$and $\hat{f}_2$ are the UDs of animals 1 and 2 respectively. The VI score ranges from 0 (no overlap) to 1 (complete overlap). To determine animal site fidelity, I calculated the VI scores for all combinations of seasonal UDs for all animals. I determined the degree of inter- and intra-sexual territoriality by estimating VI scores for all pairs of animals tracked during the same season and year. I used a script written for ArcView 3.2

(Environmental Systems Research Institute, Redlands, CA, USA) to calculate VI indices across all animal combinations (A. Singh pers comm. Appendix I). I used estimates of overlap only from those animals, whose territorial neighbours were also radio-collared. I omitted from subsequent analysis any pair of individuals with non-adjacent territories with a VI score of <0.02 (as per Lesmeister 2007). I used two-way ANOVA to test whether sex and season affected site fidelity as measured by VI scores. I also tested for differences in the number of associations between individuals across the seasons by comparing the number of inter and intra-sexual overlaps per season. For instance, I tested for seasonal differences in the number of females each male overlapped with using an ANOVA.

Habitat selection analysis

I evaluated second order and third order resource selection by Indian foxes. The second order of selection is the selection of home-range within a geographic range and third order is selection of habitats within the home-range (Johnson 1980). The extent of the intensive study area (130.4 km^2) was defined by calculating a minimum convex polygon around the collective home-ranges of all the study animals (Fig. 1). A multispectral (LISS-IV), high resolution (5.8m) satellite imagery from the Indian Remote Sensing Satellite (IRS-P6) obtained for the month of March 2006 was used to generate a landuse/landcover map of the study area. From the landcover map I determined that the intensive study area consisted of 41% grasslands and plantations, 16% fallow land and 42% of human modified areas (Fig. 3). I over-laid individual UD grids on a GIS layer derived from the landcover map for the study area within ArcGIS 9.1.I used compositional analysis to determine second order resource selection (Aebischer et al. 1993) but with a modification that assigns values based on the UD (Millspaugh et al. 2006). In this way, an individual's use of the habitat is defined by the proportion of UD volume in each habitat type within that individual's home-range (Millspaugh et al. 2006). I used Resource Selection for Windows (RSW) to conduct the compositional analysis (Leban 1999).

I determined third-order resource selection using discrete choice analysis (Cooper and Millspaugh 1999; Cooper and Millspaugh 2001). Discrete choice analysis is advantageous since resource availability can be defined separately for each site. I defined a choice set for each individual as a circular buffer around each used point with a radius derived from the average distance between 28-hr relocations for that individual. In cases where relocations were obtained later than 28 hr, the radius of the buffer was increased correspondingly with the number of days between relocations, i.e. radius=2x, 3x and so on. However, since I was interested in resource selection at the home-range level, I clipped the outer boundaries of all choice-sets to fit within the 95% kernel home-range of that individual. Within each choice-set, I then randomly assigned four available points associated with each used point (Cooper and Millspaugh 1999). I overlaid these points in a GIS with data layers consisting of roads, settlements, water bodies, protected area boundaries and a landcover map. I measured distance from each point in the choice-set to all the features in the GIS and determined the landcover category of each point.

I tested the data for effects of human disturbance, habitat type, and seasonality on habitat use. Human disturbance factors were quantified by distance to nearest roads and settlements. Habitat type was categorised by landcover: grasslands, fallow, plantation, agriculture, ploughed land and bare-soil. I also measured distance to protected area boundary and distance to nearest water source for each location. If the location fell within the protected area, then a value of zero was returned for that point. I used an information-theoretic approach to develop *a priori* models that might best explain the patterns of resource selection (Burnham and Anderson 2002). I developed a global model which included all the above variables. From the global model, I selected variables to fit six sets of sub-global models: human disturbance factors, habitat variables, protection status and combination of human disturbance, habitat variables and protection status (Table 1). I tested for multicollinearity in the data set and excluded fallow land as a variable because its minimum tolerance was <0.0001. All other variables had a tolerance range between 0.560-0.999.

I used Akaike's Information Criterion corrected for small sample size (AIC_c) to assess model weights and ranked candidate models using ΔAIC_c (Burnham and Anderson 2002). I used Akaike weights (w_i) to determine the relative support for a model given the data for the set of models within each season. Since the difference between the top models may not be very large, I accounted for this model uncertainty by averaging the estimates of the coefficients of main effect variables in each model with $\Delta AIC \leq 2$ (Burnham and Anderson 2002). I implemented discrete choice analysis using the PROC MDC function in SAS 9.1 (SAS Institute Inc. Cary, NC).

RESULTS

From April 2006 to May 2007, I captured 40 individual foxes of which 35 were fitted with radio-collars. Location data of ≥ 30 points for at least one season were collected for 32 individuals. I tracked 16 Indian foxes (10 males, 6 females) during the cool-dry season, 26 animals (17 males, 9 females) during the hot-dry season, and 12 animals (6 males, 6 females) during the wet season. Of these I have data on all seasons for seven animals (3 males, 4 females).

I observed significant differences in home-range size among sexes, with males (307.9 ha ± 48 SE) having larger mean home-ranges than females (164.7 ha ± 37.8 SE; t = -2.34, p= 0.025, Table 2). Males also had larger home-range sizes in all seasons compared to females ($F_{1, 48}$= 11.335, P=0.0015, Table 2). Home-range sizes did not differ seasonally within sexes ($F_{2, 48}$=1.598, P= 0.213, Table 2). However, after I removed non-breeding individuals (3 males, 3 females) from the analysis, I found differences in seasonal ranges within breeding females ($F_{2, 14}$=3.67, P= 0.052), but not within males ($F_{2, 17}$=1.72, P= 0.21). Home-range size of breeding females was smaller during the cool-dry season than during the wet season (Fisher's PLSD, p=0.017).

Home-range overlap

Overlap between Indian foxes based on the VI index indicated the existence of adult male-female dyads and strong territoriality between adjacent pairs. Annual intra-pair overlap was moderate to high ($\bar{X}$ VI index = 0.52±0.03 SE, n= 10). However, overlap between adjacent non-pair male-female, male-male and female-female combinations was low to negligible (Table 3). Paired male-female associations showed greater overlap (VI) than unpaired male-female or same sex associations for all seasons ($F_{3, 57}$ =32.54, p<0.0001). There was no difference in the number of male-male ($F_{2, 22}$ =0.49, p=0.62) and female-female ($F_{2, 10}$ =1.07, p=0.38) associations across seasons. Of the 31 male-female combinations that showed concurrent overlap, 21 were between putatively non-paired individuals with low overlap ($\bar{X}$ VI index = 0.07±0.022 SE). Male Indian foxes overlapped with a greater number of females during the wet season than during the subsequent cool-dry season or the hot-dry season ($F_{2, 19}$ =3.53, p=0.049).

Indian foxes displayed low site fidelity between seasons (Fig. 2) as measured by the volume of intersection between adjacent seasons. There was no significant difference in VI scores among foxes across all adjacent seasonal combinations ($F_{2, 23}$ =0.63, p=0.94). There was also no significant difference in site fidelity between sexes for each seasonal combination ($F_{1, 23}$ =0.59, p=0.45).

Habitat selection - Compositional Analysis

Compositional analysis of habitat selection by Indian foxes ranked grassland use as the highest among all seasons followed by fallow land and plantation. There were no significant differences in how foxes selected among habitats between seasons (Table 4, Fig. 3). Human modified habitats such as ploughed land, bare soil, agricultural land and human habitations ranked among the lowest over all seasons (Table 4, Fig. 3).

Discrete choice analysis

The main factors affecting Indian fox use of habitats at the third order of selection within the home-range differed among seasons and no single model best explained patterns of habitat use (Table 5). Four models constituted the choice set for the hot-dry season, five for the wet season and four models for the cool-dry season. For the hot-dry and cool-dry seasons, the model featuring grassland was the top-ranked model, whereas during the wet season, a habitat+disturbance model with grassland, plantation and agricultural land was highest ranked (Table 5).

Within the choice set, the presence of grassland was the most influential covariate among all seasons (Table 5). Other influential covariates included the presence of agriculture and ploughed land. Variables such as distance to roads and distance to settlements were also present in the models, but their weights were very low (Table 6). The model-averaged importance values for each parameter indicated that grassland had a positive influence in explaining fox presence for all seasons (Table 6). For instance, in the hot-dry season, the odds of fox use of an area increased by 1.44 times if the choice-set was a grassland habitat. This figure was 2.09 times and 1.2 times for the wet and cool-dry seasons respectively. In the wet season the presence of plantations had a positive influence and agricultural land had a negative influence on fox selection of habitat. The odds of fox selection of an area increased by 2.2 times if the choice-set included plantations and decreased by 0.55 times if it included agricultural land.

DISCUSSION

Habitat selection

Grassland habitats were consistently selected for within Indian fox home-ranges across all seasons at the landscape level. Although Indian foxes have been described as habitat generalists, occurring in a wide variety of dry habitats (Johnsingh and Jhala 2004), they are most common in dry grassland areas similar to our study site (Gompper and Vanak 2006; Vanak 2005). Indeed grassland habitats made up more than 57% of selected habitats at the landscape level. Native grassland along with plantations and fallow land, constituted 91% of all selected habitats within fox home-ranges.

The importance of grasslands as habitats for Indian foxes is further supported at the third order of selection. The presence of grassland was among the main predictors of fox habitat use among the discrete choice models across all seasons. Fox habitat selection in the wet season was also positively influenced by the presence of plantations, but agricultural land had a negative effect. The negative effect of agricultural land in the wet season in particular is not surprising, since most of the agriculture in this area is rain-fed. With the onset of the monsoons, human activity in the agricultural fields increases, and as a result foxes may avoid using these areas during this season.

In general, both kinds of analyses indicate that Indian foxes avoid human-modified habitats such as agricultural lands, ploughed habitat, and settlements. Thus, Indian foxes are more similar to swift foxes rather than kit foxes, in that they select for natural grasslands over human-modified habitat. The selection for natural grasslands may be a function of food acquisition as Indian foxes are highly dependent on wild caught food such as invertebrates, small mammals, reptiles, birds and seasonal fruit (Vanak Chapter 4). The avoidance of human-modified habitat may be a function of interference competition and predation from free-ranging domestic dogs (Vanak, Chapter 5, 6) as well as poaching by humans, two of the most important causes of mortality for Indian foxes (Vanak, Chapter 1).

Home-range size and overlap

Indian foxes live in pairs, but male foxes had consistently larger home-ranges than females across all seasons. Although male home-ranges did not differ between seasons, female home-ranges decreased in size from the wet season to the cool-dry season. The cool-dry season is the denning period for Indian foxes as most pups are born between December to January (Gompper and Vanak 2006). During this time females restricted most of their movement to the vicinity of the den site (Vanak Chapter 6) resulting in considerably smaller home-range sizes. Consequently the UD values for both males and females show pronounced peaks at breeding den sites during this period.

Individuals of a mated pair of foxes displayed higher intra-pair overlap in home-range than with any combination of adjacent individuals indicating that pairs are highly territorial. However, because males had larger home-ranges than females, more males than females overlapped marginally with neighboring foxes of both sexes. Males also showed marginal overlap with more females during the wet season than during any other season. The courting and mating season for Indian foxes occurs towards the end of the wet season and it is possible that males explore the possibility of extra-pair copulations beyond their own territories. Such wider ranging during the breeding season and extra-pair paternity has been observed for several other canids including jackals, *C. mesomelas* and *C. adustus* (Loveridge and Macdonald 2003), red foxes *V. vulpes* (Cavallini 1996; Voigt and Macdonald 1984; White et al. 1996), island foxes, *Urocyon littoralis* (Roemer et al. 2001) and swift foxes (Kitchen et al. 2005).

There was a distinct shift in patterns of home-range by Indian foxes use between seasons as evidenced by the low site fidelity observed between seasons. This was driven primarily by shifts in habitat selection and den use, either for day-time resting or for breeding. During the hot-dry season foxes used dens as primary day-time roosts, but switched to sheltering under shrubs with the onset of the wet season.

The home-range dynamics of Indian foxes are similar to that of several other fox species (Kamler et al. 2003; Kitchen et al. 2005; Roemer et al. 2001), and especially to swift foxes, in that their habitat selection is specialized towards grassland habitats. The loss of short grassland habitat is reported to be one of the primary factors leading to declining Indian fox populations (Johnsingh and Jhala 2004). Given the results of our analysis, this is not surprising. In India, dry habitats are classified as wastelands and are being aggressively converted to other uses such as agro-forestry and bio-fuel plantations (Singh et al. 2006). Indian foxes therefore, have the potential to be good indicators of grassland health. As Vanak et al. (in press) have pointed out, greater protection of dry-land biomes would be positive, not only for the Indian fox, but also for other obligate dry grassland species such as the critically endangered Indian bustard, Indian grey wolf, and blackbuck.

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Table 1. Hypotheses, a priori models, model structure and expected result explaining Indian fox selection of habitat within the home-range.

Hypothesis	Model	Model Structure	Expected result
1) Habitat Positive effect of grasslands	Grass	$\beta_0 + \beta_{grass}$	$\beta_{grass}>0$
2) Habitat Positive effect of grasslands and plantations	Grs + Plnt	$\beta_0 + \beta_{grass} + \beta_{plnt}$	$\beta_{grass}>0$, $\beta_{plnt}>0$
3) Habitat Negative effect of distance to water	Dist_water	$\beta_0 + \beta_{water}$	$\beta_{water}<0$
4) Protection Negative effect of distance to PA	Dist_PA	$\beta_0 + \beta_{PA}$	$\beta_{PA}<0$
5) Habitat+Protection Positive effects of grassland and negative effects of distance to PA and water	Grs + Dist_PA + Dist_water	$\beta_0 + \beta_{grass} + \beta_{water} + \beta_{PA}$	$\beta_{grass}>0$, $\beta_{water}<0$, $\beta_{PA}<0$
6) Habitat+Protection Positive effects of grassland and plantations and negative effects of distance to PA and water	Grs + Plnt + Dist_PA + Dist_water	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{water} + \beta_{PA}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{water}<0$, $\beta_{PA}<0$
7) Disturbance Negative effects of agriculture, ploughed land and bare soil and positive effects of distance to buildings and roads	Ag+ Plgh+ Soil + Dist_Bld + Dist_Rd	$\beta_0 + \beta_{Ag} + \beta_{Plgh} + \beta_{soil} + \beta_{build} + \beta_{Rd}$	$\beta_{Ag}<0$, $\beta_{Plgh}<0$, $\beta_{soil}<0$, $\beta_{build}>0$, $\beta_{Rd}>0$
8) Disturbance+Habitat Negative effects of agriculture and positive effects of grassland and plantation	Grs + Plnt + Agri	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$
9) Disturbance+Habitat Negative effects of agriculture and ploughed land and positive effects of grassland and plantation	Grs + Plnt + Agri + Plgh	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag} + \beta_{Plgh}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh}<0$,
10) Disturbance+Habitat Positive effects of grassland and distance to buildings	Grs + Dist_Bld	$\beta_0 + \beta_{grass} + \beta_{build}$	$\beta_{grass}>0$, $\beta_{build}>0$
11) Disturbance+Habitat Negative effects of agriculture, ploughed land and bare soil and positive effects of grassland	Grs + Plnt + Agri + Soil + Plgh	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag} + \beta_{Plgh} + \beta_{soil}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh}<0$, $\beta_{soil}<0$

and plantation			
12) Disturbance+Habitat Positive effects of grassland, plantation and distance to roads and buildings	Grs + Plnt + Dist_Rd + Dist_Bld	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{build} + \beta_{Rd}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{build}>0$, $\beta_{Rd}>0$
13) Disturbance+Habitat Negative effects of agriculture, ploughed land and positive effects of grassland, plantation and distance to roads and buildings	Grs + Plnt + Agri + Plgh + Dist_Rd + Dist_Bld	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag} + \beta_{Plgh} + \beta_{build} + \beta_{Rd}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{build}>0$, $\beta_{Rd}>0$
14) Disturbance+Habitat Negative effects of agriculture, ploughed land and bare soil and positive effects of grassland, plantation and distance to roads and buildings	Grs + Plnt + Agri + Plgh + Soil + Dist_Rd + Dist_Bld	$\beta_0+ \beta_{grass}+ \beta_{plnt} +\beta_{Ag}+ \beta_{Plgh} + \beta_{soil} + \beta_{build} + \beta_{Rd}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{soil}<0$, $\beta_{build}>0$, $\beta_{Rd}>0$
15) Disturbance+Habitat Negative effects of agriculture, ploughed land, bare soil and distance to water and positive effects of grassland, plantation and distance to roads and buildings	Grs + Plnt + Agri + Plgh + Soil + Dist_water + Dist_Rd + Dist_Bld	$\beta_0+ \beta_{grass}+ \beta_{plnt} +\beta_{Ag}+ \beta_{Plgh} + \beta_{soil} +\beta_{water} + \beta_{build} + \beta_{Rd}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{soil}<0$, $\beta_{water} <0$, $\beta_{build}>0$, $\beta_{Rd}>0$
16) Disturbance+Protection Positive effect of distance to roads and buildings and negative effects of distance to PA	Dist_Rd + Dist_Bld + PA	$\beta_0+\beta_{build}+ \beta_{Rd} +\beta_{PA}$	$\beta_{PA}<0$, $\beta_{build}>0$, $\beta_{Rd}>0$

Table 2. Fixed kernel home ranges in ha (95% of utilization distribution by volume) by season and sex of the Indian fox at the Great Indian Bustard Sanctuary from 2006-2007. Rows represent sample size (n), mean (SE), and range.

	Season		
	Cool-dry (Nov – Feb)	Hot-dry (Mar - June)	Wet (Jul - Oct)
Male			
n	10	17	6
mean (SE)	302.48 (56.44)	205.19 (41.53)	423.72 (137.89)
range	108.12 - 597.96	20.37 - 768.90	122.85 - 957.79
Female			
n	6	9	6
mean (SE)	72.95 (11.20)	158.19 (42.19)	160.11(69.86)
range	35.22 - 100.99	30.57- 383.55	11.23 - 471.84

Table 3. Volume of intersection (VI) scores from utilization distributions of paired female-male, unpaired female-male, male-male, and female-female combinations of Indian foxes across three seasons.

	Season		
	Cool-dry (Nov – Feb)	Hot-dry (Mar - June)	Wet (Jul - Oct)
Paired Male-Female			
n	3	9	4
mean (SE)	0.434 (0.067)	0.425 (0.058)	0.443 (0.096)
range	0.303 – 0.523	0.184 – 0.648	0.269 – 0.675
Unpaired Male-Female			
n	7	9	7
mean (SE)	0.014 (0.005)	0.106 (0.043)	0.118 (0.026)
range	0.0001 – 0.031	0.001 – 0.396	0.047 – 0.200
Male-Male			
n	6	11	5
mean (SE)	0.092 (0.031)	0.093 (0.028)	0.104 (0.034)
range	0.023 – 0.213	0.002 – 0.249	0.016 – 0.223
Female-Female			
n	1	4	4
mean (SE)	0.00013	0.060 (0.033)	0.109 (0.058)
range	-	0.003 – 0.130	0.009-0.253

Table 4. Matrices and habitat ranking of Indian fox resource selection in the Great Indian Bustard Sanctuary, India, 2006-2007. The direction of the interaction is indicated with + or -, and --- and +++ represent significant deviation from random at $p<0.05$. Higher ranks indicate higher level of selection.

	Habitat type							
Habitat type	Grass	Fallow	Plantation	Ploughed	Soil	Agriculture	Human habitation	Rank
Cool-Dry								
Grass	.	+++	+++	+++	+++	+++	+++	6
Plantation	- - -	+	.	+++	+++	+++	+++	5
Fallow	- - -	.	-	+++	+++	+++	+++	4
Soil	- - -	- - -	- - -	+	.	+++	+++	3
Ploughed	- - -	- - -	- - -	.	-	+	+++	2
Agriculture	- - -	- - -	- - -	-	- - -	.	+++	1
Human habitation	- - -	- - -	- - -	- - -	- - -	- - -	.	0
Wet								
Grass	.	+++	+++	+++	+++	+++	+++	6
Fallow	- - -	.	+	+++	+++	+++	+++	5
Plantation	- - -	-	.	+++	+++	+++	+++	4
Soil	- - -	- - -	- - -	.	+	+	+++	3
Ploughed	- - -	- - -	- - -	-	.	+	+++	2
Agriculture	- - -	- - -	- - -	-	-	.	+++	1
Human habitation	- - -	- - -	- - -	- - -	- - -	- - -	.	0
Hot-Dry								
Grass	.	+++	+++	+++	+++	+++	+++	6
Fallow	- - -	.	+	+++	+++	+++	+++	5
Plantation	- - -	-	.	+++	+++	+++	+++	4
Ploughed	- - -	- - -	- - -	.	+	+	+++	3
Soil	- - -	- - -	- - -	-	.	+	+++	2
Agriculture	- - -	- - -	- - -	-	-	.	+++	1
Human habitation	- - -	- - -	- - -	- - -	- - -	- - -	.	0

Table 5. *A priori* hypothesized models in the choice set ranked by AIC_c score. Models relate habitat and disturbance variables to Indian fox site selection in the great Indian bustard sanctuary in 2005-2006. Columns include the number of variables (K), Akaike's Information Criterion adjusted for small sample sized (AIC_c), distance from the lowest AIC_c (Δ AIC_c), and Akaike's model weight (w_i).

Hypotheses	K	AIC_c	Δ AIC_c	ω_i
Hot-dry season				
1) Grass	1	2584.889	0	0.258
9) Grs+Plnt+Agri+Plgh	4	2584.923	0.034	0.254
13) Grs+Plnt+Agri+Plgh+Dist_Rd+Dist_Bld	6	2585.314	0.425	0.209
2) Grs+Plnt	2	2586.884	1.99	0.095
Wet season				
8) Grs+Plnt+Agri	3	1698.263	0	0.252
12) Grs+Plnt+Dist_Rd+Dist_Bld	4	1699.095	0.832	0.166
13) Grs+Plnt+Agri+Plgh+Dist_Rd+Dist_Bld	6	1699.400	1.137	0.143
2) Grs+Plnt	3	1699.494	1.231	0.136
9) Grs+Plnt+Agri+Plgh	4	1699.604	1.341	0.129
Cool-dry season				
1) Grass	1	2133.234	0	0.287
2) Grs+Plnt	3	2134.057	0.823	0.190
3) Dist_water	1	2135.086	1.852	0.114
10) Grs+Dist_Build	1	2135.160	1.926	0.109

Table 6. Most influential *a priori* model parameter estimates, odds ratios, 95% confidence intervals of odds ratios, model-averaged parameter estimates and unconditional standard errors (SE) of variables in the top models explaining Indian fox site selection.

Parameter	Model averaged estimate	Uncond. SE	Odds Ratio	Lower CI	Upper CI	Model weights
Hot-dry season						
Grass	0.321	0.018	1.44	1.22	1.71	1.000
Plantation	-0.010	0.142	0.91	0.68	1.22	0.684
Agriculture	-0.159	0.059	0.75	0.35	1.62	0.567
Ploughed land	-0.504	0.262	0.41	0.18	0.92	0.567
Dist. to roads	0.0001	0.0001	1.00	1.00	1.001	0.256
Dist. to buildings	<0.00001	<0.00001	1.00	1.00	1.00	0.256
Wet season						
Grass	0.766	0.016	2.09	1.57	2.77	1.000
Plantation	0.826	0.012	2.20	1.58	3.07	1.000
Agriculture	-0.472	0.151	0.45	0.17	1.17	0.634
Ploughed land	0.080	0.059	1.27	0.72	2.24	0.329
Dist. to roads	0.0002	0.0001	1.001	1.00	1.001	0.000
Dist. to buildings	<0.00001	<0.00001	1.00	0.99	1.001	0.374
Cool-dry season						
Grass	0.177	0.031	1.18	0.97	1.44	0.573
Plantation	0.046	0.012	1.18	0.88	1.60	0.272

Dist. to water	<0.00001	<0.00001	1.00	1.00	1.001	0.162
Dist. to buildings	<0.00001	<0.00001	1.00	1.00	1.001	0.156

Figure 1. Map of study area showing the Great Indian Bustard Sanctuary (white polygons), state highway (white line), major habitat types and minimum convex polygon of combined fox kernel HRs (black polygon). In this imagery from Google Earth, the lighter colored strip in the center of the map is the primary grassland habitat flanked by darker agricultural fields, ploughed lands and villages.

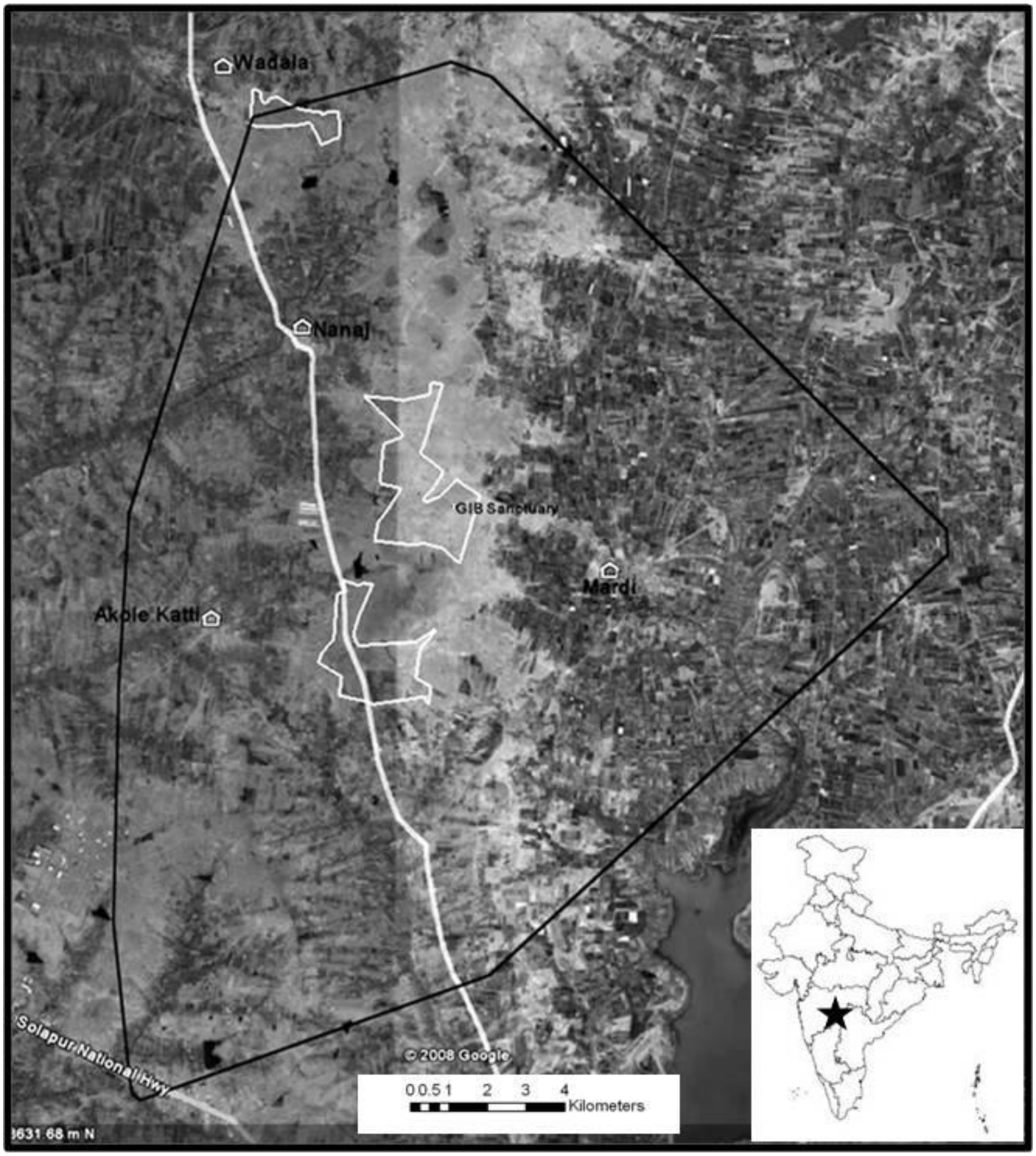


Figure 2. Proportion of habitat available and used during various seasons at the second-order level by Indian foxes.

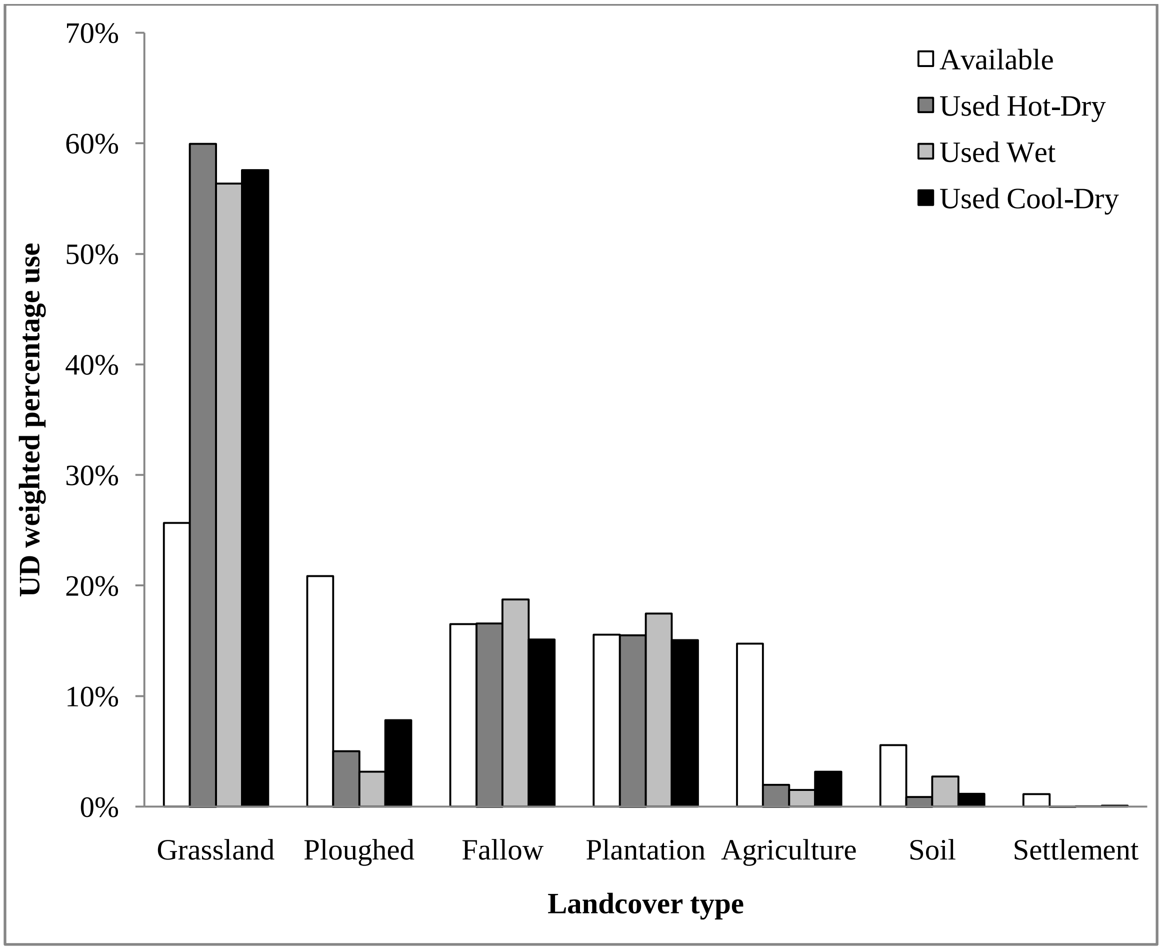
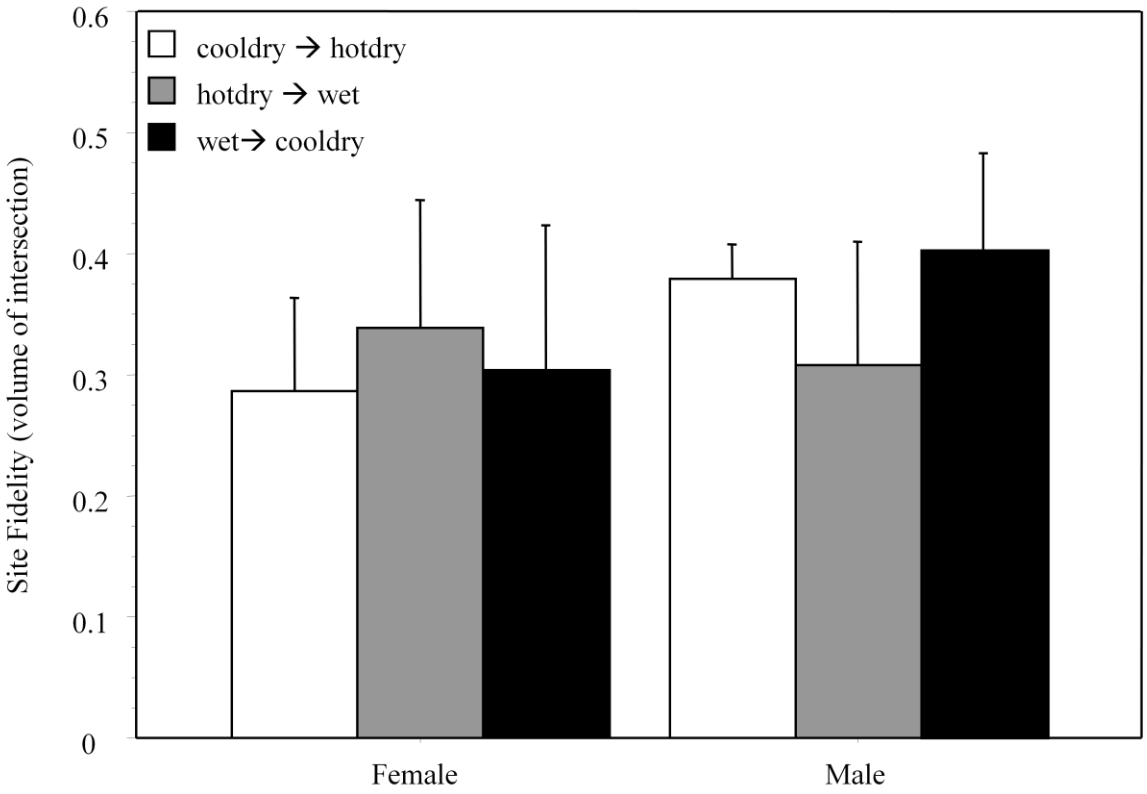


Figure 3. Site fidelity between consecutive seasons as measured by volume of intersection (Mean ± SE). There was no significant difference in site fidelity between seasons and sexes.



Chapter 4: DIETARY NICHE SEPARATION BETWEEN SYMPATRIC FREE-RANGING DOMESTIC DOGS AND INDIAN FOXES IN CENTRAL INDIA

ABSTRACT

The structure of carnivore communities is heavily influenced by resource driven intraguild competition. Larger bodied carnivores can have a profound effect on the resource use, density and distribution of smaller carnivores through aggression, displacement and predation. In this context, the competitive dynamics between domestic and native carnivores is poorly studied. I examined competition for food between sympatric populations of domestic dogs *Canis familiaris* and Indian foxes *Vulpes bengalensis*, through dietary analysis in a protected dry grassland habitat in central India where dogs are known to kill foxes and foxes avoid dogs at food resources. Dogs subsisted largely on human derived material from direct feeding, and scavenging on garbage, crop residue and livestock carcasses (83% relative occurrence). Wild caught foods constituted only 11% relative occurrence of dog diet. Indian foxes were omnivorous and included a wide variety of food types in their diet. The majority of Indian fox diet consisted of invertebrates (33% relative occurrence), rodents (20% relative occurrence) and fruits of *Zizyphus mauritiana* (18.5% relative occurrence). Indian foxes did not include any human derived material, nor did they scavenge from large mammal carcasses, and included only a small portion of agricultural produce in their diet. The diet of free-ranging domestic dogs is typical of dogs from other parts of the world. However, the low contribution of human-derived food sources to the diet of Indian foxes was surprising since the species is a generalist carnivore. Although there

was limited dietary overlap between dogs and foxes in this study, I discuss the possibility that dogs may be preventing foxes from accessing agricultural lands and human associated foods by interference competition.

INTRODUCTION

Competition between sympatric carnivores can have dramatic effects on the structure of carnivore communities (Caro and Stoner 2003; Palomares and Caro 1999). In particular, interference competition is a fundamental feature of carnivore communities (Linnell and Strand 2000) and has been well documented in the Canidae (Berger and Gese 2007; Johnson et al. 1996). The directionality of the interactions is driven by body size, with larger carnivores displacing or killing smaller carnivores (Creel et al. 2001; Johnson et al. 1996; Palomares and Caro 1999). Competition for resources is assumed to be the main driver of these interactions (Holt and Polis 1997) because carnivores with greater dietary overlap also display the most intense competition (Creel et al. 2001; Linnell and Strand 2000).

Given the importance of intra-guild competitive dynamics among carnivores, and the potential for large carnivores to negatively influence smaller carnivores, it is surprising that the extent of resource competition between native and domestic free-ranging carnivores such as the dog *Canis familiaris* is relatively unstudied. The domestic dog is probably the most numerous carnivore in the world today (Daniels and Bekoff 1989; Wandeler et al. 1993; WHO/WSPA 1990), and in much of the world dogs are free-ranging. Free-ranging dogs may be owned or affiliated with humans, but because they are free-ranging, they can interact with local wildlife as predators, prey, competitors, and reservoirs or vectors of diseases (Butler et al. 2004; Edgaonkar and Chellam 2002; Fiorello et al. 2006; Funk et al. 2001; Kruuk and Snell 1981). Despite massive global populations of dogs in rural or natural environments, outside of Australia (Glen and Dickman 2008; Glen et al. 2006; Mitchell and Banks 2005) only a handful of studies have quantified the diets of free-ranging dogs (Atickem 2003; Butler and du Toit 2002; Butler et al. 2004; Campos et al. 2007).

Although dogs are known to kill and feed on wildlife, most of the information on the diet of dogs has come from anecdotal reports or from studies focused on specific wild prey species (Lowry and McArthur 1978; Manor and Saltz 2004; Yanes and Suárez 1996). Most of these studies indicate that although free-ranging dogs may supplement their diets with wild caught food, they rely extensively on human-derived food (Campos et al. 2007; Kruuk and Snell 1981) either through direct feeding (Meek 1999; Scott and Causey 1973) or scavenging (Boitani et al. 1995; Daniels and Bekoff 1989). This dependence on human derived food is one of the main criteria for distinguishing free-ranging and truly feral dogs (Boitani and Ciucci 1995; Green and Gipson 1994).

Only a few studies have examined the role of free-ranging dogs as competitors for resources with wild carnivores (Boitani et al. 1995; Butler et al. 2004). Herein I examine the potential for resource competition between free-ranging dogs and a little studied canid, the Indian fox *Vulpes bengalensis*, in a semi-arid grassland ecosystem of central India using data on dietary overlap. The Indian fox is a small (mean adult body weight ≈ 2.5kg; Vanak 2007) crepuscular to nocturnal canid found in open short grassland habitats (Gompper and Vanak 2006; Vanak and Gompper 2007). This species is endemic to the Indian subcontinent but despite being one of the most common canids, little is known about the basic ecology of this species. It is described as an opportunistic omnivore that depends on small vertebrates, invertebrates and fruits for the majority of its dietary needs (Gompper and Vanak 2006; Johnsingh and Jhala 2004).

I expected that competition between dogs and Indian foxes would be high for several reasons. First, experimental analyses have shown that Indian foxes avoid foraging from food patches when dogs are present (Vanak, Chapter 6). Secondly, telemetry-based data show that dogs are an important cause of Indian fox mortality by direct predation and spread of disease (Vanak 2007, Appendix I). Finally, similar studies in Australian systems have shown high dietary overlap and competitive exclusion of introduced red foxes, *V. Vulpes* by Australian wild dogs (Glen and Dickman 2008; Mitchell and Banks 2005).

MATERIALS AND METHODS

Study Area

This study was conducted in the Great Indian Bustard Sanctuary (GIBS) at Nannaj, Maharashtra, in central India (17° 49’ 40”N and 75° 51’35” E). The sanctuary consists of 6 protected grassland patches within a matrix of sugarcane fields, seasonal crops, communal grazing lands, and forestry plantations. The study area is bordered by several villages with a combined human population of approximately 50,000 largely dependent on agro-pastoralism (http://solapur.gov.in/htmldocs/dgraphy.htm accessed on 11/Jun/08). This region experiences a wet season from Jul–Oct during which 95% of the precipitation occurs (Temp. range = 16-32 °C, mean annual precipitation = 600mm), a cool-dry from Nov–Feb (Temp. range = 6-37 °C) and a hot-dry season from Mar–Jun (Temp. range =18-47 °C).

Indian foxes are a common carnivore in the natural grassland habitats of GIBS, as they are in many grassland habitats of India (Vanak and Gompper 2007), and are also regularly observed in surrounding grazing and agricultural lands (Vanak 2007). Dogs are ubiquitous in the study area and occur at high densities ranging from 24 dogs/km^2 in farm lands to 113 dogs/km^2 in the villages (Vanak 2007). Free-ranging adult dogs in this area weigh approximately 17 kg (Vanak 2007) and may be grouped into three categories: 1) herding dogs that accompany grazing livestock in grasslands during the day, 2) farm dogs that are a continuous presence on the interface between farmlands and natural grasslands, and 3) village dogs that may occasionally pass through fox habitat.

Dietary Analyses

I determined the diet of dogs and Indian foxes by fecal analysis. Scats from dogs were collected opportunistically every month from the vicinity of farms and in grassland habitat outside villages where known ear-tagged and radio collared dogs were observed (see Vanak 2007). Village dogs rarely ventured into grassland habitats and I did not collect scats from within the villages thus restricting our sampling to mainly herding and farm dogs. Dog scats were distinguished from wolf scats based on size and shape (Habib 2007).

Scats of Indian foxes were collected every month from the vicinity of dens of active radio collared foxes (n = 23) and from trails used by foxes that I regularly monitored. Fox scats were differentiated from scats of dogs and other carnivores based on size and shape (Vanak and Mukherjee in press). Although I collected both adult and pup scats from den sites, I only report results from analyses of adult scats since I do not have comparable data from domestic dog pups. Only recent scats with no signs of color loss or perceptible erosion were collected (after List et al. 2003).

All scats were placed in paper bags marked with the date and site of collection and air-dried for 7 to 10 days. Dried scats were softened with 90% alcohol, broken apart in a Petri-dish and examined macroscopically (Reynolds and Aebischer 1991). Mammalian hairs were cleared with xylene and mounted on glass slide using DPX mountant to observe medullary patterns. Casts of cuticular scale patterns of mammalian hair were made on clear nail enamel polish (Mukherjee et al. 1994). Mammalian jaw fragments were cleaned and photographed for comparison with known specimens (Mukherjee et al. 2004). Reptile scales were mounted on glass slides using DPX mountant to examine scale micro-ornamentation (Joseph et al. 2007).

Regionally derived reference collections were used to identify the remains to the lowest taxonomic category. Mammals were identified to genus or species and reptiles were identified to order or species. Feathers and egg fragments were grouped as bird remains (except for poultry feathers), but were not identified further due to inadequate reference materials. Invertebrates were classified as termites, ants, beetles, and grasshoppers, or were classified as “others” (other insects, scorpions, and centipedes) if they were found in less than 5% of scats. Scats also contained human derived materials (HDM), which included garbage, millet bread, and human feces. These were identified by texture and appearance (e.g. grains of millet bread, remains of plastic bags). Dogs were regularly observed consuming human feces and remains of undigested tomato skin in dog scats confirms this.

Because identification of dietary remains was sometimes limited to the family level or higher, the number of taxonomically different food items under-represents the true number of species consumed. To standardize for differences in the level of identification of taxa consumed by dogs and foxes, I grouped items into 8 broad categories: invertebrates, mammals, birds, reptiles, seeds, vegetation, crops and human derived material (HDM).

Representation of each food type in the diet was expressed as frequency of occurrence (FO), defined as:

$$FO = \frac{s(100)}{N}$$

where s is the number of samples containing each prey type and N is the total number of samples, and as relative percent occurrence (RO), defined as:

$$RO = \frac{p(100)}{T}$$

where p is the number of occurrences of each prey type and T is total occurrences of all prey types in all samples which represents the relative importance of a given food type in the diet of the species (Loveridge and Macdonald 2003). Although FO overemphasizes the importance of small prey types (Loveridge and Macdonald 2003), I used this measure because I am mainly interested in comparing diets between species.

I compared the FO of each food item between seasons and species using a χ^2 test (Reynolds and Aebischer 1991). I calculated the dietary diversity (B_A) for both species using the Levins' Index (Krebs 1999; Levins 1968),

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

where p_i is the RO of each dietary item, and n is the total number of dietary items.

Dietary overlap (O_{fd}) between species was discerned by RO,

$$O_{fd} = \frac{\sum f_i d_i}{\sqrt{(\sum f_i^2 \sum d_i^2)}}$$

where f_i is the RO of food item i in foxes and d_i is the RO of food item i in dogs (Pianka 1973). This index varies between 0 (complete separation) to 1 (complete overlap). I used ECOSIM 7 software (Gotelli and Entsminger 2006) to test for significance of overall and intra-season niche overlap by comparing observed values with values obtained from 10,000 random iterations of the original matrices.

RESULTS

From November 2005 to July 2007 I collected 436 Indian fox scats (Cool-dry season = 236; Hot-dry season = 145; wet season = 55) and 320 domestic dog scats (Cool-dry = 90; Hot-dry = 150; wet = 80). Scat numbers are low for the wet season as rains and dung beetle activity quickly eroded fresh scats. I identified 48 items (fox = 27, dog = 21) to the lowest taxonomic level possible. However, much identification was limited to higher taxonomic levels and therefore the number of food items is likely an underrepresentation of the actual number of species consumed. This underrepresentation may be greater for foxes than for dogs due to the more diverse diets of foxes (see below).

Diet of free-ranging dogs

I identified several categories of food used by dogs, including HDM (mainly from household garbage, millet bread, human feces), domestic ungulates (cattle, water buffalo, goat and sheep), two occurrences of blackbuck *Antilope cervicapra*, rodents *Golunda elliotti, Rattus* spp., lagomorph *Lepus nigricollis*, birds (poultry), reptiles (mainly *Calotes versicolor*), insects (mainly Coleopterans), fruit (*Zizyphus*, grapes, guava) and crops (millet, sorghum, corn, wheat, peanut). The main constituent of the diet of free-ranging dogs over all seasons was HDM, which occurred in 90.6% of all scats and comprised 40% of all items found in dog diet (Table 1). Crops such as millet, sorghum, and corn were the second most common food item consumed by dogs, collectively occurring in almost 52% (FO) of all scats and comprising 23.3% (RO) of dog diet. The third most important component of the diets of dogs were the remains of domestic ungulates (41% FO, 18.3% RO), which they likely scavenged. Wild-caught food such as small mammals, birds, reptiles and invertebrates combined contributed a relatively small proportion to the diet of dogs. Remains of wild-caught food were found in 22.5% of all dog scats, and contributed 10.1% (RO) to their diets.

There was no significant difference in the consumption of HDM and crops across seasons. The diets of dogs appeared relatively stable across all seasons, and apart from large mammal remains, seasonal differences were observed in only three other minor categories (Table 2). Dogs consumed significantly less carrion during the hot-dry season than during the other two seasons (Table 2). Birds (poultry) and beetles were consumed in significantly greater portions during the wet season, and the fruits of *Zizyphus* were consumed in greater proportion during the cool-dry season. The overall niche breadth of dogs was 2.75.

Diet of Indian fox

I identified a diversity of food items in scats of Indian fox including lagomorph (*Lepus nigricollis*), rodents (*Golunda elliotti, Tatera indica, Mus* spp., *Rattus* spp.), shrews (*Suncus* spp.), birds (including eggs), reptiles (*Calotes versicolor, Sitana ponticeriana*, Scincidae, and *Echis carinatus* and other snakes), fruits (*Zizyphus* spp., *Cassia* spp.), crops (corn, sorghum, millet, grapes, melons, gourds), insects (termites, ants, beetles, grasshoppers) and other invertebrates (scorpions, centipedes). Vegetation and soil were also found in a large percentage of scats, and were considered non-dietary items.

The main constituent of Indian fox diet was invertebrates (termites, ants, grasshoppers and beetles) based on an RO of 33% (Table 1). Small mammals occurred in 57.1% of all scats with a RO of 20.6%. Among the small mammals eaten by Indian fox, the Indian bush rat *Golunda elliotti* was the most common prey (FO = 61.4%), followed by mice (*Mus* spp.; FO = 24%) and Indian hare *Lepus nigricollis* (FO = 19.6%). Other small mammals detected in the feces of Indian fox were Indian gerbils *Tatera indica*, shrews *Suncus* spp, and palm squirrels *Funambulus tristriatus*. The third most important food item eaten by Indian fox was the fruits of *Zizyphus mauritiana* (FO = 51.4%, RO = 18.5%). Other food items in Indian fox diet included reptiles and birds. Reptiles were found in 35.8% FO of all fox scats and contributed nearly 13% RO to fox diet. Of these, the garden lizard *Calotes versicolor* was the most commonly consumed, being found in 83% of all scats that contained reptile scales, followed by saw-scaled vipers *Echis carinatus* which were found in 15% of all reptile remains. Bird remains consisted mostly of ground nesting species such as quails (*Perdicula* spp.), partridges (*Francolinus* spp.) and sandgrouse (*Pterocles* spp.) although I was unable to more fully verify this due to insufficient reference materials.

There was a general lack of human-associated foods in Indian fox diet; HDM consisting of garbage or other human refuse was not found in any fox scat. Foxes consumed a very small proportion of agricultural produce including grapes, corn, millet, gourds and melons, but all these combined contributed < 3% RO to fox diet (Table 1). There was no indication that foxes scavenged from large-mammal carcasses, and the overall niche breadth (B_a) for foxes was 6.1.

The importance of various types of invertebrates differed among seasons; e.g. termites were consumed more during the hot-dry season and beetles were consumed more during the wet season (Table 2). Mammals remained an important part of fox diet all year round as there was no significant seasonal difference in the occurrence of small mammal remains in fox scats (Table 2). *Zizyphus* fruits formed the main component of Indian fox diet during the cool-dry season (RO = 24.2%) and were consumed in significantly lower proportions in other seasons (Table 2). There were no seasonal differences in reptile and bird occurrence in fox diet.

Dietary comparisons

Indian foxes and dogs exhibited low dietary overlap (Pianka's index O_{fd} = 0.13) and this overlap was non-significant at the 5% level based on the randomly simulated matrices (mean = 0.38, var = 0.027, $P_{obs>exp}$ = 0.96). A number of food items consumed by dogs were absent from the diets of foxes, such as HDM and large mammals. Similarly, invertebrates were a minor component of the diets of dogs (Table 1). There were significant quantitative and taxonomic differences in diet within all the categories (except grapes) that dogs and foxes overlapped (Table 1). Small mammals, birds, reptiles, invertebrates, *Zizyphus* and other vegetation were consumed in proportionally lower amounts by dogs in comparison to foxes. Crops were the only shared food item that dogs consumed more than foxes (Table 1).

DISCUSSION

The diet of dogs in the GIBS appeared typical of that reported from other rural areas of the world, such as Zimbabwe, Ethiopia and Italy where free-ranging dogs subsist largely on human-derived food materials. For example, Butler and Du Toit (2002) reported that 88% of dog diet in rural Zimbabwe consisted of human-derived food.

Boitani et al. (1995) reported that free-ranging dogs in rural Italy depend on garbage dumps as a main source of food. Dogs in rural Ethiopia depend on HDM for > 90% of their dietary needs (Atickem 2003). In our study area, human-derived food, crops and large mammal remains formed 83% (RO) of the diet while wild-caught food contributed just 11% (RO) to their overall diet. Dogs are either fed left over food from households that they are associated with, or scavenge garbage and human feces from the vicinity of houses and farmlands.

Large mammal remains found in dog diet were mainly from livestock carcasses that villagers discarded on the periphery of the village. Goat and sheep, however, were most likely scavenged from wolf *C. lupus* kills; there was no evidence of dogs attacking and killing livestock as has been reported from other areas (Boitani et al. 1995). The availability of livestock carcasses, particularly sheep and goats decreases in the hot-dry season because villagers move their livestock to better pastures or stall feed valuable milk cattle during the height of the dry-season. Blackbuck remains in dog diet may be a result of predation as seen in other sites (Jhala 1993) or scavenging, most likely from wolf kills.

Seasonal differences were seen in three minor categories of importance in dog diet: birds, beetles and *Zizyphus* fruits. The monsoon season is a period of high mortality among chicken in poultry farms near the village of Nannaj, and dogs were regularly seen scavenging partially incinerated poultry from carcass dumps. The wet season is also a time of high insect abundance, and dogs often forage for large scarabid beetles then. Dogs also consumed *Zizyphus* fruits during the peak fruiting season between November and January. However, no significant seasonal differences in other major food types were observed (HDM, crops). This is unsurprising because HDM and staple crops such as corn, sorghum and millets are a stable source of food for dogs throughout the year.

Indian foxes had a diet typical of fox species in semi-arid regions, generally including a wide variety of food types. Indian foxes have been described as opportunistic omnivores: small mammals, fruits and insects are reported to form a major component of their diet (Gompper and Vanak 2006; Home 2005; Johnsingh 1978b; Manakadan and Rahmani 2000). Indian foxes had a much wider niche breadth than dogs. Invertebrates, small mammals, *Zizyphus* fruits and reptiles combined contributed > 85% to Indian fox diet (Table 1). Seasonal differences were seen in several important categories of Indian fox diet (Table 2), presumably due to the changes in availability of fruits and invertebrates. For example, the cool-dry season is the peak fruiting season for *Zizyphus* and this item was heavily consumed by foxes, to the extent that most scats collected from this period consist almost entirely of *Zizyphus* berries. Beetles were consumed more during the wet season, but during the hot-dry season when insect resources were scarce, foxes dug-up termitaria in search of termites. Vegetable farming in this area is highly dependent on monsoonal rains, and therefore vegetable crops such as melons and gourds are easily available and thus consumed more by foxes during the wet season.

Overall, dogs and Indian foxes in this region had low and non-significant dietary niche overlap. Foxes relied almost entirely on wild caught food, while dogs relied heavily on human-derived food. This pattern does not match that found among introduced red foxes and wild dogs in Australia. Several studies in Australia have found high overlap between wild dog and red fox diets (Glen and Dickman 2008; Mitchell and Banks 2005). Most free-ranging dogs in Australia are wild or truly feral and thus, by avoiding human habitats, they are not dependant on human-derived food. On the other hand, free-ranging dogs in other parts of the world are largely dependent on HDM (Atickem 2003; Butler and du Toit 2002; Daniels and Bekoff 1989).

Unlike dogs, Indian foxes consumed a very small proportion of HDM (<3% RO including grapes and crops). Foxes that subsist on or include HDM and agricultural crops in their diet have been found to have better body condition and size (Cypher and Frost 1999; Yom-Tov et al. 2007). The lack of HDM in the diets of Indian fox was surprising because the species is similar to other generalist opportunistic fox species and will readily consume human provided food when available (Vanak, Chapter 6). In general, several studies have shown other vulpine foxes living in rural, urban or suburban habitats to include HDM in their diet (e.g. red fox - Contesse et al. 2004; Blanford's fox *V. cana* - Geffen et al. 1992; kit fox *V. macrotis* - Warrick et al. 2007). The limited consumption of agricultural crops and locally grown fruits and vegetables such as grapes, pomegranate, gourds and melons was also contrary to what is known for other fox species. Red foxes are known to include a wide variety of human-derived fruits and vegetables in their diet (e.g. Contesse et al. 2004), as are swift foxes *V. velox* and kit foxes (Kamler et al. 2007; Warrick et al. 2007).

Indian foxes in this area did not scavenge on large mammals, whereas this food contributed up to 5% of fox diet in Gujarat, western India (Home 2005). The Gujarat study area has a low human population, low agricultural productivity and a general lack of dogs (Home 2005). In contrast, most of the grassland habitat in our study area is fragmented and the landscape is dominated by agriculture and human settlements. This human-modified landscape may, however, represent a foraging opportunity for foxes in terms of increased rodent abundance (Bhaskaran 2006; Mukherjee et al. 2004), HDM, and agricultural produce.

Even though our findings suggest low resource competition between these two species our data does not exclude the possibility that dogs are preventing Indian foxes from accessing HDM and agricultural produce (especially seasonally abundant foods such as grapes). In our study area, human and domestic dog densities are high, and dogs are the most common carnivore on the landscape. Therefore, the likelihood of foxes encountering both human modified landscapes and dogs in this area is high. Interference competition and intraguild predation are common interactions between Indian foxes and dogs in this area (Vanak 2007; Vanak, Chapter 6) as they are among native canids (Johnson et al. 1996). Thus, given that the directionality of these interactions is driven by body size (Creel et al. 2001; Johnson et al. 1996; Palomares and Caro 1999), it is very likely that dogs are directly or indirectly excluding Indian foxes from accessing possible resources in this area.

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Table 1. Comparison of the diets of the domestic dog and Indian fox in the Great Indian Bustard Sanctuary, Nannaj, India (*indicates significant differences at P<0.05 and ** indicates significant differences at P<0.0001).

Food category	*Frequency of occurrence*			*Relative occurrence*	
	Domestic dog	Indian fox	χ^2	Domestic dog	Indian fox
Human-derived	90.63	0.00	-	40.73	0.00
Large Mammal (Total)	40.63	0.00	-	18.26	0.00
Cattle	13.75			6.18	
Water buffalo	3.44			1.54	
Goat	22.19			9.97	
Sheep	6.56			2.95	
Blackbuck *Antilope cervicapra*	0.63			0.28	
Unidentified	2.50			1.12	
Small Mammal (Total)	5	57.11	43.61**	2.25	20.61
Bush Rat *Golunda elliotti*	1.56	35.06		0.7	12.65
Mice *Mus* spp.	0.00	13.74		0.00	4.96
Indian gerbil *Tatera indica*	0.00	4.34		0.00	1.57
Rats *Rattus* spp.	1.56	0.00		0.7	0.00
Palm squirrel *Funambulus* spp.	0.00	1.08		0.00	0.39
Shrews *Suncus* spp.	0.00	1.81		0.00	0.65
Indian hare *Lepus nigricollis*	0.63	11.21		0.28	4.04
Unidentified	1.25	9.40		0.58	3.39
Bird	8.13	19.72	5.14*	3.65	7.12
Reptile	1.25	35.78	33.12**	0.56	12.91
Garden lizard *Calotes versicolor*	1.25	29.66		0.56	10.71
Saw-scaled viper *Echis carninatus*		5.50			1.99
Fan-throated lizard *Sitana ponticeriana*		3.36			1.21
Unid snakes and skinks		3.36			1.21
Invertebrates					
Isoptera	0.00	43.81	-	0.00	15.81
Hymenoptera	0.00	6.65	-	0.00	2.40
Orthoptera	0.00	13.76	-	0.00	4.97
Coleoptera	6.88	28.21	11.11**	3.12	10.18
Others+Unid	2.5	1.15	-	1.13	0.41
Zizyphus mauritiana	11.25	51.38	25.81**	5.06	18.54
Grapes	3.75	3.67	0.00	1.69	1.32
Crops	51.88	4.36	41.43**	23.32	1.57
Vegetation	1.88	11.47	6.23*	0.84	4.14

Table 2. Seasonal occurrences of food categories in the diets of the Indian fox and domestic dog in the Great Indian Bustard Sanctuary, Nannaj, India (*indicates significant differences at $P<0.05$ and ** indicates significant differences at $P<0.001$).

Food category	*Indian fox*							*Domestic dog*						
	Frequency occurrence				Relative occurrence			Frequency occurrence				Relative occurrence		
	Cool-Dry	Hot-Dry	Wet	χ^2	Cool-Dry	Hot-Dry	Wet	Cool-Dry	Hot-Dry	Wet	χ^2	Cool-Dry	Hot-Dry	Wet
Human-derived	0.00	0.00	0.00	-	0.00	0.00	0.00	93.33	92.00	82.93	0.679	33.33	56.56	31.48
Large mammal	0.00	0.00	0.00	-	0.00	0.00	0.00	64.44	10.67	68.29	42.48**	23.02	6.56	25.93
Small mammal	57.2	53.79	65.45	1.102	20.58	18.62	27.07	4.44	4.00	7.32	1.2	1.59	2.46	2.78
Bird	19.92	22.76	10.91	4.33	7.16	7.88	4.51	6.67	2.67	19.51	15.8**	8.73	3.28	2.78
Reptile	37.71	35.86	27.27	2.04	13.57	12.41	11.28	0.00	0.00	4.88	-	4.76	0.00	0.00
Termites	37.71	57.93	32.73	8.14*	13.57	20.05	13.53	-	-	-	-	-	-	-
Ants	8.05	5.52	3.64	1.33	2.90	1.91	1.50	-	-	-	-	-	-	-
Grasshoppers	11.02	17.24	16.36	1.41	3.96	5.97	6.77	-	-	-	-	-	-	-
Coleopterans	27.54	24.14	41.82	5.72*	9.91	8.35	17.29	6.67	0.00	24.39	26.7**	22.22	28.69	18.52
Zizyphus	65.68	40.00	20.00	25.33**	23.63	13.84	8.27	24.44	5.33	7.32	18.16**	1.59	0.82	0.00
Grapes	5.93	1.38	0.00	-	2.13	0.48	0.00	13.33	0.00	0.00	-	2.38	1.64	7.41
Crops	0.42	5.52	18.18	18.32**	0.15	1.91	7.52	62.22	46.67	48.78	2.52	0.00	0.00	1.85
Vegetation	5.93	23.45	3.64	19.82**	2.13	8.11	1.50	4.44	1.33	0.00	3.0	2.38	0.00	9.26

Chapter 5: EXPERIMENTAL EXAMINATION OF BEHAVIOURAL INTERACTIONS BETWEEN FREE-RANGING WILD AND DOMESTIC CANIDS

ABSTRACT

The structure of mammalian carnivore communities is strongly influenced by intraguild competition and intraguild predation. However, intraguild interactions involving the world's most common carnivore, the domestic dog *Canis familiaris*, have rarely been investigated. I experimentally examined the behavioral responses of a small canid, the Indian fox *Vulpes bengalensis*, to the presence of dogs and dog odors. Since resource competition between dogs and foxes is low, it is unclear whether foxes perceive dogs as interference competitors. To test this I exposed foxes to neutral, live dog, and animal odor cues at food trays and recorded the amount of food eaten, time spent at food trays, and vigilance and non-vigilance behaviors. When dogs were visible, foxes continued to visit the food trays, but reduced the amount of time spent (by 83%) and food eaten (by 70%) at those trays. Foxes were 10 times more vigilant during dog trials than during neutral and odor trials and also exhibited lower levels of non-vigilance behavior (resting, playing) when dogs were visible. In contrast, dog odors did not affect fox foraging and activity. These results show that vigilance/foraging tradeoffs due to interference competition can occur between native and domestic carnivores as well, despite low dietary overlap. These negative effects of dogs on a smaller member of the carnivore guild raise conservation concerns especially for endangered carnivores. In many parts of the world, free-

ranging dog densities are high due to human subsidies and these subsidized predators have the potential to exacerbate the indirect effects of human presence.

INTRODUCTION

Mammalian carnivores can dramatically influence the distribution and density of co-predators through direct and indirect competition (Caro and Stoner 2003; Palomares and Caro 1999). Theoretical and empirical studies of intraguild competition and the associated occurrence of intraguild predation, suggest that this dynamic is unidirectional, with larger carnivores negatively influencing smaller carnivores (Linnell and Strand 2000). Interference competition results in direct interaction which in turn results in spatial exclusion, harassment, or at an extreme, mortality by intraguild predation (Holt and Polis 1997). Interference competition, has been well documented among mammalian Carnivora and especially in the family Canidae (Johnson et al. 1996).

In most cases of interference competition, the subordinate competitor uses one of two behavioral strategies to reduce encounters with dominant competitor(s): avoiding range overlap, or modifying range use to reduce interactions while still allowing for home range overlap. For example, red foxes *Vulpes vulpes* avoid coyotes *Canis latrans* (Fedriani et al. 2000; Gosselink et al. 2003), and Arctic foxes *Alopex lagopus* avoid red foxes (Elmhagen et al. 2002; Tannerfeldt et al. 2002). In these cases, interference competition results in non-overlapping territories, in favor of the dominant competitor. In contrast, canids such as kit foxes *V. macrotis* have home ranges that overlap those of coyotes despite the fact that coyotes are the main cause of mortality for kit foxes (Cypher and Spencer 1998; Ralls and White 1995; White and Garrott 1997). Here, kit foxes use anti-predatory tactics such as multiple diurnal den use and habitat partitioning to reduce interference interactions with coyotes (Nelson et al. 2007).

At the population level, the costs of intraguild interference interactions are unambiguous for the subordinate competitor: increased mortality rates and decreased population sizes (Creel et al. 2001; Linnell and Strand 2000). At the level of the individual however, the behavioral effects of these interactions are less well understood and are likely more subtle, involving the need to temporally and spatially avoid particular areas or alter activity budgets (Nelson et al. 2007; St-Pierre et al. 2006). For example, African hunting dogs *Lycaon pictus* incur a cost in hunting efficiency by avoiding prey-rich habitat due to the presence of lions *Panthera leo* (Creel et al. 2001). After the reintroduction of wolves *C. lupus* into Yellowstone, coyotes reduced foraging and increased vigilance when in wolf territories or approaching ungulate carcasses (Atwood and Gese 2008; Switalski 2003). Similar foraging-vigilance trade-offs were also experimentally demonstrated by Scheinin et al. (2006), who exposed red foxes to a larger competitor (golden jackal; *C. aureus*) at food trays. Foxes decreased food consumption at food trays when a jackal was present. Such examples demonstrate that the mere presence of a dominant competitor results in risk aversion that is manifested by reduced willingness to use an area, and the associated loss of access to high quality resources.

Given these strong intraguild interactions between carnivores, it is striking that the effect of one of the most common carnivores, the domestic dog *C. familiaris*, on sympatric native carnivores has received little attention. Dogs have been introduced wherever humans have settled and are probably the most numerous carnivore in the world today (Daniels and Bekoff 1989;

Wandeler et al. 1993; WHO/WSPA 1990). Throughout rural areas of much of the world dogs are free-ranging; that is, although they may be owned by individuals or affiliated with specific human habitations, much of their daily activity budget involves free-ranging behavior (Butler et al. 2004; Fiorello et al. 2006). During the course of this ranging these animals have numerous opportunities to interact with native carnivore species at multiple levels, for example as predators, prey, and disease reservoirs (Butler and du Toit 2002; Butler et al. 2004; Edgaonkar and Chellam 2002; Fiorello et al. 2006).

There is little information on the competitive dynamics of dogs and native canids. Such interactions deserve close examination because the direct and indirect effects of dogs on other carnivores may be far-reaching. For example, in Australia, dogs fulfill the role of a larger predator in their interactions with non-native meso-predators such as introduced red foxes and feral cats *Felis catus* (Glen et al. 2007; Johnson et al. 2007; Mitchell and Banks 2005). However, Australian dogs are truly feral (sensu Boitani et al. 1995; Green and Gipson 1994) and there is high overlap in diet between these species (Glen et al. 2006; Mitchell and Banks 2005). Moreover, since these red foxes and cats are recent introductions to the Australian landscape, it is not clear if these competitive dynamics reflect those seen in settings where dogs interact with native smaller carnivores.

Contrary to popular belief, few dog populations are truly feral with regards to food acquisition (but see Campos et al. 2007; Kruuk and Snell 1981), as they are typically subsidized by human derived food sources to a large extent (Butler and du Toit 2002; Daniels and Bekoff 1989). Presumably, competition for resources is a primary driver of interference interactions among carnivores (Atickem 2003; Caro and Stoner 2003; Case and Gilpin 1974; Linnell and Strand 2000). However, even where dogs do not compete with wild carnivores for food (Butler and du Toit 2002), they may still influence the behavior of smaller predators if they are perceived as predators or interference competitors. Especially in areas where the carnivore community is disarticulated, domestic dogs could fulfill the role of a medium-sized carnivore through interference competition and intraguild predation (Glen and Dickman 2005; Johnson et al. 2007).

Domestic dogs in rural India are typical of free-ranging dogs elsewhere in the world as they are heavily dependent on human subsidies and show low dietary niche overlap with wild canids such as Indian foxes *Vulpes bengalensis* (Vanak , Chapter 4). Indian foxes are a typical small canid and are common throughout the Indian subcontinent (Gompper and Vanak 2006). I designed a field experiment to determine whether dogs, like wild canids, can induce behavioral changes indicative of interference competition in the smaller Indian fox merely by their presence. I predicted that foxes will react to the presence of dogs because dogs are a mid-sized canid similar to golden jackals *Canis aureus*. Specifically, the presence of live dogs will cause foxes to a) reduce visitation rates to, and consume less food at high value food sources and b) exhibit greater levels of vigilance. In contrast, given that dogs are widespread and occur at high densities in the study area, I expect that foxes will be habituated to the presence of dog odors and thus odors alone will be insufficient to induce a change in the foraging and activity of foxes.

MATERIALS AND METHODS

Study area and species

This study was conducted in a grassland ecosystem adjacent to the Great Indian Bustard Sanctuary (GIBS) at Nannaj, Maharashtra, in central India. The regional landscape consists of a matrix of sugarcane fields, seasonal crops, communal grazing lands, protected grasslands and forestry plantations. The intensive study area of approximately 50 km^2 comprises the protected grasslands of Nannaj which is bordered by several villages with a combined human population of approximately 50,000. This region is semi-arid and experiences a wet season from Jul–Oct during which 95% of the precipitation occurs (Temp. range = 16-32 °C, mean annual precipitation = 600mm), a cool-dry from Nov–Feb (Temp. range = 6-37 °C) and a hot-dry season from Mar–Jun (Temp. range =18-47 °C).

The local economy is based on agro-pastoralism, and as such, domestic dogs in this region (avg. adult body weight 17.04 kg ± 3.1 SD, n = 74) can be roughly categorized into three types: 1) herding dogs that accompany grazing livestock in grasslands (fox habitat) during the day, 2) village dogs that occasionally traverse fox habitat during the day or at night, and 3) farm dogs that are a continuous presence in peripheral fox habitat. Farm dogs occur at densities of 28 dogs/km^2 (± 3.2 SE) in the 50km^2 study region and are a major presence in the landscape. Dog diet consists primarily of human-derived food materials (garbage, crops) and scavenging from livestock carcasses. A small component of their diet consists of wild caught food, mainly rodents (*Rattus* spp.) and black-naped hare *Lepus negricollis* (Vanak, Chapter 4). The primary source of dog mortality appears to be enzootic viral diseases, intraguild predation by wolves, and targeted killing of problem animals by humans (A. T. Vanak and M. E. Gompper, unpublished data).

The Indian fox is a typical small fox (avg. adult body weight 2.47 kg ± 0.35 SD, n= 35) endemic to the Indian subcontinent. It is crepuscular and nocturnal and is an opportunistic omnivore that is common in open short grasslands (Gompper and Vanak 2006; Vanak and Gompper 2007). It is the most common wild carnivore in the study area, where it inhabits protected grasslands as well as grazing lands and agricultural fields. It does not compete directly with dogs for food, as rodents, insects, fruits, and reptiles make up a large part of the fox's diet (Vanak, Chapter 4). The main causes of mortality for foxes in this region are poaching by humans, disease, and predation by larger carnivores, including dogs (Vanak 2007a). Indian foxes breed during the winter, at which time foxes use a den that is maintained by both individuals of a mated pair. The breeding season coincides with the beginning of the dry season (January to May) when water and food resources become increasingly scarce and grassland height decreases dramatically.

Experimental design

Trials were conducted from February to April 2007, during which time foxes were localized at breeding dens and had predictable daily activity patterns. Behavioral trials were centered on fox dens which were inhabited by a resident breeding pair (except for 1 den, which had only 1 adult female), and 2-4 pups aged 3-4 months old. Behaviors were recorded for all foxes at each den during these trials but a den was considered the sampling unit.

To determine if and how the presence of dogs influences fox activity and foraging behavior, foxes at each den-site were exposed to three trials: 1) neutral (no stimulus), 2) live dog and 3) animal odors. The neutral trial consisted of two un-manipulated foraging trays for the foxes. The dog and animal odor trials consisted of two foraging trays with either a control condition (a non-threatening stimulus) or a treatment condition with a potentially threatening stimulus. The difference in fox responses between these paired foraging trays and across the three trials indicates the level of interference that dogs have on fox foraging and activity.

Each set of trials was preceded by 2-3 days of habituation of foxes to the food source and the observers. Two plastic trays (34 x 24 x 6 cm deep) were placed 200 m apart on opposite sides of the main den entrance. The plastic trays were lined with soil obtained from the site to reduce unfamiliar smells. Two boiled chicken eggs divided into 8 equal pieces and 200 g of locally grown grapes were placed on each tray. I assumed that this type of food would be a highly attractive foraging option because of the presence of pups at the den sites at a time of seasonal food scarcity. The amount of food in the trays was also appropriate as foxes would often eat all the food in both trays during the habituation period, thus indicating that they did not satiate after foraging at a single tray. Each pair of trays was placed 100 m from the den site one hour prior to sunset and observations were recorded continuously from the time the first fox (either adult or pup) was sighted within 100 m of either tray until one hour after sunset. Behaviors of foxes were recorded by two people from the back of a pickup truck 150 m from the den site using a spotting scope and two Sony miniDV camcorders. Videos were then scored by ATV. Foxes were considered habituated when they visited and ate from both food trays during the 2 hr observation period.

During the habituation period, all foxes showed a preference for one tray over another, and therefore I assigned the treatments for the dog and animal odor trials non-randomly to control for initial tray bias (Fig. 1). A "preferred" tray was identified as the tray where foxes consumed more food (> 50%) or spent more time (> 50%) during the habituation period and was often the first tray discovered (5 of 7 trials). Initial preference for a tray was mostly reduced by the time the neutral trial was conducted 2-3 days later (see results). Following this initial habituation period I exposed each set of foxes to the neutral, dog, and animal odor trials on consecutive days in that order. The order of the trials was explicitly set to test predictions. Odor cues are likely to be reinforced by the actual presence of a dog during the live dog trial. Therefore, a lack of difference between treatment and control trays during the odor trial would be stronger support for our prediction that dog odors do not affect fox foraging and activity.

For the neutral trial, no stimulus was placed at either tray, thus providing a baseline measure of undisturbed activity and foraging behavior. For the dog trial, a trained dog was placed in a cage (100 x 50 x 65 cm) in line-of-sight 20 m from one tray (treatment) and a similar-sized empty cage was placed at the other tray (control). The dog treatment was intentionally placed at the "preferred" tray (Fig. 1). The stimulus dog was a local mixed-breed animal raised by ATV and was habituated to the cage prior to these trials. Thus the dog sat calmly in the cage during the trials and was not agitated except in one instance when he growled at an approaching fox. While the cage was designed to collect any excrement from the dog to reduce confounding odors at the site, the dog did not urinate or defecate during any of the trials. The dog had received all relevant vaccinations to reduce chances of disease transmission. I did not use a goat or other domestic animal as a control for the live dog treatment because their association with humans (who use dogs for herding and hunting) would be a confounding factor. Further, I did not use an inanimate model (as in Scheinin et al. 2006) because the novelty of the object could potentially confound the experiment. Thus an inherent assumption of the live dog trial is that changes in fox behavior are a result of the dog being recognized as a threat (interference competitor) by the fox, rather than a response to the novelty of the dog.

For the animal odor trial, I reversed the position of the treatment and control at the food trays (Fig. 1) to ensure that a specific tray was not associated with dog stimuli. The odor treatment was a cotton-ball soaked with fresh (< 1 day old) dog urine and dog scat, and the odor control was a water-soaked cotton-ball and fresh (< 1 day old) dung from blackbuck (*Antilope cervicapra*). Blackbuck are common in the study area and are presumably a non-threatening native herbivore.

During each 2-hr trial period, I recorded the presence of pups at the den-site and at trays and all occurrences and duration of the following behaviors by adult foxes: time of first appearance of at least one fox at the site, number of visits to each tray, and time spent at each tray irrespective of the number of foxes that visited the tray. I also recorded the duration of vigilance behaviors by any adult fox and duration of non-vigilant behaviors by all foxes. Vigilance behaviors were defined as alert postures, alarm barks and agitated movements, while non-vigilance included grooming, sleeping, resting, play, and suckling. For statistical analyses I grouped these behaviors in the two categories because not all foxes exhibited all behaviors (for example, males did not suckle and pups did not alarm call). I combined the durations of each behavior exhibited by all foxes at each den-site to reflect the occurrences of behaviors per den site. For example if more than one fox was present at a tray, I only recorded that as one event and did not tally the time spent by all individual foxes present concurrently at the tray. I ended trials one hour after sunset and measured the remaining food present in each tray. As each set of trials took between 5-6 days to complete, I was able to test the behavioral responses of 13 adult foxes and their pups at seven den-sites.

Data analysis

All behavioral measures met the assumptions of normality as determined by Kolmogorov-Smirnov tests and assumptions of sphericity were met according to Mauchly's sphericity test. For each trial (neutral, live dog, animal odor), I used a paired t-test to determine whether the proportion of food eaten and number of visits by foxes differed between control and treatment trays. There was no significant difference in the proportion of eggs and grapes consumed during each trial so these food types were combined for analysis. I calculated the difference between the number of visits to, and the proportion of food eaten from, the control tray and treatment tray for each trial and used a Repeated Measures Analysis of Variance (RM ANOVA) to test for the effect of trial on these differences. I also tested whether foxes differed in the time they spent at control and treatment trays during each trial using paired t-tests. I quantified the duration of vigilance and non-vigilance behaviors, and of total time spent at both trays, as proportions of total trial duration to correct for the differences in observation periods between trials. Using a RM ANOVA I determined the effect of stimulus on allocation of time spent at trays, and in vigilance and non-vigilance behaviors. All statistical analyses were conducted using SPSS 15.0.

RESULTS

The number of foxes that visited the trays did not differ among trials ($F_{2,12} = 1.5$, *P* = 0.26, mean ± SE = 2.62 ± 0.016). Pups were present and active at all den sites during the trials and most visited the trays with adults except for 2 cases when pups independently visited a tray and 2 cases when they did not visit the trays at all. During the neutral and odor trials, there was no difference in which tray was first visited. Foxes did recognize the odor cues, as at 4 of the 7 sites foxes investigated both odor cues by sniffing or licking the urine-soaked cotton ball (treatment) and water-soaked cotton ball (control). In contrast to the neutral and odor trials, the first tray visited by any fox during the dog trial was always the control tray with the empty cage. During the dog trials, the latency to arrive at any tray by any fox (time first arrival - time tray set-up) was longer than the latencies during the neutral and odor trials ($F_{2,12} = 7.78$, *P* = 0.007, Table 1 for means).

There was no difference between proportion of food eaten at the two trays for the neutral trial (t = -1.903, *P* = 0.106, Table 1, Fig. 2a), thus indicating that initial "preference" for a tray was lost after the habituation period. There was also no difference in the proportion of food eaten at the two trays during the odor trial (t = 0.801, *P* = 0.454, Table 1, Fig. 2a). In contrast, foxes significantly reduced food consumption at the live dog tray compared to the empty cage tray (t = 9.033, *P* = 0.0001, Table 1, Fig. 2a). Therefore, the mean difference in proportion of food consumed between control and treatment trays was significantly greater during the live dog trial than during the neutral and animal odor trials ($F_{2,12}$ = 21.89, P < 0.0001). Foxes did not completely avoid the live dog tray, but rather they made significantly fewer visits compared to the empty cage tray (t = 2.856, *P* = 0.029, Table 1, Fig. 2b). There was no difference between the number of visits at trays for the neutral (t = -2.295, *P* = 0.062) and animal odor (t = 1.291, *P* = 0.244) trials (Table 1, Fig. 2b). Similarly, the mean difference in the number of visits between control and treatment trays was significantly greater during the live dog trial than during the neutral and animal odor trials ($F_{2,12}$ = 8.3, *P* = 0.006). Foxes did not compensate for the decrease in the number of visits and proportion of food consumed at the live dog tray by increasing these behaviors at the control tray during the live dog trial as their responses at control trays were similar for all three trials (Table 1).

During the neutral trial, foxes spent marginally less time at the non-preferred tray compared to the preferred tray (t = -2.408, *P* = 0.053, Table 1, Fig. 2c) and thus I assigned the preferred tray to the treatment condition during the following day's dog trial. Foxes spent 83% less time at the tray within sight of the caged dog compared to the empty cage tray (t = 3.258, *P* = 0.017, Table 1, Fig. 2c).There was no difference in time spent at the two trays during the following day's odor trial (t = 0.754, *P* = 0.48, Table 1, Fig. 2c).

There were significant differences among the trials in the total proportion of time spent at both trays ($F_{2,12}$ = 11.13, *P* = 0.0018) and in vigilance ($F_{2,12}$ = 55.24, *P* < 0.0001) and non-vigilance ($F_{2,12}$ = 17.186, *P* = 0.0003) behaviors by foxes. Compared to the dog trial, foxes spent twice as much time at the food trays during the neutral trial (Table 1, Fig. 3). However, there was no significant difference in the time spent at the trays between the animal odor and dog trials (Table 1, Fig. 3). During the dog trials, foxes reduced time spent on non-vigilant behaviors compared to the neutral and animal odor trials (Table 1, Fig. 3). Consequently, foxes were most vigilant during the dog trials as they increased vigilance activity by >10 times compared to the neutral trial (Table 1, Fig. 3). For all three behaviors, there was no significant difference in how time was allocated between the neutral and animal odor trials (Table 1, Fig. 3).

DISCUSSION

This experiment demonstrates the profound effect domestic dogs can have on the activity and foraging behavior of Indian foxes. When a dog was visible, foxes reduced their visitation rates and spent less time at the food trays. Not only did this result in less food consumed at the tray within sight of the dog, but foxes ate less overall than they did when exposed to no stimuli or animal odors. Foxes were more vigilant when a dog was visible, exhibiting alert postures, agitated movements and alarm calling. As a result, foxes arrived much later at food trays, spent less time foraging at the trays and reduced other non-vigilance activities such as resting, playing, and grooming. The presence of dog odors (fresh urine and scat) had little effect on fox foraging and activity. These results are similar to those reported by Scheinin et al. (2006), where the presence of a live jackal, but not jackal odors elicited change in red fox foraging and behavior. Although unlikely, it is possible that foxes could not distinguish between the odors of dogs and blackbucks, as their behavioral responses at both trays were similar. However, dogs are present at very high densities in the study area and foxes are likely to encounter dog scat and urine often.

Therefore the presence of dog odors is unlikely to be a novel or a particularly threatening stimulus. Since olfaction is an important component of canid communication (Gorman and Trowbridge 1989), it is possible that dog and blackbuck odors may provide some information which would explain why foxes investigated the odors during the trials. In any case, the reduction of foraging time during the odor trials compared to the neutral trials was marginal ($\bar{X}$ <1 minute).

The results indicate that overall, foxes are not affected by the indirect indicators of dog presence (urine and scat), but instead react to the potentially more direct threat posed by actual dog presence. This response is expressed as a reduction of food intake and an increase in vigilance. Such vigilance has been observed in other carnivores as well, such as coyote *Canis latrans*, (Switalski 2003), cheetah *Acinonyx jubatus* (Hunter et al. 2007), dwarf mongoose *Helogale undulate* (Rasa 1989) and eastern quoll *Dasyurys viverrinus* (Jones 1998). In each of these cases, there was also a large trade-off between vigilance behavior and foraging. Therefore it is quite likely that the energetic costs in terms of loss of foraging opportunity during the dog trials might be high for the foxes, especially when raising pups at a time of general food scarcity. The combined effects of reducing foraging, increasing vigilance and lowering other non-vigilant activity (such as play behavior, grooming and suckling) may have important fitness and survival consequences for these individuals (Lima and Dill 1990).

The responses of Indian foxes to domestic dogs were similar to the reactions of red foxes to golden jackals described by Scheinin et al. (2006). In our study area, golden jackals occur at low densities but they likely compete for the same food resources (such as rodents and *Zizyphus* berries) as foxes (Home 2005; Mukherjee et al. 2004). Such dietary overlap could be a major driver of interference competition between those two species. However, dogs and foxes do not compete for food resources at this study area (Vanak, Chapter 4), but dogs appear to dominate foxes via interference interactions. Yet it is important to note that foxes did not completely avoid the food trays when dogs were visible as might be expected if foxes viewed dogs as predators. Rather, foxes modified their behavior while still approaching the dog and the food. Given that in other systems subordinate competitors use diverse strategies to reduce encounters with dominant competitors (Atwood and Gese 2008; Creel et al. 2001; Nelson et al. 2007), I believe the data indicates a similar competitor avoidance scenario: foxes trade-off foraging for vigilance at rich resources patches when domestic carnivores are present. These results suggest that foxes view dogs as a larger member of the canid guild and thus as an interference competitor. Dogs may therefore fulfill the role of a mid-sized canid in this community despite their close association and dependence on humans. The broader effects of interference interactions between dogs and other carnivores have been observed in at least one system. In Australia, non-native red foxes avoided areas that were recently visited by wild dogs (dingoes, feral dogs and their hybrids), although they are sympatric with dogs at the landscape level (Mitchell and Banks 2005). There, in the absence of large mammalian carnivores, dingoes and feral dogs have assumed the role of a mid-sized, apex predator in their interactions with both introduced eutherian and native marsupial carnivores (Glen et al. 2007; Johnson et al. 2007).

Domestic dogs are a classic example of a subsidized predator (Boarman 2003; Kays and DeWan 2004). They are insulated from food scarcity because of human-derived food subsidies, and are generally buffered from intraguild feedback mechanisms (for e.g. predation by larger carnivores such as wolves and leopards) by the presence of safe refuges in or near human habitations. Such a scenario is problematic for conservation practitioners since in some regions the enhanced dog populations likely influence species of conservation. Although Indian foxes are not a species of conservation concern in India (Sillero-Zubiri et al. 2004), the results from this study can be extrapolated to endangered small carnivores since the underlying mechanisms and consequences of intraguild competition likely remain the same. In such cases, the interference competition from dogs could result in lower population sizes of sympatric carnivores which in turn might increase the likelihood of local extirpation (Cypher et al. 2001; Linnell and Strand 2000).

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Table 1. Behavioral responses of Indian foxes during the neutral, live dog and animal odor trials (N=7 dens).

Fox Responses		Neutral trial	Live dog trial	Animal Odor trial
Proportion of food eaten [mean (± SE)]	Control tray	0.47 (0.10)	0.71 (0.08)	0.76 (0.09)
	Treatment tray	0.71 (0.11)	0.1 (0.05)	0.68 (0.14)
Number of visits [mean (± SE)]	Control tray	7.29 (1.74)	8.0 (2.60)	8.86 (1.32)
	Treatment tray	10.86 (2.17)	1.71 (0.57)	7.0 (1.62)
Duration of time spent at tray [minutes, mean (± SE)]	Control tray	6.65 (1.34)	8.81 (2.63)	7.94 (1.87)
	Treatment tray	10.52 (2.23)	0.8 (0.22)	6.47 (1.89)
Duration of vigilance behaviors [minutes, mean (± SE)]		2.48 (0.6)	30.34 (4.87)	5.1 (1.26)
Duration of non-vigilance behaviors [minutes, mean (± SE)]		14.27 (3.21)	5.84 (1.27)	13.9 (2.98)
Latency to arrive to trays [minutes, mean (± SE)]		59.14 (4.31)	87.43 (6.08)	57.71 (9.74)

Figure 1. Experimental design and timeline for neutral, live dog and animal odor trials. Note the alternating assignment of treatment and controls at trays.

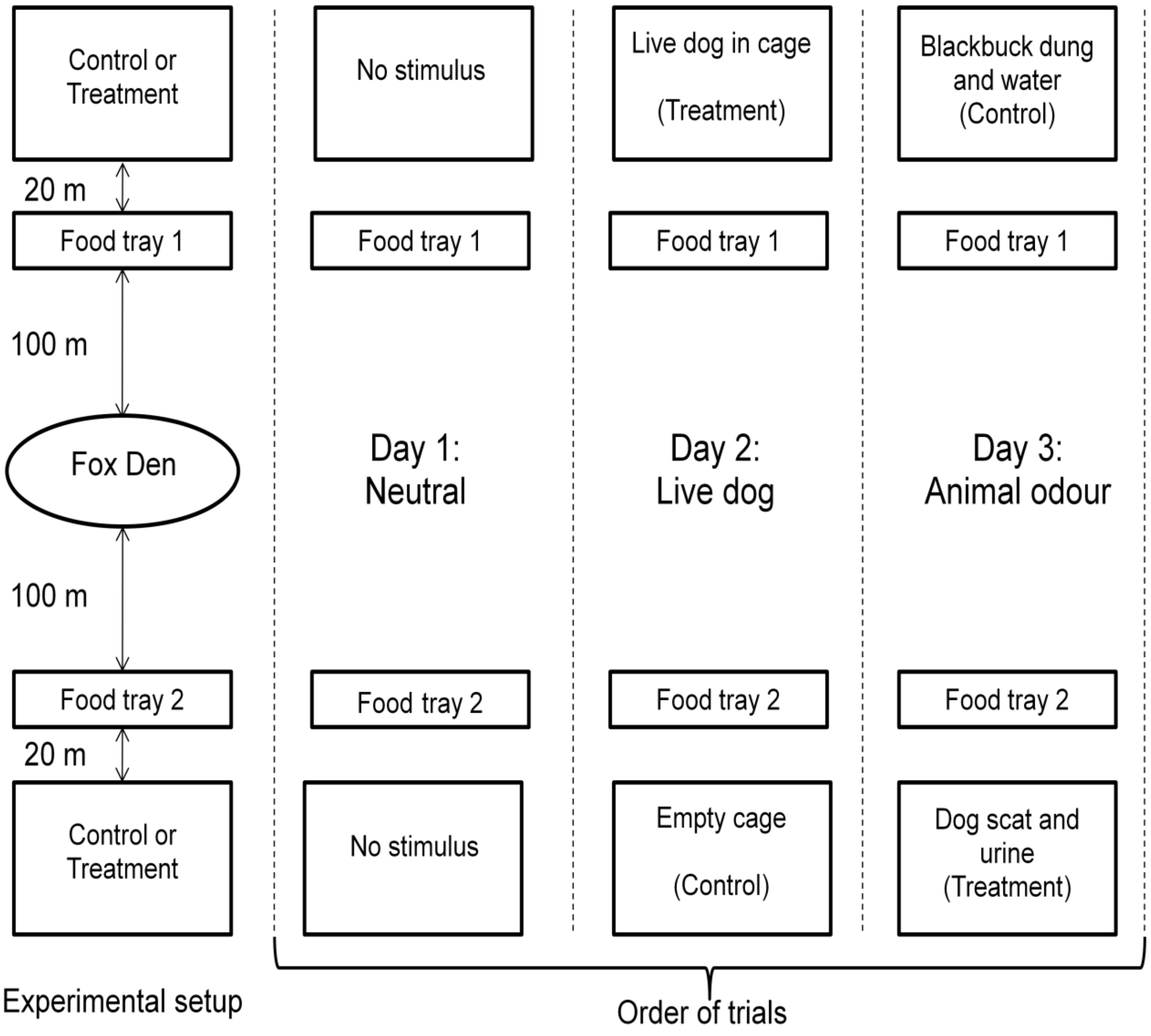


Figure 2a. Proportion of food consumed by foxes at control (unshaded bars) and treatment (shaded bars) trays during the neutral, live dog, and odor trials. * denotes significant difference between trays at $p < 0.05$ (mean ± SE, n = 7 dens).

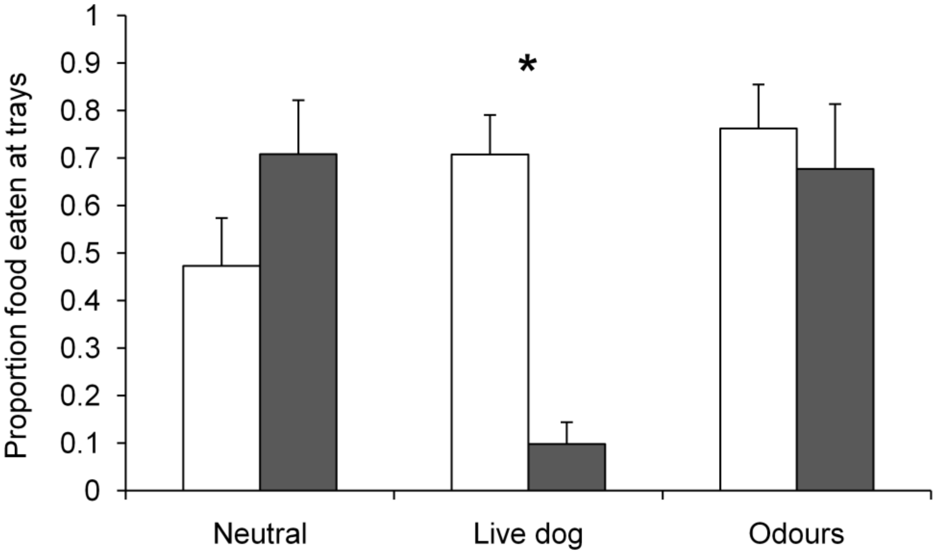


Figure 2b. Number of visits by foxes to control (unshaded bars) and treatment (shaded bars) trays during the neutral, live dog, and odor trials. * denotes significant difference between trays at $p < 0.05$ (mean ± SE, n = 7 dens).

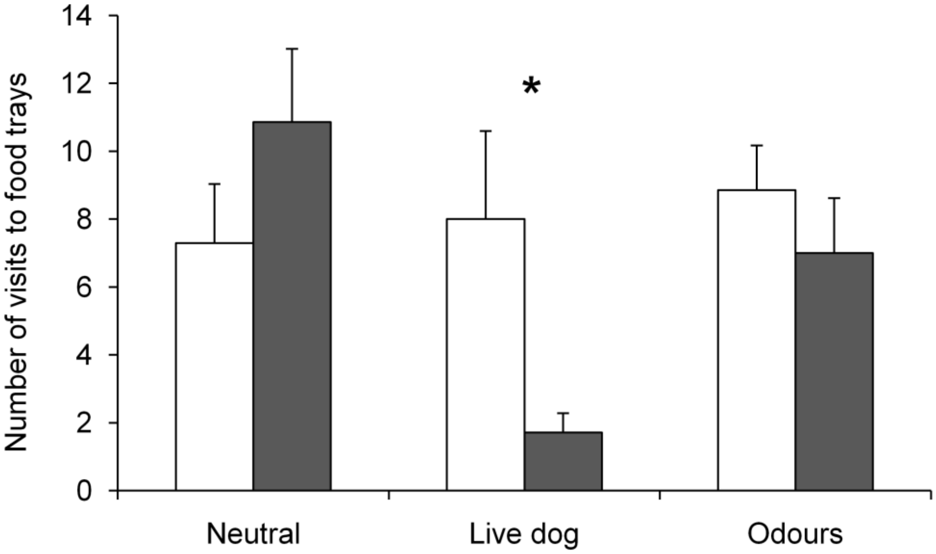


Figure 2c. Amount of time spent at control (unshaded bars) and treatment (shaded bars) trays by foxes during the neutral, live dog, and odor trials. * denotes significant difference between trays at $p < 0.05$ (mean ± SE, n = 7 dens).

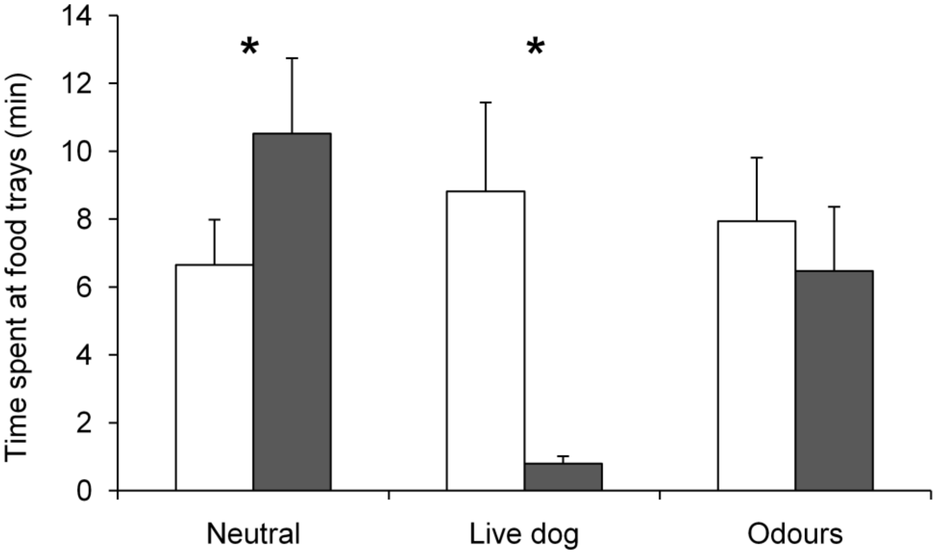
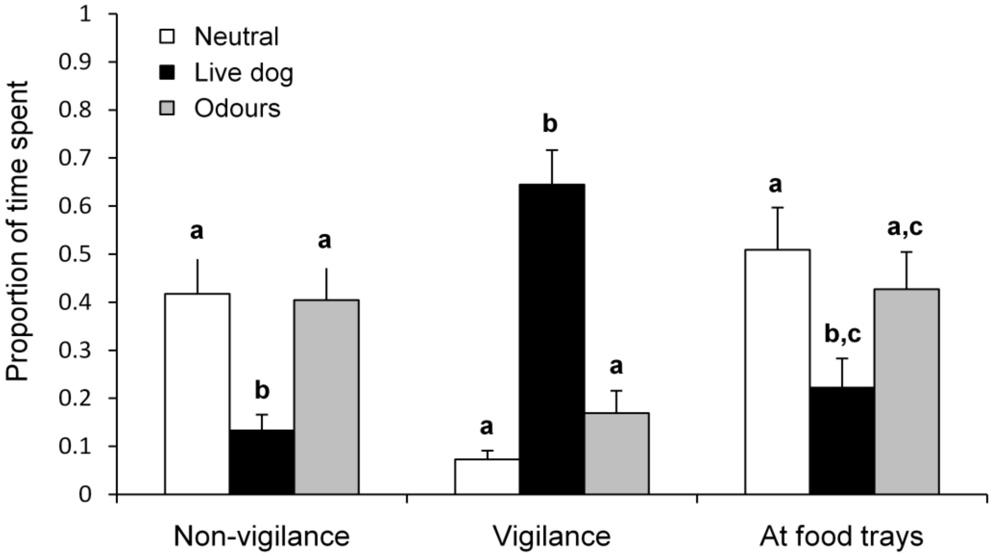


Figure 3. Proportion of time spent by foxes at the food trays and in vigilance and non-vigilance behaviors during the neutral, live dog and odor trials. Letters denote significant difference (Fisher's LSD p <0.05) among trials for each behavior (means ± SE, n=7 dens).



CHAPTER 6: SPATIAL NICHE OVERLAP BETWEEN DOMESTIC DOGS AND INDIAN FOXES IN A HUMAN DOMINATED LANDSCAPE IN CENTRAL INDIA

ABSTRACT

The distribution and space use patterns of meso-carnivores are heavily influenced by the effects of top-down intraguild competition with larger carnivores. To avoid the effects of interference competition and intraguild predation, subordinate competitors can alter space use patterns which may also result in a reduction of foraging opportunities. Whether this effect of interference competition also occurs between wild and domestic carnivores is unknown. I examined the space use patterns of 32 radio-collared Indian foxes and 25 free-ranging dogs in an endangered grassland habitat in and around the Great Indian Bustard Wildlife Sanctuary in central India. I hypothesized that Indian foxes would reduce overlap with dog territories and that fox space use patterns at the landscape level would be influenced by the presence of dogs. Using a logistic regression analysis in an information theoretic framework, I determined the effects of landcover type, primary prey abundance (rodents) and dog presence on the landscape on the space use of foxes. As expected, Indian foxes showed low overlap with dogs based on the volume of intersection index. Top models showed a positive influence of grasslands, plantations (which have grassland understoreys), and rodent abundance and a negative influence of agricultural land and dog presence. This suggests that fox space use is determined not only by habitat type and primary prey abundance, but also influenced by the presence of a mid-sized carnivore, the dog.

Free-ranging dogs are ubiquitous throughout much of the world, and here I show that a smaller carnivore is modifying its use of the landscape to avoid dogs, suggesting that interference competition from dogs may pose threats to native carnivore communities.

INTRODUCTION

The distribution and abundance of meso-carnivores are limited by habitat availability, prey abundance, competition, and predation. In the absence of a competitor or predator, meso-carnivores should be distributed based on habitat quality and preferred food availability. For example, Nelson et al. (Nelson et al. 2007) suggested that in the absence of coyotes *Canis latrans*, kit foxes *Vulpes macrotis* would select for shrub habitats which have a greater abundance and diversity of prey than grassland habitats. However, small carnivores are often the subordinate intraguild competitor in most communities and thus are potentially subject to top-down effects that mediate their ability to use preferred habitat.

Competitive dynamics among carnivores are asymmetric and interference competition and the associated occurrence of intraguild predation are unidirectional, with larger carnivores negatively influencing smaller carnivores (Linnell and Strand 2000). Competition can affect the subordinate competitor in several ways: by limiting spatial distributions resulting in scattered interspecies territories (Creel et al. 2001; Johnson et al. 1996), constraining habitat selection (Nelson et al. 2007), reducing prey encounter rates and food intake or requiring increased hunting effort (Atwood and Gese 2008; Creel et al. 2001; Gorman et al. 1998; Palomares et al. 1996).

Subordinate competitors may however, use two behavioral strategies to reduce encounters with dominant competitor(s): avoiding range overlap, or modifying range use to reduce interactions while still allowing for home range overlap. For example, at the landscape level, red foxes *V. vulpes* avoid coyotes (Gosselink et al. 2003), and Arctic foxes *Alopex lagopus* avoid red foxes (Elmhagen et al. 2002; Tannerfeldt et al. 2002). When ranges do overlap, such as between kit foxes *V. macrotis* and coyotes (Cypher and Spencer 1998; Ralls and White 1995; White and Garrott 1997), kit foxes use anti-predatory tactics such as multiple diurnal den use and habitat partitioning to reduce interference interactions with coyotes (Nelson et al. 2007). Avoidance of certain habitats can also result in a cost in hunting efficiency, as seen when African hunting dogs *Lycaon pictus* avoid prey-rich habitat in the presence of lions *Panthera leo* (Creel et al. 2001). Therefore, the above examples demonstrate that the mere presence of a dominant competitor results in risk aversion that is manifested by reduced willingness to use an area, and the associated loss of access to high quality resource patches.

Intraguild interactions between native and domestic carnivores such as the dog have rarely been investigated (Vanak, Chapter 2). Dogs are a mid-sized canid, and when free-ranging into wild habitats, can exert a top-down influence on smaller carnivores via interference competition (Vanak, Chapter 2). For example, the avoidance of rich food sources by a native meso-carnivore in the presence of dogs has been demonstrated experimentally by Vanak (Chapter 5). Indian foxes reduced consumption of food by 70% and displayed increased vigilance behavior when exposed to a live dog at food trays. Whether this avoidance of dogs at the local scale extends to avoidance of prey-rich habitats at the landscape level by any meso-carnivore is unknown. Here I address this issue.

I hypothesize that domestic dogs are interference competitors of a native meso-carnivore, the Indian fox. Given that smaller carnivores may avoid spatial overlap with dominant competitors or modify space use to reduce encounters, I predict that dogs and Indian foxes will have non-overlapping home-ranges and that the presence of dogs will negatively influence fox space use. If dogs did not exert competitive dominance, I would expect that the space use of foxes would be primarily determined by habitat preference and prey abundance. In our study area, Indian foxes select for native grasslands over human-modified habitats at both the landscape and home-range level (Vanak, Chapter 3). Although the habitat preferences of domestic dogs in this region are unknown, they occur at high densities in the farm lands bordering grassland habitats (28/km^2; Vanak, 2007) suggesting a preference for human dominated habitats and the associated resource subsidies (Vanak, Chapter 4). The Indian fox is an opportunistic omnivore that depends mainly on wild caught food such as small mammals, invertebrates and seasonally available fruits. On the other hand dogs in this area are mainly dependent on human-derived food and thus, have low dietary niche overlap with foxes (Vanak, Chapter 4). Despite the preference for grassland habitats and rodents in their diet, I predict that the presence of dogs in the landscape will also be an important predictor of fox space use.

STUDY AREA AND METHODS

This study was conducted in and around the Great Indian Bustard Sanctuary (GIBS) at Nannaj, Maharashtra, in central India (17° 49’ 40” N and 75° 51’35” E). The sanctuary consists of six protected grassland patches (6 km^2 out of 8,698 km^2 GIBS) within a matrix of sugarcane fields, seasonal crops, communal grazing lands, and forestry plantations. The study area is bordered by several villages with a combined human population of approximately 50,000 largely dependent on agro-pastoralism (http://solapur.gov.in/htmldocs/dgraphy.htm accessed on 11/Jun/08). This region experiences a wet season from Jul–Oct during which 95% of the precipitation occurs (Temp. range = 16-32 °C, mean annual precipitation = 600mm), a cool-dry from Nov–Feb (Temp. range = 6-37 °C) and a hot-dry season from Mar–Jun (Temp. range =18-47 °C). A detailed description of the study area is given in Chapter 3.

Capture and handling

I captured and radio-collared 35 Indian foxes and 25 domestic dogs from November 2005 to April 2007. Details of capture and handling protocols of Indian foxes are given in Vanak (Chapter 3) and Belsare and Vanak (in prep). I targeted dogs on farms bordering fox habitat for radio-collaring, under the assumption that this group of animals is most likely to range into wild habitat and thus have an effect on fox space use. Most domestic dogs were handled after obtaining permission from their owners, although others had to be captured using box traps, padded foot-hold traps, throw-nets or by chemical immobilization using a blow-pipe. After physically restraining the captured animals, I immobilized them with a mixture of xylazine hydrochloride and ketamine hydrochloride. Animals were closely monitored until they were fully recovered following the same protocol observed for foxes (chapter 3).

Radio Telemetry and joint space use analysis

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, I collected all triangulation data for each non-stationary animal by obtaining simultaneous fixes from at least three stations or within a 2 minute interval. Locations were collected every 28 hours to provide an independent and approximately equal number of locations in every part of the day. Further details on telemetry data collection are given in chapter 3.

To determine home-range and space use patterns of foxes and dogs I calculated 95% kernel home ranges for all individuals with ≥30 locations to minimize potential bias in home-range estimation due to small sample sizes (Kernohan et al. 2001; Seaman et al. 1999). I calculated fox and dog utilization distributions (UD) using a fixed kernel estimator. Kernel size or bandwidth was selected with the “plug-in” method using the KDE function in Matlab (The Mathworks Inc, Natick, MA USA; Beardah and Baxter 1995). I excluded the outer 5% of the UD by volume using Hawth’s tools in ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA, USA) to reduce potential bias in home-range estimates resulting from extremely low use areas on the tails of the UD. I 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, Chapter 3).

I estimated overlap of space use between dogs and foxes by calculating the Volume of Intersection (VI) index (Fieberg and Kochanny 2005; Kernohan et al. 2001). This index measures the degree of overlap between individual UDs as:

$$VI = \iint \min[\hat{f}_1(x,y), \hat{f}_2(x,y)]dxdy$$

where $\hat{f}_1$and $\hat{f}_2$ are the UDs of animals 1 and 2 respectively. The VI score ranges from 0 (no overlap) to 1 (complete overlap). I determined the degree of overlap by estimating VI scores for all pairs of animals tracked during the same season and year. I used an AML script for ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, USA) to calculate VI indices across all animal combinations (A. Singh pers. comm. Appendix I). I omitted from subsequent analysis any pair of individuals with a VI score of <0.02 to reduce bias from low use areas in the tail of the UD (similar to Lesmeister 2007). Since we radio-collared all adjacent pairs of foxes in the intensive study area, but not all dogs, our measure of overlap is likely an underestimate.

Estimating rodent relative abundance

To determine rodent abundance on the landscape, I first enumerated rodent burrows as an index of relative abundance. I overlaid a 1km x 1km grid on a map of the study area and randomly selected 41 sample grids representing 29% of the intensive study area. Within each grid I walked a square strip-width transect of 1600 x 2 m and enumerated rodent burrows. Grids falling on human settlements were excluded from sampling. I did not differentiate between ploughed land and agriculture and combined the two categories. I did not systematically sample bare-soil landcover type because it occupied a small proportion of the total area and was highly patchy and because I did not find any rodent burrows in any of the patches that were encountered I assigned a zero value to bare-soil. I also did not sample in human settlements because of logistic reasons, and assigned zero value to this landcover type assuming that rodent species of interest were unlikely to be found in human settlements. I 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, burrow counts of the Indian desert jird *Merriones hurrianae* were highly correlated ($R^2 = 0.97$, n=7) with density estimates. Although the Indian desert jird does not occur in our study area, similar burrowing species such as the Indian gerbil *Tatera indica* and *Mus booduga* are found here and are of high importance in the diet of the Indian fox across all seasons (Vanak, Chapter 4).

I created a GIS layer of rodent relative abundance by mapping mean number of burrows/ha in each habitat (Table 1) to its associated habitat type at 5.6 meter resolution on a landcover map derived from a LISS IV multispectral imagery (IRS P3). Habitat type was categorized by landcover as grasslands, fallow, plantation, agriculture, ploughed land, bare-soil and human settlements. I then re-sampled the resultant raster image to a 30 m resolution using a bilinear function to smoothen the estimate for each pixel (Fig. 1). I chose 30 m resolution as it was the minimum bandwidth value for fox UD estimates.

Estimating dog use of landscape

To determine how landcover categories predicted dog space use, I first conducted a logistic regression analysis of habitat use (Keating and Cherry 2004) to determine the probability of a habitat being selected by dogs. From the radio-telemetry data, I compared landcover attributes of point locations of dogs to an equal number of paired random points generated within the intensive study area. From the logistic regression output, I used the estimated parameter coefficients (Table 1) for each landcover category as a surrogate measure of dog presence in the landscape. The parameter estimates were plotted onto the landcover map using the raster calculator in ArcGIS to generate a GIS layer that predicted dog use of the landscape.

Modeling fox space use as a function of habitat, dogs and rodents

To determine the effect of food resources, landcover and competitor covariates on fox space use patterns, I 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, I determined the landcover category, rodent relative abundance and estimate of dog presence on the landscape. I used a logistic regression analysis to compare attributes at each point location to random sites. All the statistical analysis was conducted in SAS 9.1 (SAS Institute Inc. Cary, NC) using the PROC LOGISTIC function. I tested the data for multicollinearity and excluded fallow land as a variable because its minimum tolerance was <0.001. All other variables had a tolerance range between 0.34-0.650.

I used an information-theoretic approach to develop *a priori* models that best explained Indian fox space use patterns. I developed a global model that included relative abundance of rodents, dog presence and landcover variables that are considered as important predictors of Indian fox habitat use (Vanak, Chapter 3), and assessed the significance of this model using a likelihood ratio test. Using variables derived from the global model, I developed seven sets of candidate sub-global models (Table 2). These candidate models reflect specific hypotheses about the relationship between the variables and space use by Indian foxes (Table 2).

I used Akaike's Information Criterion (AIC) to assess model weights and ranked candidate models using ΔAIC (Burnham and Anderson 2002). I used Akaike weights (w_i) to determine the relative support for a model given the data for the set of candidate models. To account for model selection uncertainty I averaged the estimates of the coefficients of main effect variables in each model with $\Delta AIC \leq 2$ (Burnham and Anderson 2002). I determined the magnitude of the effect of each predictor variable on the response variable by the odds ratio (Allison 1999). The odds ratio indicates the change in the odds of the response variable (i.e., probability of use) for an increase in the predictor variable, when all other predictor variables are held constant.

Model validation

I estimated the validity of the models in the choice-set by generating a receiver operating characteristic (ROC) curve. ROC curves are calculated by evaluating sensitivity and specificity values at different probability cut-off levels within the data to produce to pairs of sensitivity/specificity values. Plotting sensitivity as a function of 1 – specificity for each threshold yields the ROC curve. The area under the curve (AUC) is used as an assessment of model performance or predictive power, wherein a model with no predictive power has an AUC of 0.5, while an AUC of 1.0 indicates a perfect model. Since the area under the curve (AUC) is a threshold-free index of classification performance, it does not require designation of an arbitrary cutoff for specifying presence or absence from probability values (Fielding and Bell 1997). I fitted the used/available dataset with the the model averaged parameter estimates and calculated specificity/sensitivity values using a web-based ROC software (Eng et al. 2005). The software computes the ROC and provides an AUC value. Values of AUC 0.7 – 0.9 indicate good model predictive ability, while values >0.9 indicate excellent model performance.

RESULTS

I obtained sufficient telemetry data to calculate home-ranges and utilization distributions for 32 foxes between April 2006 to May 2007 and for 24 dogs from November 2005 to April 2007. Mean Indian fox 95% kernel home-range sizes were 2.39 km^2 (± 0.31 SE) and mean dog home-range sizes were 0.45 km^2 (± 0.11 SE). The mean VI index of overlap between Indian foxes and dogs was 0.08 (± 0.01 SE, range = 0.02 – 0.23, n = 45; Fig. 2).

Rodent abundance in the landscape varied by habitat types with fallow land having the highest densities of burrows and plantations having the lowest densities (Table 1). Logistic regression analysis of dog habitat use indicated selection of human modified habitat, with human settlements, agricultural land, bare-ground, and plantations having a positive effect on dog selection and grasslands, fallows and ploughed land having a negative effect (Table 1).

Model selection

The best fit model with the lowest AIC score among the candidate models with an AIC weight of 0.686 supported the hypothesis that habitat parameters as well as the presence of dogs influenced Indian fox space use (Table 3). The next best supported model included habitat parameters and presence of dogs and rodents with an AIC weight of 0.314. All other models had a ΔAIC >10 and therefore provided little support. Model averaged parameter coefficients for the top ranked model showed negative effects of dog presence, agriculture, plantations and ploughed land and positive effects of grasslands and rodents (Table 4). The odds ratio estimates indicate that grassland, ploughed land and dogs have the strongest effects on fox space use (Table 4). The odds of an area being used by foxes increases by a factor of 9.5 if it is grassland habitat, decreases by a factor of 0.73 in the case of ploughed land, and decreases by a factor of 0.99 if dog presence increases. Other variables in the model such as plantations and agriculture have little effect as the confidence intervals of the odds ratio include 1.00. The AUC value for the ROC curve (Fig. 3) of the final model was 0.79 with a 77.6:19.4 percent concordance to discordance ratio with the remaining 2.9% tied.

DISCUSSION

Scattered interspecies territories and avoidance of competitor presence are indicators of interference competition. Our results show that Indian fox space use is influenced by the presence of dogs at the home-range and landscape level. The low overlap between Indian fox and dog 95% kernel home ranges indicates a clear partitioning of space use between the species. This pattern of spatial segregation has been observed in other canids as well (e.g. coyotes and red foxes; Harrison et al. 1989; Sargeant et al. 1987). However, this segregation may simply be a function of differential preferences in habitat or prey selection (Gosselink 2003; Todd et al. 1985) rather than competitive exclusion. Indian foxes prefer grasslands over human-modified habitats (Vanak, Chapter 3), whereas dogs may select for agricultural fields and human settlements.

Indian fox space use was not explained by habitat alone, since habitat only models had no support among the top ranked models. This was also true for dog presence and rodent abundance models, indicating that competitor presence and/or primary prey alone were not good predictors of fox space use. Instead, candidate models with combined effects of landcover type, the presence of dogs and rodent abundance were the best predictors of fox space use. Based on the model averaged estimates from the top AIC models, grasslands are the main positive influence on fox space use, whereas human modified habitats such as ploughed land and the presence of dogs are the main negative influences. Thus, although Indian fox space use is determined primarily by habitat type, the presence of an interference competitor also has an important influence on space use.

The avoidance of prey rich habitats due to the presence of an interference competitor is also seen in the similar sized kit fox. Kit foxes partition habitat, space and diet with larger coyotes (Nelson et al. 2007). The preferred prey of kit foxes, Heerman’s kangaroo rat *Dipodomys heermani,* is more abundant in shrub habitats than in grassland habitats, but kit foxes had less shrub habitat in core use areas compared to the rest of the home range. This suggests that avoiding the risk of encountering coyotes in shrub habitats is a greater influence on kit fox habitat selection than relative prey abundance (Nelson et al. 2007). This is understandable since coyotes and kit foxes compete for similar prey, and coyotes are one of the main intraguild predators of kit foxes, and thus are expected to displace foxes from the best foraging habitats. However, Indian foxes and domestic dogs show low dietary overlap and therefore do not appear to compete for the same food resources (Vanak, chapter 4). Furthermore, even though rodent abundances are higher in agricultural lands than in grasslands or plantations these habitats are negatively associated with fox use. Dogs on the other hand are positively associated with agricultural habitats. The presence of dogs in agricultural fields may have a negative effect on fox space use and may preclude foxes from foraging in prey rich habitats such as fallow and agricultural lands (Table 1). This further supports the argument that dogs play the role of a mid-sized canid in intraguild interactions with smaller carnivores (Vanak, Chapter 5), resulting in risk aversion behavior at the cost of foraging opportunities for the subordinate competitor.

These results suggest that the competitive intraguild dynamics that are seen among wild carnivores can also occur between wild and domestic carnivores, despite a seeming lack of competition for food and other resources. The role of dogs as intraguild competitors of wild carnivores has thus far been under-recognized (Vanak, Chapter 2). Dogs are among the world’s most common carnivores and are heavily subsidized by humans. As a result, they can occur at high densities even in rural areas, where they tend to range freely into wild habitats. Therefore, dogs can pose threats to native carnivore communities, and extend the edge of anthropogenic disturbance well beyond the borders of human settlements.

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

Landcover	Rodent burrows/ha	SD	n	Dog parameter estimates	SE
Grassland	25.66	21.24	26	-0.021	0.09
Fallow	55.79	32.11	7	-0.272	0.12
Agriculture	34.37	29.88	19	0.295	0.10
Ploughed*	34.37	29.88	19	-0.896	0.12
Plantation	7.48	8.69	4	0.291	0.10
Bare ground	0	0	0	0.210	0.15
Human settlements	0	0	0	0.340	0.05

* Rodent estimates for ploughed land are the same as for agriculture.

Table 2. *A priori* hypotheses and specific models to test the influence of habitat, primary prey, and competitor presence on the space use patterns of Indian foxes.

Hypothesis	Model	Model Structure	Expected result
1) Habitat Positive effect of grasslands	Grass	$\beta_0 + \beta_{grass}$	$\beta_{grass}>0$
2) Habitat Positive effect of grasslands and plantations	Grs + Plnt	$\beta_0 + \beta_{grass} + \beta_{plnt}$	$\beta_{grass}>0$, $\beta_{plnt}>0$
3) Habitat Negative effects of agriculture and ploughed land and positive effects of grassland and plantation	Grs + Plnt + Agri + Plgh	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag} + \beta_{Plgh}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$,
4) Habitat Negative effects of agriculture, ploughed land and bare soil and positive effects of grassland and plantation	Grs + Plnt + Agri + Plgh + Soil	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag} + \beta_{Plgh} + \beta_{soil}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{soil}<0$
5) Dog Negative effects of dog presence	Dogs	$\beta_0 + \beta_{dogs}$	$\beta_{dogs}<0$
6) Rodents Positive effects of rodents	Rodents	$\beta_0 + \beta_{rodents}$	$\beta_{rodents}>0$
7) Dog+Habitat Positive effects of grassland and negative effects of dog presence	Grs + Dogs	$\beta_0 + \beta_{grass} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{dogs}<0$
8) Dog+Habitat Negative effects of agriculture, ploughed land and dog presence and positive effects of grassland and plantation	Grs + Plnt + Agri + Plgh + Dogs	$\beta_0 + \beta_{grass} + \beta_{plnt} + \beta_{Ag} + \beta_{Plgh} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{dogs} <0$
9) Dog+Habitat Negative effects of agriculture and dog presence and positive effects of grassland	Grs + Agri + Dogs	$\beta_0 + \beta_{grass} + \beta_{Ag} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{Ag}<0$, $\beta_{dogs} <0$
10) Dog+Rodents Positive effects of rodents and negative effects of dog presence	Rodents + Dogs	$\beta_0 + \beta_{rodents} + \beta_{dogs}$	$\beta_{rodents}>0$, $\beta_{dogs}<0$

11) Habitat+Dog+Rodents Positive effects of grassland and rodents and negative effects of dog presence	Grs + Rodents + Dogs	$\beta_0 + \beta_{grass} + \beta_{rodents} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{rodents}>0$, $\beta_{dogs} <0$
12) Habitat+Dog+Rodents Negative effects of agriculture and dog presence and positive effects of grassland and rodents	Grs + Agri + Rodents + Dogs	$\beta_0 + \beta_{grass} + \beta_{Ag} + \beta_{rodents} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{Ag}<0$, $\beta_{rodents}>0$, $\beta_{dogs} <0$
13) Habitat+Dog+Rodents Negative effects of agriculture, ploughed land bare soil and dog presence and positive effects of grassland, plantation and rodents	Grs + Plnt + Agri + Plgh + Rodents + Dogs	$\beta_0+ \beta_{grass}+ \beta_{plnt} +\beta_{Ag}+ \beta_{Plgh} + \beta_{rodents} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{rodents}>0$, $\beta_{dogs} <0$
14) Global Negative effects of agriculture, ploughed land bare soil and dog presence and positive effects of grassland, plantation and rodents	Grs + Plnt + Agri + Plgh + Soil + Rodents + Dogs	$\beta_0+ \beta_{grass}+ \beta_{plnt} +\beta_{Ag}+ \beta_{Plgh} + \beta_{soil} + \beta_{rodents} + \beta_{dogs}$	$\beta_{grass}>0$, $\beta_{plnt}>0$, $\beta_{Ag}<0$, $\beta_{Plgh} <0$, $\beta_{soil}<0$, $\beta_{rodents}>0$, $\beta_{dogs} <0$

Table 3. Models ranked by AIC values that best explain the contribution of various parameters to Indian fox space use in the great Indian bustard sanctuary in 2005-2006. Columns include the number of variables (*K*), Akaike's Information Criterion (AIC), distance from the lowest AIC (Δ AIC), and Akaike's model weight (w_i).

Model	AIC	K	Δ AIC	ω_i
8) Grs+plnt+agri+plgh+dog	3869.364	5	0	0.686
13) Grs+plnt+agri+plgh+dog+rdnts	3870.93	6	1.566	0.314
14) Grs+plnt+agri+plgh+soil+dog+rdnts	3889.983	7	20.619	0.000
4) Grs+plnt+agri+plgh+soil	3899.482	5	30.118	0.000
9) Grs+agri+dog	3922.148	3	52.784	0.000
12) Grs+agri+dog+rdnts	3923.122	4	53.758	0.000
7) Grs+dog	3923.178	2	55.814	0.000
11) Grs+dog+rdnts	3940.630	3	71.626	0.000
3) Grs+plnt+agri+plgh	3974.870	4	105.506	0.000
2) Grs+Plnt	4205.318	2	335.954	0.000
1) Grs	4347.646	1	478.282	0.000
10) Dogs+rdnts	4973.163	2	1100.84	0.000
5) Dogs	4973.613	1	1104.25	0.000
6) Rdnts	5108.357	1	1234.82	0.000

Table 4. Most influential *a priori* model parameter estimates, odds ratios, 95% confidence intervals of odds ratios, model-averaged parameter estimates and unconditional standard errors (SE) of variables in the top models explaining Indian fox space use patterns.

Parameter	Estimate	Odds Ratio	Lower CI	Upper CI	Model averaged estimate	Uncond. SE
Intercept	-1.13				-1.16	0.158
Grass	2.23	9.496	7.158	12.597	2.24	0.142
Plantation	-0.036	1.004	0.772	1.304	-0.02	0.149
Agriculture	-0.16	0.852	0.442	1.640	-0.16	0.338
Ploughed	-1.32	0.27	0.190	0.385	-1.32	0.179
Dog	-4.29	0.014	0.005	0.038	-4.28	0.537
Rodents	0.003	1.003	0.995	1.011	0.001	0.0008

Figure 1. Raster image of rodent landscape based on estimates of rodent burrows in different habitat types in and around the Great Indian Bustard Sanctuary, Maharashtra, India. Darker areas represent higher rodent abundance.

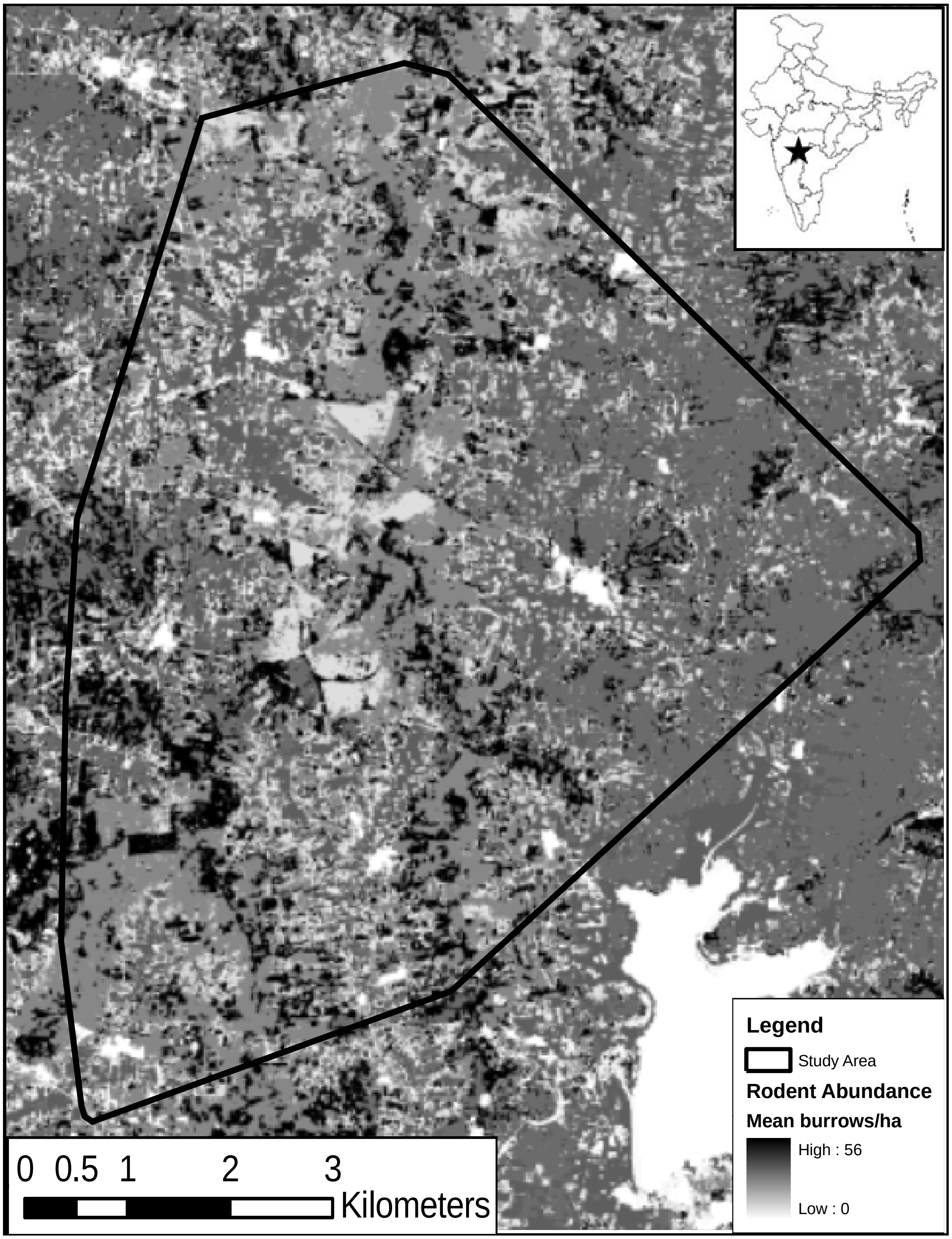


Figure 2. Map of study area with 95% kernel home ranges of foxes (n= 18, grey shading) and dogs (n=25, pink shading) illustrating the low overlap between dogs and foxes in the landscape. Note that not all fox home-ranges have been plotted on this map for the sake of clarity.

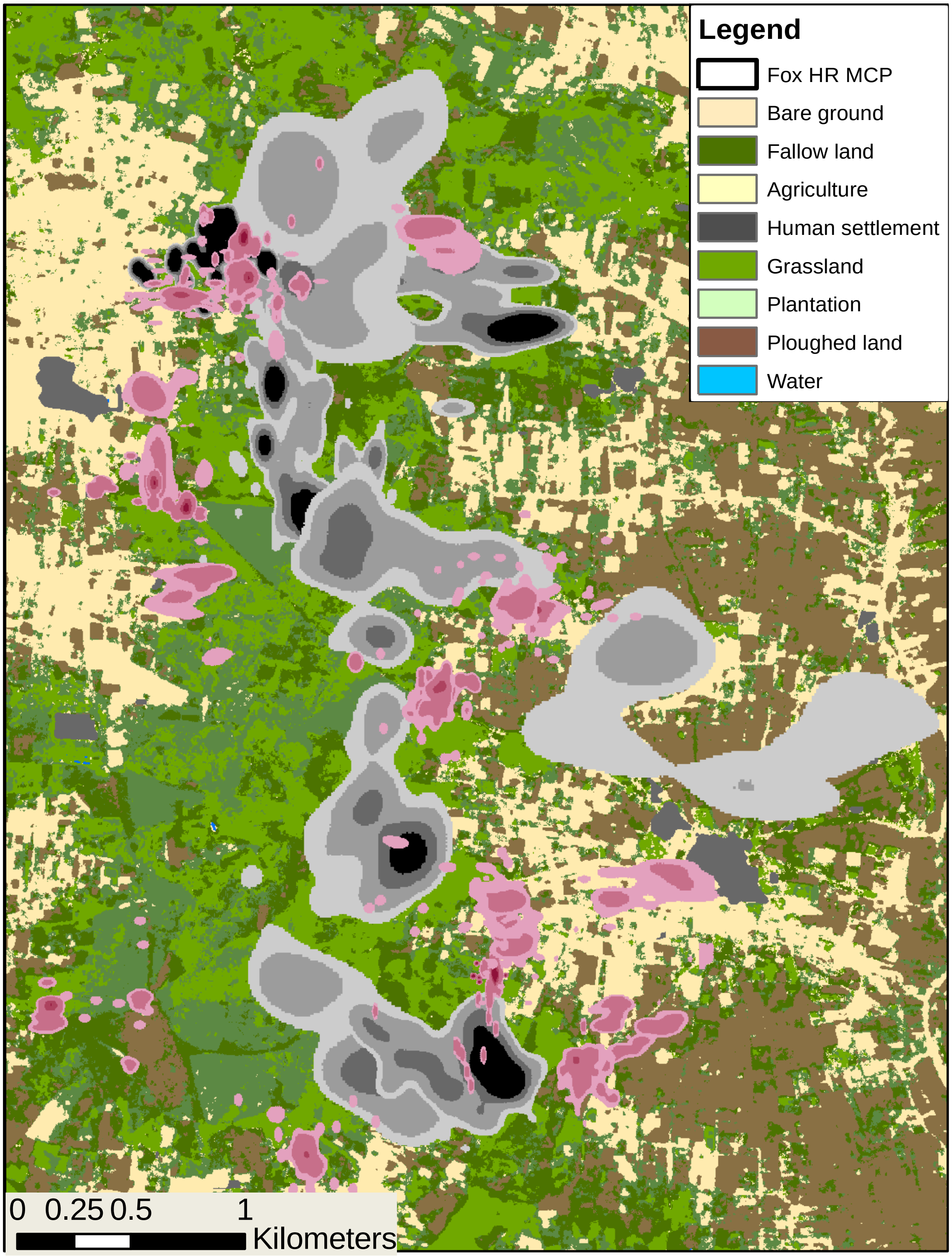
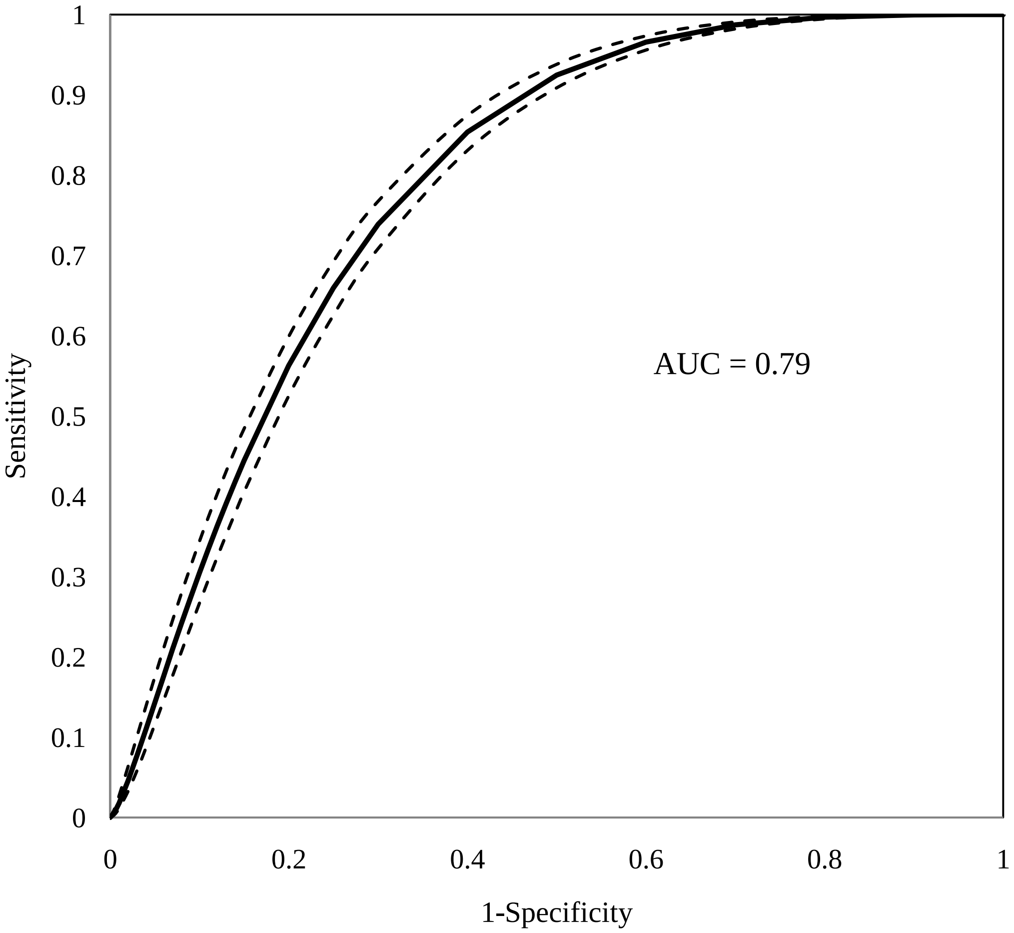


Figure 3. Receiver operating characteristic curve for Indian fox logistic regression model. Dashed lines indicate upper and lower 95% confidence intervals.



APPENDIX I

Record of Indian fox captures in the Great Indian Bustard Wildlife Sanctuary, India, showing the date of capture, sex, estimated age, and weight, and confirmed or suspected cause of mortality if dead.

Fox ID	Date of capture	Sex	Estimated age	Weight (Kg)	Status at end of study (Jul -07)
F01	13/02/06	M	Old Adult	1.98	Dead 13/02/06 High CDV infection
F02	25/04/06	F	Adult	2.34	Alive
F03	26/04/06	M	Adult	2.76	Alive
F04	27/04/06	F	Young adult	2.26	Alive
F05	05/05/06	M	Young adult	1.82	Dead 22/05/06 – possible CDV infection
F06	05/05/06	M	Adult	2.58	Dead 27/05/06 – High CDV infection
F07	06/05/06	M	Old Adult	2.32	Dead 29/08/06 – Possible dog predation
F08	06/05/06	F	Adult	2.04	Suspected poaching 04/06/06
F09	18/05/06	F	Juvenile	1.86	Dead 20/06/06 – Possible dog predation
F10	19/06/06	M	Adult	2.66	Alive
F11	21/06/06	F	Adult	2.36	Dead 30/06/06 – High CDV infection
F12	05/07/06	F	Adult	2.28	Dead – 19/04/07 Possible dog predation
F13	05/07/06	M	Adult	2.6	Alive – Collar dropped
F14	05/07/06	M	Adult	2.93	Alive – Collar dropped
F15	14/07/06	M	Young Adult	2.3	Dead 25/07/06 High CDV infection
F16	15/07/06	F	Adult	2.3	Alive
F17	15/07/06	M	Old Adult	2.36	Dead 23/01/07 – Possible territorial fight
F18	25/07/06	F	Adult	2.5	Alive
F19	25/07/06	F	Young adult	2.08	Dead 26/08/06 Poaching
F20	25/07/06	F	Young Adult	2.08	Dead 25/09/06 Possible dog predation
F21	28/10/06	M	Adult	2.94	Alive
F22	25/02/07	M	Adult	3.26	Dead 18/01/07 Poaching
F23	25/02/07	M	Adult	2.58	Alive
F24	26/02/07	F	Adult	2.26	Presumed poached – Collar not found
F25	26/02/07	M	Adult	2.74	Alive
F26	03/03/07	M	Adult	2.78	Alive
F27	03/03/07	F	Adult	2.92	Alive
F28	04/03/07	M	Adult	3.1	Alive
F29	04/03/07	F	Old Adult	2.1	Alive
F30	04/03/07	F	Adult	2.02	Alive
F31	05/03/07	M	Adult	2.64	Dead 27/05/07– Presumed poached
F32	22/03/07	F	Adult	2.18	Alive
F33	22/03/07	M	Adult	3.06	Alive
F34	22/03/07	M	Adult	2.82	Alive
F35	23/03/07	F	Adult	2.52	Alive
F36	23/03/07	M	Subadult	2.12	Alive

APPENDIX II

ArcView 3.3 AML script to estimate the volume of intersection index (VI) between overlapping utilization distributions developed by Aditya Singh (aditya.arch@gmail.com)

LOADING SCRIPTS

1. Double-click on an empty area on the bar containing all buttons, The "Customize" dialog appears

2. In the "Type" pull-down, select "View"

3. In the "Category" pull-down, select "Buttons", The display right below the pull down changes to show an array of buttons

4. Slide the scrollbar (below the button display) to the right and select the last button by clicking on it, Now click on "New"

5. A new blank button appears. Double-click on the blank area to the right of the entry "Click" (just below the button display)

6. The "Script Manager" Dialog appears, Click on "New", Enter a new name in the input box

7. A new blank script document (with the name just specified) appears. Delete its contents.

8. Either copy-paste this ENTIRE script on the document, or, click on the button with the open-folder icon (tooltip reads "Load text file") and navigate to this file.

9. Click on the button with the tick-mark icon ("compile"). Make sure spatial analyst is loaded first.

10. After the script is compiled, close the script window and return to the view

11. Click on the new button to run the script

#SCRIPT 1 – Load Matlab UD files with X Y and Z columns

```
theView = av.GetActiveDoc

TheThemes=TheView.GetActiveThemes

GridList={}
GridName={}

for each t in TheThemes
   if (t.Is(GTheme)) Then
     g1=t.GetGrid
     g2=g1/g1.GetStatistics.Get(1).AsGrid
     g3=(g2.IsNull).con(0.AsGrid,g2)
     NRows=g3.GetNumRowsAndCols.Get(0)
     NCols=g3.GetNumRowsAndCols.Get(1)
     TheMean=g3.GetStatistics.get(2)
     TheSum=NRows*NCols*TheMean
     g4=g3/TheSum.AsGrid
     GridList.Add(g4)
     GridName.Add(t.GetName)
   end
end
```

#SCRIPT 2: Calculate VI index by selecting active themes

```
GridCount=GridList.Count

aFN=FileDialog.Put("CrossTab.dbf".AsFileName,"*.dbf","Specify location of Crosstab file")
NewVtab=VTab.MakeNew (aFN,dBase)

RefFld =Field.Make("Cross",#FIELD_CHAR,10,0)
AddField={RefFld}
for each f in GridName
  NewField=Field.Make(f,#FIELD_DECIMAL,40,10)
  Addfield.Add(NewField)
end
NewVtab.AddFields(AddField)

ctr=0

GridList1=GridList.DeepClone
GridList2=GridList.DeepClone

for each d in 0..(GridCount-1)
  NR=NewVTab.Addrecord
  NewVtab.SetValue(RefFld,NR,GridName.Get(d))
  for each f in 0..(GridCount-1)
    if (d>=f) then
      Grid1=GridList1.Get(d)
      Grid2=GridList2.Get(f)

      VI=Grid1.LocalStats(#GRID_STATYPE_MIN,{Grid2})

      st=VI.GetStatistics.Get(2)

      gd=(VI.GetNumRowsAndCols.Get(0))*(VI.GetNumRowsAndCols.Get(1))*st
      TheFld=NewVtab.FindField(GridName.Get(f))
      NewVtab.SetValue(TheFld,NR,gd)

    end
  end
end

msgbox.info("Process complete","Process complete")
```

VITA

Abi Tamim Vanak was born in India and graduated with a Bachelor of Science degree in Zoology from Loyola College, Madras University in 1995. He went on to complete his Masters degree in Wildlife Sciences at the Wildlife Institute of India, Dehradun in 1997. After his masters, Abi worked for several years as a research associate with several conservation and research organisations in India, namely the Wildlife Institute of India, Wildlife Protection Society of India, Centre for Wildlife Studies and Ashoka Trust for Research in Ecology and the Environment. In 2003 he started his doctoral program at the University of Missouri.

Abi and his wife Maria Thaker (who is scheduled to complete her Ph.D. in April of 2009 from Indiana State University) hope to continue to integrate their passion for science and conservation in the developing world.