

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

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The competitive dynamics between domestic and native carnivores are poorly studied. We examined competition for food between sympatric populations of free-ranging dogs (*Canis familiaris*) and Indian foxes (*Vulpes bengalensis*) through dietary analysis in a protected, dry grassland habitat in central India. We expected significant dietary overlap between dogs and foxes because of clear evidence of interference competition between dogs and foxes in this area. However, dogs subsisted largely on human-derived foods (HDFs) from direct feeding, and scavenging on garbage, crop residue, and livestock carcasses (83% relative occurrence [RO]). Wild-caught foods constituted only 11% RO of the diet of dogs. The majority of the diet of Indian foxes consisted of invertebrates (33% RO), rodents (20% RO), and fruits of *Zizyphus* (18.5% RO). Indian foxes did not consume HDF, nor did they scavenge from large-mammal carcasses, and included only a small portion of agricultural produce in their diet. The low contribution of HDF and agricultural food sources to the diet of Indian foxes was surprising because this species is a generalist omnivore. Dogs may be preventing foxes from accessing agricultural lands and human-associated foods by interference competition.

Key words: *Canis familiaris*, dietary overlap, human-derived food, interference competition, *Vulpes bengalensis*

Sympatric carnivores often compete for similar resources. The directionality of the competitive interaction 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). Interference competition, including intraguild predation, 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). It is assumed that competition for resources may be one of the main drivers of interference competition (Case and Gilpin 1974; Palomares and Caro 1999; Polis et al. 1989). For example, coyotes (*Canis latrans*) compete for similar food resources with swift foxes (*Vulpes velox*) and kit foxes (*V. macrotis*), as indicated by a high dietary overlap (Kamler et al. 2007a; Kitchen et al. 1999; Nelson et al. 2007; White et al. 1995). Coyotes also are interference competitors, as well as one of the main causes of mortality for swift foxes and kit

foxes (Cypher and Spencer 1998; Kamler et al. 2003; Kitchen et al. 1999; Nelson et al. 2007; Ralls and White 1995).

Given the potential importance of competitive dynamics between carnivores, it is surprising that resource competition between native carnivores and free-ranging domestic carnivores such as the dog (*C. familiaris*) is relatively unstudied. The dog is probably the most numerous carnivore in the world today (Daniels and Bekoff 1989; Wandeler et al. 1993; World Health Organization–World Society for the Protection of Animals 1990), and in much of the world, dogs are free-ranging. Although dogs may be owned or affiliated with humans, free-ranging dogs are not confined, and can therefore 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; Vanak and Gompper, in press). Despite large global populations of dogs in rural or natural environments, 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; Glen and Dickman 2008; Glen et al. 2006; Mitchell and Banks 2005).

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Although dogs are known to kill and feed on wildlife, much 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 (HDF—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 HDF is 1 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 (Atickem 2003; Boitani et al. 1995; Butler et al. 2004). Herein, we examine the potential for resource competition between free-ranging dogs and a little-studied canid, the Indian fox (*Vulpes bengalensis*), in a semiarid grassland ecosystem of central India using data on dietary overlap. The Indian fox is a small (mean adult body weight \approx 2.5 kg—Vanak 2008) 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 a putatively common canid, little is known about its basic ecology. 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).

We expected that competition for food between dogs and Indian foxes would be high for several reasons. First, experimental studies conducted at the same site as our study showed that Indian foxes reduced consumption rates at experimental food trays and displayed increased vigilance behavior when exposed to a caged dog placed 20 m from the trays (Vanak 2008). Second, the avoidance of dogs appears to manifest itself at the landscape level as well. The presence of dogs had a negative influence on the space-use and habitat-selection patterns of Indian foxes. The home ranges of Indian foxes and dogs show low overlap, and the habitat use of radiotracked Indian foxes was negatively associated with presence of dogs (Vanak 2008). Third, dogs are a direct source of mortality of Indian foxes. Of 14 recorded mortalities (including 5 deaths due to poaching) of radiomonitored Indian foxes, 4 were due to direct killing by dogs (Vanak 2008). Importantly, the Indian foxes killed by dogs were not consumed, fitting the expected patterns of intraguild predation due to interference competition. Competition for resources is assumed to be the main driver of interference interactions in carnivores (Holt and Polis 1997) because carnivores with greater dietary overlap also display the most intense competition (Creel et al. 2001; Linnell and Strand 2000). Thus, the interference interactions between dogs and Indian foxes may be a manifestation of competition for resources. In this study area, we predicted that dietary overlap between

Indian foxes and dogs would be ecologically significant, because both species should use agricultural food sources and small vertebrates. However, given that dogs were directly fed or scavenged human refuse, we expected low overlap of HDF in the diets of these 2 species.

MATERIALS AND METHODS

Study area.—Our study was conducted in the Great Indian Bustard Sanctuary at Nannaj, Maharashtra, in central India (17°49'40"N, 75°51'35"E). The sanctuary consists of 6 protected grassland patches (34–200 ha) within a matrix of sugarcane fields, vineyards, seasonal crops, communal grazing lands, and forestry plantations. The study area was bordered by several villages with a combined human population of approximately 50,000 that is largely dependent on agropastoralism (<http://solapur.gov.in/htmldocs/dgraph.htm>, accessed 11 June 2008). This region experiences a wet season from July to October, during which 95% of the precipitation occurs (temperature range = 16–32°C, mean annual precipitation = 600 mm), a cool-dry season from November to February (temperature range = 6–37°C), and a hot-dry season from March to June (temperature range = 18–47°C).

Indian foxes are a common carnivore in the natural grassland habitats of the Great Indian Bustard Sanctuary, as they are in many grassland habitats of India (Vanak and Gompper 2007), and also are 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/km² in farmlands to 113 dogs/km² in the villages (Vanak 2007). Free-ranging adult dogs in this area weigh approximately 17 kg (Vanak 2007) and may be grouped into 3 categories: herding dogs that accompany grazing livestock into grassland habitat during the day, farm dogs that are a continuous presence on the interface between farmlands and natural grasslands, and village dogs that rarely foray into grassland habitats. Other carnivores that are found in the study area include the Indian gray wolf (*C. lupus pallipes*); the home range of 1 wolf pack overlapped the study area—Habib 2007), golden jackal (*C. aureus*), jungle cat (*Felis chaus*), and gray mongoose (*Herpestes edwardsi*). However, unlike foxes and dogs, none of these species are common, and are rarely encountered (A. T. Vanak, pers. obs.).

Dietary analyses.—We determined the diet of dogs and Indian foxes by fecal analysis. Scats from dogs were collected opportunistically every month for 20 months (2005–2007) from the vicinity of farms and in grassland habitat outside villages where known ear-tagged and radiocollared dogs were observed (Vanak 2007, 2008). Village dogs rarely ventured into grassland habitats and we 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 during the same time period from the vicinity of dens of radiocollared foxes ($n = 23$) and from trails used by foxes that we regularly

monitored. Fox scats were differentiated from scats of dogs and other carnivores based on size and shape (Vanak and Mukherjee 2008). Although we collected scats from both adults and pups from den sites, we only report results from analyses of scats of adults because we do not have comparable data from dog pups. Only recent scats with no loss of color or perceptible signs of erosion were collected (List et al. 2003). All scats were placed in paper bags marked with the date and site of collection and air-dried for 7–10 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 slides 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. Except for poultry feathers, feathers and egg fragments were grouped as bird remains but were not identified further because of inadequate reference materials. Invertebrates were classified as termites, ants, beetles, grasshoppers, or “other” (including other insects, scorpions, and centipedes) if they were found in <5% of scats. Scats also contained HDF, which included garbage, millet bread, and human feces. These were identified by texture and appearance (e.g., grain fragments or fibrous millet bread, and remains of plastic bags). Although we could not specifically identify the remains of human feces in dog scats, dogs were regularly observed consuming human feces from the vicinity of households and farms.

Because identification of dietary remains was sometimes limited to the family level or higher, the number of taxonomically different food groups underrepresents the true number of species consumed. To standardize for differences in the level of identification of taxa consumed by dogs and Indian foxes, we defined a food group as consisting of remains that were broadly categorized as invertebrates, mammals, birds, reptiles, seeds (fruit), vegetation, crops, and HDF. We did not contrast seasonal differences in the diet of dogs and Indian foxes because this information is available elsewhere (Vanak 2008) and our main aim was to compare overall diets of these 2 species. 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 percent relative 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), we used this measure because we are mainly interested in comparing diets between species.

We compared the FO of each food item between species using a chi-square test (Reynolds and Aebischer 1991). We 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). We used EcoSim 7 software (Gotelli and Entsminger 2006) to test for significance of 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, we collected 436 Indian fox scats (cool-dry season = 236; hot-dry season = 145; wet season = 55) and 320 dog scats (cool-dry = 90; hot-dry = 150; wet = 80). Scat numbers are low for the wet season because rains and dung beetle activity quickly eroded fresh scats. We 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 because of the more diverse diets of foxes (see below).

Diet of free-ranging dogs.—We identified several categories of food used by dogs, including HDF (mainly from household garbage and millet bread), domestic ungulates (cattle, water buffalo, goats, and sheep), 2 occurrences of blackbuck (*Antelope cervicapra*), rodents (*Golunda ellioti* and *Rattus*), lagomorphs (*Lepus nigricollis*), birds (poultry), reptiles (*Calotes versicolor*), insects (mainly coleopterans), fruit (*Zizyphus*, grapes, and guava), and crops (millet, sorghum, corn, wheat, and peanuts). The main constituent of the diet of dogs was HDF, which occurred in 90.6% (FO) of all scats and comprised 40% (RO) of all items identified (Table 1). Crops such as millet, sorghum, and corn were the 2nd most common food item consumed by dogs, collectively occurring in almost

TABLE 1.—Comparison of the diets of dogs (*Canis familiaris*) and Indian foxes (*Vulpes bengalensis*) 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	
	Dog	Indian fox	χ^2	Dog	Indian fox
Human-derived	90.6	0		40.7	0
Large mammal (total)	40.6	0		18.3	0
Cattle	13.8			6.2	
Water buffalo	3.4			1.5	
Goat	22.2			10.0	
Sheep	6.6			3.0	
Blackbuck (<i>Antelope cervicapra</i>)	0.6			0.3	
Unidentified large mammal	2.5			1.1	
Small mammal (total)	5	57.1	43.6**	2.3	20.6
Bush rat (<i>Golunda ellioti</i>)	1.6	35.1		0.7	12.7
Mice (<i>Mus</i>)	0	13.7		0	5.0
Indian gerbil (<i>Tatera indica</i>)	0	4.3		0	1.6
Rats (<i>Rattus</i>)	1.6	0		0.7	0
Palm squirrel (<i>Funambulus tristriatus</i>)	0	1.1		0	0.4
Shrews (<i>Suncus</i>)	0	1.8		0	0.7
Indian hare (<i>Lepus nigricollis</i>)	0.6	11.2		0.3	4.0
Unidentified small mammal	1.3	9.4		0.6	3.4
Bird	8.1	19.7	5.1*	3.7	7.1
Reptile	1.3	35.8	33.1**	0.6	12.9
Garden lizard (<i>Calotes versicolor</i>)	1.3	29.7		0.6	10.7
Saw-scaled viper (<i>Echis carinatus</i>)		5.5			2.0
Fan-throated lizard (<i>Sitana ponticeriana</i>)		3.4			1.2
Unidentified snakes and skinks		3.4			1.2
Invertebrates					
Isoptera	0	43.8		0	15.8
Hymenoptera	0	6.7		0	2.4
Orthoptera	0	13.8		0	5.0
Coleoptera	6.9	28.2	11.1**	3.1	10.2
Others + unidentified	2.5	1.2		1.1	0.4
<i>Zizyphus mauritiana</i>	11.3	51.4	25.8**	5.1	18.5
Grapes	3.8	3.7		1.7	1.3
Crops	51.9	4.4	41.4**	23.3	1.6
Vegetation	1.9	11.5	6.2*	0.8	4.1

52% (FO) of all scats and comprising 23.3% (RO) of their diet. The 3rd most important component of the diet of dogs was the remains of domestic ungulates (41% FO, 18.3% RO). Remains of wild-caught food such as small mammals, birds, reptiles, and invertebrates combined were found in 22.5% of all dog scats, and contributed 10.1% (RO) to their diets. The overall niche breadth of dogs was 2.75.

Diet of Indian foxes.—We identified a greater diversity of food items in scats of Indian fox ($B_A = 6.1$). The main constituent of the diet of Indian foxes 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 an RO of 20.6%. Among the small mammals eaten by Indian foxes, bush rats (*G. ellioti*) were the most common prey (FO = 61.4%), followed by mice (*Mus*; FO = 24%) and Indian hares (*L. nigricollis*; FO = 19.6%). Other small mammals detected in the feces of Indian foxes were Indian gerbils (*Tatera indica*), shrews (*Suncus*), and palm squirrels (*Funambulus tristriatus*). The 3rd most important food item eaten by Indian foxes was the fruit of *Zizyphus* (FO = 51.4%, RO = 18.5%). Other food items in the diet of Indian foxes

included reptiles and birds. Reptiles were found in 35.8% FO of all fox scats and contributed nearly 13% RO to their diet. Of these, the garden lizard (*C. 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 scats that contained reptile remains. Bird remains most likely consisted of ground-nesting species such as quail (*Perdica*), partridges (*Franco-linus*), and sandgrouse (*Pterocles*), although we were unable to more fully verify this due to insufficient reference materials. Vegetation and soil also were found in a large percentage of scats, and were considered nondietary items.

There was a general lack of human-associated foods in Indian fox diet; HDF 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, and all these combined contributed <3% RO to fox diet (Table 1). There was no indication that foxes scavenged from carcasses of large mammals.

Dietary comparisons.—Indian foxes and dogs exhibited low dietary overlap ($O_{fd} = 0.13$) and this overlap was nonsignif-

icant at the $\alpha = 5\%$ level based on the randomly simulated matrices ($\bar{X} = 0.38$, variance = 0.027, $P_{\text{obs}>\text{exp}} = 0.96$). A number of food categories consumed by dogs were absent from the diets of Indian foxes, such as HDF 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) for which dogs and foxes overlapped (Table 1). Small mammals, birds, reptiles, invertebrates, *Zizyphus* fruits, 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 Indian foxes (Table 1).

DISCUSSION

In the Great Indian Bustard Sanctuary, the diet of dogs appeared typical of free-ranging dogs in other rural areas of the world, with a primary reliance on human-associated foods. Similarly, Indian foxes had a diet typical of fox species in semiarid regions, consuming a diversity of food items including invertebrates, small mammals, and fruits. As a consequence, dogs and Indian foxes in the Great Indian Bustard Sanctuary had low and nonsignificant dietary niche overlap. This finding was contrary to our predictions given the extent to which dogs may be interference competitors with foxes.

The diet of dogs in the Great Indian Bustard Sanctuary consisted largely of HDF and other human-associated foods, similar to those of free-ranging dogs in rural Zimbabwe, Italy, and Ethiopia, where nearly 90% of the diets of dogs consist of HDF (Atickem 2003; Boitani et al. 1995; Butler and du Toit 2002). Dogs in our study area are either fed leftover food from households that they are associated with, or scavenged garbage and human feces from the vicinity of houses and farmlands. Thus, HDF, crops, and large-mammal remains (human-associated foods) formed 83% (RO) of the diet of dogs. Although large-mammal remains were a component of the diet of dogs, they were mainly livestock carcasses that villagers discarded on the periphery of the village (A. T. Vanak, pers. obs.). There was no evidence of dogs attacking and killing livestock, as has been reported from other areas in the world (Boitani et al. 1995). The relatively few instances of blackbuck remains in the diet of free-ranging dogs indicate low overlap between diets of dogs and wolves in this area as well, because the latter species is highly dependent on blackbuck at the Great Indian Bustard Sanctuary (Habib 2007). It is unclear if the blackbuck remains identified in dog feces were due to direct predation or scavenging of wolf-killed animals.

Indian foxes had a diet typical of fox species in semiarid regions, and also similar to that found elsewhere in India for this species (Gompper and Vanak 2006; Home 2005; Johnsingh 1978; Manakadan and Rahmani 2000). Because a variety of invertebrates, small mammals, *Zizyphus* fruits, and reptiles contributed $>85\%$ to diets of Indian foxes (Table 1), foxes had a much wider niche breadth than dogs. Indian foxes

in this area did not scavenge on large mammals, whereas this food contributed up to 5% of the diet of foxes in Gujarat, western India (Home 2005). The Gujarat study area had 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 was fragmented and the landscape was dominated by agriculture and human settlements. However, this human-modified landscape should represent a foraging opportunity for foxes in terms of increased rodent abundance (Bhaskaran 2006; Vanak 2008), HDF, and agricultural produce. Yet HDF and agricultural produce contributed little to the overall diet of Indian foxes.

In general, dogs and Indian foxes in this region had low and nonsignificant dietary niche overlap. Foxes relied almost entirely on wild-caught food, whereas dogs relied heavily on human-associated foods. However, other vulpine foxes living in rural, urban, or suburban habitats include human-associated foods in their diet (e.g., *V. vulpes* [Contesse et al. 2004], *V. cana* [Geffen et al. 1992], and *V. macrotis* [Warrick et al. 2007]). The limited consumption of agricultural crops and locally grown fruits and vegetables by Indian foxes was unexpected. Red foxes are known to include a wide variety of fruits and vegetables from agriculture in their diet (e.g., Contesse et al. 2004), as do swift foxes and kit foxes (Kamler et al. 2007b; Warrick et al. 2007). Indeed, foxes that subsist on or include HDF 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 dietary overlap between Indian foxes and dogs also does not mirror that found for introduced red foxes and dogs in Australia. Several studies in Australia have found high overlap between diets of dogs and red foxes (Glen and Dickman 2008; Mitchell and Banks 2005) as well as spatial exclusion of red foxes by dogs (Mitchell and Banks 2005). Notably, however, most free-ranging dogs in Australia are wild or truly feral and hence not dependent on HDF.

The low resource overlap between dogs and Indian foxes may be a function of the differences in body size between these species: dogs in our study region weigh about 17 kg whereas foxes weigh 2.5 kg, and thus may have distinct dietary niches. However, difference in body size alone is unlikely to explain the general lack of HDF, and particularly agricultural produce, in the diets of Indian foxes. In our study area, population densities of humans and dogs 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 among native canids (Johnson et al. 1996), and also have been observed between Indian foxes and dogs in this area (Vanak 2008). Given that the directionality of these interactions is driven by body size (Creel et al. 2001; Johnson et al. 1996; Palomares and Caro 1999; Vanak 2008), it is possible that dogs may directly or indirectly exclude Indian foxes from accessing HDF and agricultural produce (especially seasonally abundant foods such as grapes).

In protected and intact native habitats, this lack of access to human-associated food sources may not necessarily have a negative impact on Indian fox populations. However, prime Indian fox habitats in India are poorly represented in the protected area network (Vanak et al. 2008). Rather, grassland habitats outside protected areas are becoming increasingly human-impacted (Singh et al. 2006). It is in such areas that competition with domestic carnivores may play an important negative role in the continued persistence of small carnivores such as the Indian fox.

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