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Occupancy and diet of the Indian desert fox *Vulpes vulpes pusilla* in a *Prosopis juliflora* invaded semi-arid grassland

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Encroachment by woody invasive plants has been recognized as a major driver of structural change in grasslands ecosystems. The impact of invasive plant-mediated changes on mammalian species from higher trophic levels is relatively less understood. This study aims to understand the impact of woody encroachment on the ecology of a relatively understudied mesopredator, the Indian desert fox *Vulpes v. pusilla* in a semi-arid saline grassland ecosystem in Western India. We examined the site occupancy of the Indian desert fox at the landscape level, and den site selection at the micro-habitat scale. We also examined the diet of desert foxes during winter and summer season. We found that at the landscape level the desert fox selects more open *Suaeda* saline habitats over dense invasive *Prosopis juliflora* dominated habitats. At the scale of the den, proximity to water and vegetation cover were the main drivers of den site selection. Similar to other arid zone foxes, insects, plant materials and small mammals were the main components of the diet of Indian desert fox. Given its selection of open habitats, invasive shrub encroachment is likely to result in a loss of habitat as well as resources for this species, potentially impacting on the conservation status of this already range-restricted species in India.

Keywords: Banni grasslands, desert fox, invasive plants, *V. vulpes pusilla*, Western India, white-footed fox, woody encroachment

Grasslands are among the most altered terrestrial ecosystem across the globe, facing threats from rapid urbanization, fragmentation, overgrazing, land conversion for agriculture and introduction of non-native species (White et al. 2000). A total of 24% geographic area of India is covered by various kinds of grasslands (Rawat and Adhikari 2015), yet these ecosystems face a fundamental problem of recognition. Arid and semi-arid grasslands of India are classified as wastelands in government policies and are prone to land conversion and afforestation under land restoration or development schemes (Vanak et al. 2017).

Large scale plantation initiatives across the country have caused the degradation of these ecosystems through the introduction of non-native species (Vanak et al. 2017). Encroachment of woody vegetation into grasslands and savannah has been recognized as a major driver of change in the biodiversity and functioning of these ecosystems. The rapid expansion of woody vegetation has been associated with the suppression of fire cycles, change in herbivore species composition, overgrazing and poor land management practices. Global climate change due to an increase in CO_2 and rising temperatures has also been linked to increasing woody cover at planetary scales (Archer et al. 2001, Popp et al. 2007, Auken 2009, Ratajczak et al. 2012).

Woody encroachment in grasslands not only affects the soil nutrient cycle and carbon storage (Peltzer et al. 2010) but also alters the physical structure of a landscape from an open grassland habitat to dense woodland. The impact of these structural changes in grasslands on native fauna has gained much attention from researchers. Studies have shown the species-specific impact of these structural changes on the diversity, distribution (Bateman et al. 2008, Pike et al. 2011), activity (Bachen et al. 2018, Jayadevan et al. 2018, Guiden and Orrock 2019), abundance (Smith et al. 2017) and predation risk (Schmidt and Whelan 1999, Mattos and Orrock 2010) of many species. Recent studies in African savannah ecosystems have highlighted varying impacts of bush encroachment on the relative abundance of multiple mammalian species (Blaum et al. 2007). Reducing grass cover due to the expansion of woody shrubs has altered herbivore species composition from grazing dominated to browsing dominated communities (Smit and Prins 2015).

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However, the impact of such woody encroachment on species from higher trophic levels such as predators or meso predators (as in absence of larger predator they become major predators in the landscape, Prugh et al. 2009) is relatively less understood, specifically in the context of depleting grasslands of India. Rapidly encroaching woody vegetation cover can affect carnivore communities through different pathways. For example, increasing woody cover can alter prey availability thus influencing carnivore abundance and distribution (Dutra et al. 2011). Secondly, woody vegetation cover may provide shelter from other intraguild predators thus positively affecting smaller carnivore species (Popp et al. 2007). Structural changes in habitat due to bush encroachment can directly affect habitat selection of grassland specialist carnivore species.

Here, we study the impact of rapid colonization of a semi-arid grassland by a woody invasive species *Prosopis juliflora*, on the ecology of lesser-known dry grassland meso-predator, the Indian desert fox *Vulpes vulpes pusilla*. The Indian desert fox is one among three subspecies of red fox found in India. The other two subspecies are the Kashmir fox *V. v. griffithi*, found in the temperate regions of the Himalayas, and the Tibetan red fox *V. v. montana* found in the cold deserts of the Tibetan plateau (Menon 2014). All three subspecies remain poorly studied, although it is likely that the two high altitude sub-species in India resemble temperate red fox subspecies such as *V. v. crucigera* in their ecology.

There is very little published information about the Indian desert fox, except in the compilations of faunal records, such as the Fauna of British India Mammals Vol. 2 (Pocock 1941) and some natural history articles and mammalian field guides (Prater 1990, Menon 2014, Wilson and Dookia 2019). The habitat of the Indian desert fox includes dunes, saline scrub grasslands and semi-arid scrub savannah. It shelters in burrows dug in the ground near vegetation cover of reeds and bushes (Prater 1990). It appears to be the only fox found amongst the dunes of the Rajasthan desert (Pocock 1941). Gerbils, other rodents and spiny-tailed lizards are reported as their main prey items (Sangha 2014).

This sub-species has been given the highest legal protection in India (Schedule I) under the Indian Wildlife (Protection) Act 1972. Despite its legal status, the fox is poached for its fur and meat. Rapid urbanization, industrialization and the introduction of invasive species are a threat to the habitat across its distribution range.

To gather basic ecological information about this unique but poorly studied sub-species, we investigated landscape-scale occupancy, den site selection and dietary habits in a xeric and saline ecosystem, the Banni grasslands of Kutch district in Gujarat. The Banni grasslands have undergone a massive change in vegetation structure, as the woody invasive species, *Prosopis juliflora* has turned parts of this landscape into a dense woodland from an open grassland habitat (Vaibhav et al. 2012). As the Indian desert fox is described as an open habitat species, we hypothesized that these changes could negatively affect the site occupancy (presence or absence) of the Indian desert fox (Table 1). We also studied the den-site selection of the Indian desert fox, and as with other arid environments adapted foxes (Uresk et al. 2003, Dell'Arte and Leonardi 2008), we expected that availability of water and vegetation cover would be the main predictors of den-site selection at the microhabitat scale.

Table 1. Predicted species response to each habitat type based on our hypothesis.

Covariate	Ψ
Sueda saline land (SSL)	+
Prosopis juliflora dense area (PD)	–
Moderate *P. juliflora* area with mixed vegetation (PM)	0
Water occupied area (water)	+

Black-naped hare *Lepus nigricollis*, Indian hedgehog *Paraechinus micropus*, desert hedgehog *Hemiechinus collaris*, Indian gerbil *Tatera indica* and Indian desert jird *Meriones hurrianae* are some of the potential mammalian prey species of Indian desert fox in the landscape. Red-sand boa *Eryx johnii*, saw-scaled viper *Echis carinatus*, black cobra *Naja naja*, spiny-tailed lizard *Uromastyx hardwickii* and Bengal monitor lizard *Veranus bengalensis* are some of the potential reptilian prey species. Golden jackal *Canis aureus*, Indian wolf *Canis lupus*, caracal *Caracal caracal*, striped hyena *Hyaena hyaena*, Indian fox *Vulpes bengalensis*, jungle cat *Felis chaus* and desert cat *Felis silvestris ornata* are the main mammalian co-predators in the landscape.

Material and methods

Study area

Banni, once one of Asia's largest tropical grasslands, is situated at the northern border of Kutch district in Gujarat (23°19′–23°52′N, 68°56′–70°32′E) encompassing an area of ~2500 km^2 (Jayadevan et al. 2018). It falls within the hot semi-arid region of India, with ~300 mm average annual rainfall. Maximum temperatures exceed 47°C in summer while winters are mild with the minimum temperature not dropping below 7°C. The vegetation of the Banni is typically grass-dominated along with halophilic vegetation in high saline areas. Physiognomically this area is classified as *Dichanthium–Cenchrus–Lasiurus* type of grassland (Dabadghao and Shankarnarayan 1973). The grasses commonly found here include, *Dichanthium annulatum*, *Cenchrus ciliaris*, *Cenchrus setigerus* and *Desmostachya bipinnata* (Joshi et al. 2009). High saline areas are colonized by perennial grasses such as *Aeluropus lagopoides* and *Urochondra* sp. *Acacia nilotica* is the major tree species in the area along with other shrubs such as *Capparis decidua*, *Ziziphus* sp., *Salvadora persica* and *Salvadora oleoides*. Since the extensive introduction of *Prosopis juliflora* in the 1960s, more than 50% of the Banni has been transformed into stable woody vegetation dominated landscape (Vaibhav et al. 2012). The density of woody cover of *Prosopis juliflora* can vary between years due to the regular harvest of its wood for charcoal production. However, because of the rapid regeneration of *Prosopis*, the land cover type remains the same.

Sampling approach

Site occupancy

We used the occupancy sampling design developed by Hines et al. (2010) to determine the space use by the Indian

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desert fox. This design uses a space for time substitution to produce detection probabilities that are correlated with site covariates. The size of the sample grid in an occupancy framework should be large enough to fully encompass the species' home-range (Mackenzie and Royle 2005). Thus, due to a lack of published information about the home range of the Indian desert fox, we chose an intermediate home-range size between golden jackal which is ~20–30 km² (Aiyadurai and Jhala 2006) and Indian fox which is ~2–3 km² (Vanak and Gompper 2010a). The map of the study area was overlaid by sampling grids of size 4 × 4 km. We used a modified checkerboard design (Fig. 1) to select sample grids.

The occupancy survey was done for the dry season between February and June 2014. A total of 46 grids were selected for survey across the landscape, but only 39 of them were accessible as some grids fell in the restricted army zone. A transect of 5 km length was walked diagonally in each sampling grid with each one km segment representing a spatial replicate. We searched for signs of Indian desert foxes such as spoor, scat and dens. The difference between spoor of Indian and desert fox was determined based on size and verified by direct sightings. Tracks of the Indian desert fox can be distinguished from the Indian fox by its larger hind feet and a wide gap between front digits (Pocock 1941). The scat of Indian desert fox is also slightly larger in diameter (mean = 1.48 cm, SE = 0.02, 95% CI = 0.013, Misher unpubl.) than that of the Indian fox (mean = 1.43 cm, SE = 0.31, 95% CI = 0.063) although this difference may not be significant (Vanak and Mukherjee 2008).

We used a land cover map generated from a supervised classification of a Landsat ETM+ satellite imagery dated October 2008 (<http://glcf.umd.edu/data/>) to determine site covariates such as land cover type, distance to water and distance to roads and villages. From the land cover map, we determined the proportion of different habitat types in each sampled grid. These covariates represented the structural component of the habitat and are commonly used in occupancy studies as a measure of habitat variability (Krishna et al. 2008).

We used the program PRESENCE ver. 6.4 to determine occupancy and the factors affecting occupancy. The occupancy parameters are referred to as the probability of sample unit occupied by species, referred as 'ψ' and detection probability 'p'. We used the Markov process model to estimate the occupancy parameter 'ψ' and 'p' as it can determine spatially correlated detection probability.

The null model $\psi(.)\ \Theta 0(.)\ \Theta 1(.)\ p(.)\ pi(.)$ was first fitted to the data. Parameter '$\Theta 0$' is the detection at a segment given that the sample unit is occupied by a species, but the species is not present in the previous segment. '$\Theta 1$' is the detection at a segment, given that the sample unit is occupied by a species and it is also present in the previous segment. While 'pi' is the presence of a species at an un-surveyed segment 0, given that the sample unit is occupied by the species. We then modeled 'ψ' as the function of different measured variables while 'p' was held constant because the detection probability at an occasion is dependent upon detection at the previous occasion (Hines et al. 2010). As site covariates were a proportion of different habitat types, there was strong autocorrelation. Due to limitations of small sample size and autocorrelation among covariates, we ran only a few relatively simple models (n = 8), with no more than two covariates/model. We ran

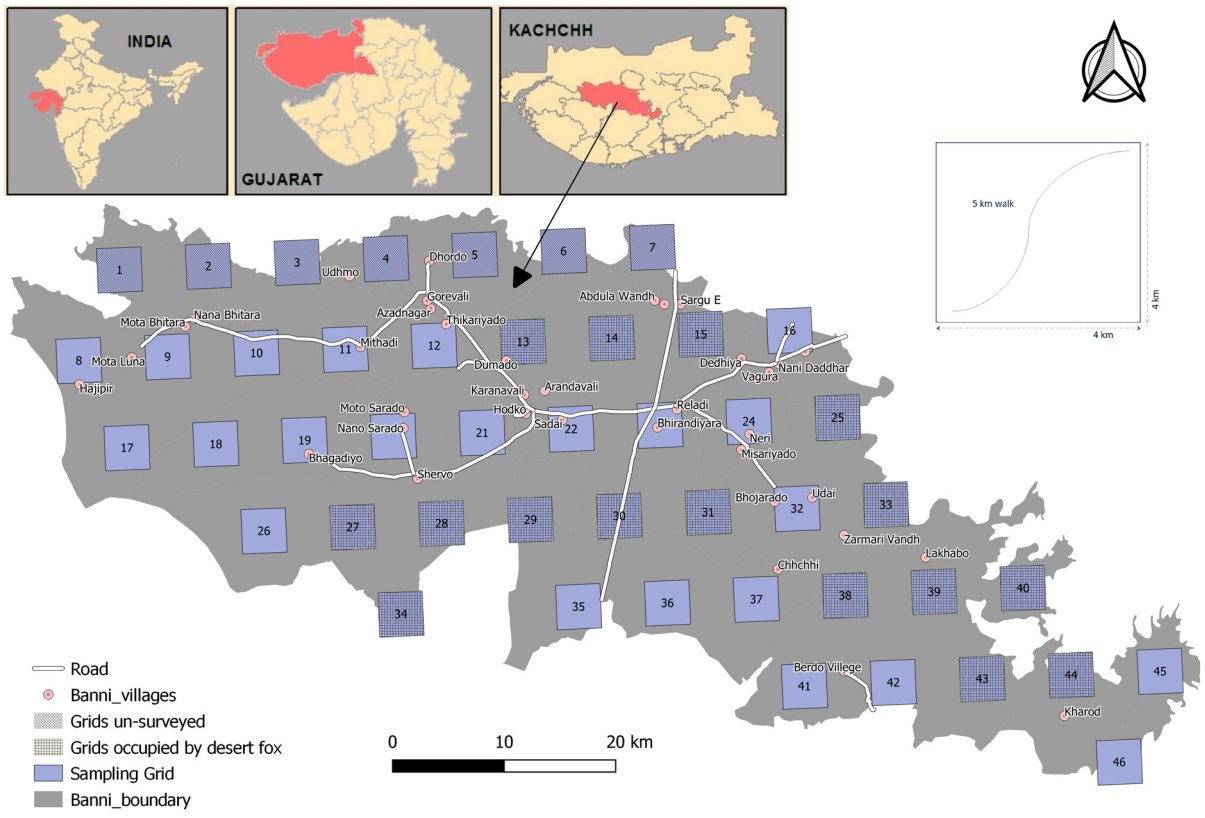


Figure 1. Map of the survey grids in the Banni landscape of Kachchh district in Gujarat, India.

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models with a single habitat variable to estimate 'ψ' and 'p'. Habitat variables SSL, PD and PM were represented equally in the modeling. Later we added water with each different habitat variable to test if the availability of water was also an important predictor of occupancy. All models were ranked according to AIC_c values and beta coefficients of the independent variables, 'ψ' and 'p' were averaged across the top candidate models based on ΔAIC_c (Burnham and Anderson 2003).

Den site selection

A systematic walking search with two to four observers was conducted to look for active resting and breeding dens of Indian desert fox in all potential areas from February 2014 to February 2015. Inquiries from local people and shepherds about desert fox den locations were also made. Active dens were identified by the presence of signs of fresh excavation, scat of pups and adults around the den site, and tracks along the path to the den opening. As the study area also has Indian foxes, we set a camera trap at each den site (n = 20) for one night to confirm the identity of the denning species.

To collect data for evaluating micro-habitat characteristics, the design implemented by Punjabi et al. (2013) was used. We recorded visibility, number of rodent burrows, spiny-tail lizard's burrows and number of shrubs within a 25 × 25 meter north-oriented plot with the den site as the center (Fig. 2). The same variables were measured for four available plots at 500 m in four directions from the den site. The visibility at the den site was measured using a standard chessboard (1.50″ square – 12″ × 12″ board). The number of visible squares were counted from 10 m in eight directions at two different heights: 0.5 and 1 m. The total number of visible squares was converted into percentage and these values were averaged for each data point. Percentage ground cover of grass, herbs and bare soil was recorded in a 5-m radius plot at each den point and available point. To determine the effect of shrubs on den site selection, the numbers of shrubs were counted at each den plot as well as putative available plots. The numbers of rodent and spiny-tailed lizard burrows were recorded as an index of food abundance, as the number of burrows is correlated with the true abundance of rodents (Ramesh et al. 2013).

We used conditional logistic regression to determine habitat factors predicting den site selection of Indian desert fox. We standardized every continuous variable by its mean and standard deviation. Site attributes for each den point were paired with four available points within the patch. All models were ranked according to AIC_c.

To determine the effect of distance from water points, human habitation and roads on the den-site selection of Indian desert fox at large-scale we performed a distance-based analysis. We calculated the minimum distance of den-site (n = 20) from these features and did the same for randomly placed points (n = 20 × 4) using QGIS ver. 2.2 (<http.//qgis.osgeo.org>). Then we performed a two-sample t-test to determine whether the distance from these features between den points and available points was significantly

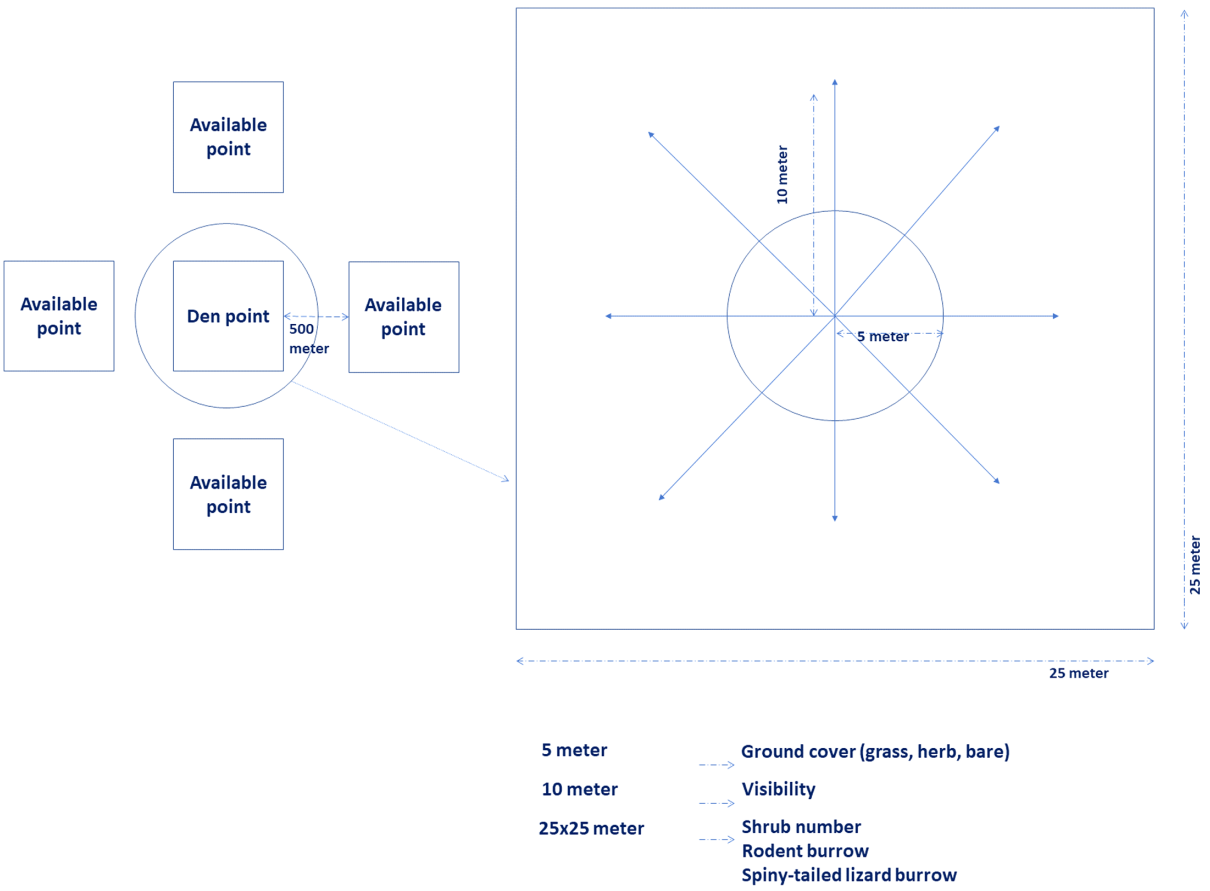


Figure 2. Sampling design to collect data to determine den-site selection of Indian desert fox.

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different. All statistical analysis was done using R ver. 3.2.0 (<www.r-project.org>).

Dietary analysis

We analyzed food remains in the scats to determine the diet of the Indian desert fox. Scat samples were collected opportunistically from six different active den sites of Indian desert foxes. Weekly visits were made to all identified den sites for scat collection during the winter (October–February) and summer (March–June) seasons. As a large part of the landscape gets waterlogged during the monsoon, we were unable to collect scats during monsoon season. Samples were collected in plastic zip-lock bags and marked with the date and site of collection and then sun-dried for laboratory analysis. To separate food remains in the scat, each sample was soaked in a sieve with diluted laundry detergent (Klare et al. 2011). Soaked remains were air-dried. Food remains or indigestible components such as seeds, hair, claws, scales, feathers, bones and insect chitin were separated using needles and forceps and were examined using a compound microscope. Vertebrates were categorized as Mammalia, Reptilia and Aves. Mammalia was further classified into Rodentia (rodents) and Erinaceinae (hedgehogs); Reptilia were differentiated as *Uromastyx hardwickii* (spiny-tailed lizards) and other reptiles based on micro-ornamentation of scales as per Vanak and Gompper (2009). Feathers and eggshell fragments were recorded as Aves (birds) remains. Invertebrata were broadly classified as Coleopteran (beetles), Isoptera (termites), Orthoptera (crickets/grasshoppers), Hymenopterans (ants), Diptera (flies), Arachnida (scorpions) and Crustacea (crabs). Amongst the vegetation remains, the only readily identifiable material included pods of *P. juliflora*, fruits of *Ziziphus* sp., seeds of Cucurbitaceae and succulent leaves of *Suaeda nudiflora*. Others were classified as the remains of root tubers and grass/leaves. Data from seasons were pooled to determine the diet of Indian desert fox. We calculated the frequency of occurrence (FO) of a prey item by using the formula

$$\mathrm{FO} = s\left(100\right) / N$$

where '*s*' is the number of samples containing each prey type and *N* is the total number of samples analyzed. Relative occurrence (RO) was calculated as

$$\mathrm{RO} = p\left(100\right) / T$$

where '*p*' is the number of occurrences of each prey type and *T* is the number of total occurrences of all prey types.

Results

Occupancy

The presence of desert fox was recorded in 16 grids out of a total of 39 sampled, which gave us a naïve occupancy rate of 0.41 whereas the estimated occupancy rate $\hat{\Psi}$ was 0.45 (95% CI, 0.20–0.70), with a $\hat{p} = 0.77$ (95% CI, 0.52–1.02). The null model psi(.),th0(),th1(),p(.),th0pi() performed poorly. The model psi(SSL+water), th0(),th1(),p(.),th0pi() ranked as the best model having lowest AIC_c value (Table 2).

The sum of model weights shows that habitats such as *Suaeda* saline land (0.73) and the proportion of the area under water (0.73) in the grid has a weak positive impact on desert fox occupancy, whereas the presence of either dense or mixed *Prosopis juliflora* were weak negative predictors (Table 3). However, there was a high variance in the beta estimates for these predictors, with 95% CI spanning zero.

Individual site estimates of occupancy probability (Ψ) averaged across the top models show a strong correlation (R = 0.93) with *Suaeda* saline land (Fig. 3). This suggests that desert foxes occupy more open habitats such as *Suaeda* saline land compared to other habitat types. Low lying areas that are seasonally inundated with water have no correlation (R = 0.04) with desert fox occupancy. Areas occupied by dense and mixed *Prosopis* were found to have a negative correlation (R = 0.36 and 0.43) with desert fox occupancy.

Den-site selection

A total of 195 km walk effort and 547 km driving effort by vehicle was done to find dens. We found a total of 20 active dens of desert fox out of which 18 were in *Suaeda* dominated open grassland habitats and two were in the moderate *P. juliflora* habitat. The top model indicates grass cover, shrub density and herbaceous cover as the best predictors of microhabitat variables for selection of den-site (Table 4). Beta estimates of variables show a significant impact of grass cover, herb cover and shrub density on den-site selection (Table 5).

Table 2. Model selection results and parameter estimates (with standard error) for desert fox occupancy in the Banni landscape.

Model	$\hat{\Psi}$ (SE)	$\hat{p}$	AIC_c	ΔAIC_c	*Wi*	K
psi(SSL+water),th0(),th1(),p(.),th0pi()	0.45 (0.13)	0.77	162.73	0	0.55	5
psi(SSL),th0(),th1(),p(),th0pi()	0.45 (0.12)	0.73	164.96	2.23	0.18	5
psi(PM+water),th0(),th1(),p(.),th0pi()	0.44 (0.12)	0.81	166.52	3.79	0.08	5
psi(PD+water),th0(),th1(),p(.),th0pi()	0.44 (0.13)	0.79	166.88	4.15	0.07	5
psi(PM),th0(),th1(),p(),th0pi()	0.45 (0.10)	0.77	167.4	4.67	0.05	5
psi(PD),th0(),th1(),p(.),th0pi()	0.44 (0.11)	0.79	168.91	6.18	0.03	5
psi(water),th0(),th1(),p(.),th0pi()	0.43 (0.11)	0.85	169.07	6.34	0.02	5
psi(.),th0(),th1(),p(.),th0pi()	0.43 (0.08)	0.53	169.77	7.04	0.02	5

$\hat{\Psi}$ is the estimated occupancy parameter, $\hat{p}$ is the estimated species detection probability, AIC is the small sample size corrected Akaike information criteria value, ΔAIC_c is the difference in AIC_c values between each model and the model with lowest AIC_c, *Wi* is the AIC_c model weight and K is the number of parameter estimated by the model.

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Table 3. Covariates influencing occupancy ranked on the basis of summed model weight with averaged beta coefficient and standard error.

Covariate	Summed AIC weight	Beta coefficient	SE	95% CI	
SSL	0.73	0.05	0.03	0.11	−0.01
Water	0.73	0.21	0.14	0.48	−0.06
PM	0.14	−0.04	0.02	0.00	−0.08
PD	0.09	−0.03	0.03	0.03	−0.09

The mean distance from water for den sites was significantly lower (1.2 km) than for random points (5.8 km; $t = -3.45$ and $p < 0.001$). The mean distances from roads (den site = 7.1 km and random point = 7.0 km) and the nearest village (den site = 6.1 km and random point = 6.2 km) were not significantly different.

Diet

During the period of February 2014–2015, a total of 80 scat samples (summer = 52 and winter = 28) were collected. The sample size for the winter season was small since most of the identified dens were abandoned during the monsoon. We identified a total of 20 items to the lowest taxonomic level possible (Table 6).

The main constituent of the diet of Indian desert fox were invertebrates based on relative occurrence (RO) of 53.43% and frequency of occurrence (FO) of 100%. A major proportion of invertebrate diet was formed of Coleoptera (FO = 91.25%), Orthoptera (FO = 87.5%) and Isoptera (FO = 82.5%). Plant materials were the second most prevalent item in the diet with an RO of 31.39% and occurring in 87.5% of total scat samples analysed. Plant materials mainly included fruits of *Suaeda nudiflora*, *Zizyphus* sp. and remains of Cucurbitaceae species. Other vegetation included pods of *P. juliflora*, tubers, grasses, leaves and some unidentified plant material. Bird remains were found in 40% of scat samples making it the third largest group of prey in diet with a relative occurrence of 6.65%. Mammal presence was relatively low in the diet with an RO of 5.20% occurring only in 28.75% of all scat samples analysed. Reptiles were the lowest occurring (FO = 155, RO = 3.33) group among prey species in the diet of Indian desert fox.

Discussion

The red fox is often described as a habitat and resource generalist. However, the sub-species *Vulpes v. pusilla* seem to have developed a high degree of habitat specificity in the western arid zone of India. Our results show that the Indian desert fox's occupancy was best predicted in the open *Suaeda nudiflora* dominated areas with availability of water in the Banni landscape, even though it has an estimated cover of 28.2% of the sampled landscape.

In the Banni, low lying areas that have high salinity, and are waterlogged for several months of the year, have escaped the rapid colonization by *Prosopis juliflora*. Therefore, these areas have remained open plains, covered with short grasses such as *Dichanthium* sp., *Cyperus* sp. and small shrubs like *Suaeda nudiflora*. Desert fox occupancy was positively associated with these kinds of areas and negatively correlated with areas of dense *P. juliflora*.

The negative impact of invasive shrub cover on Indian desert fox is similar to what has been observed for the cape

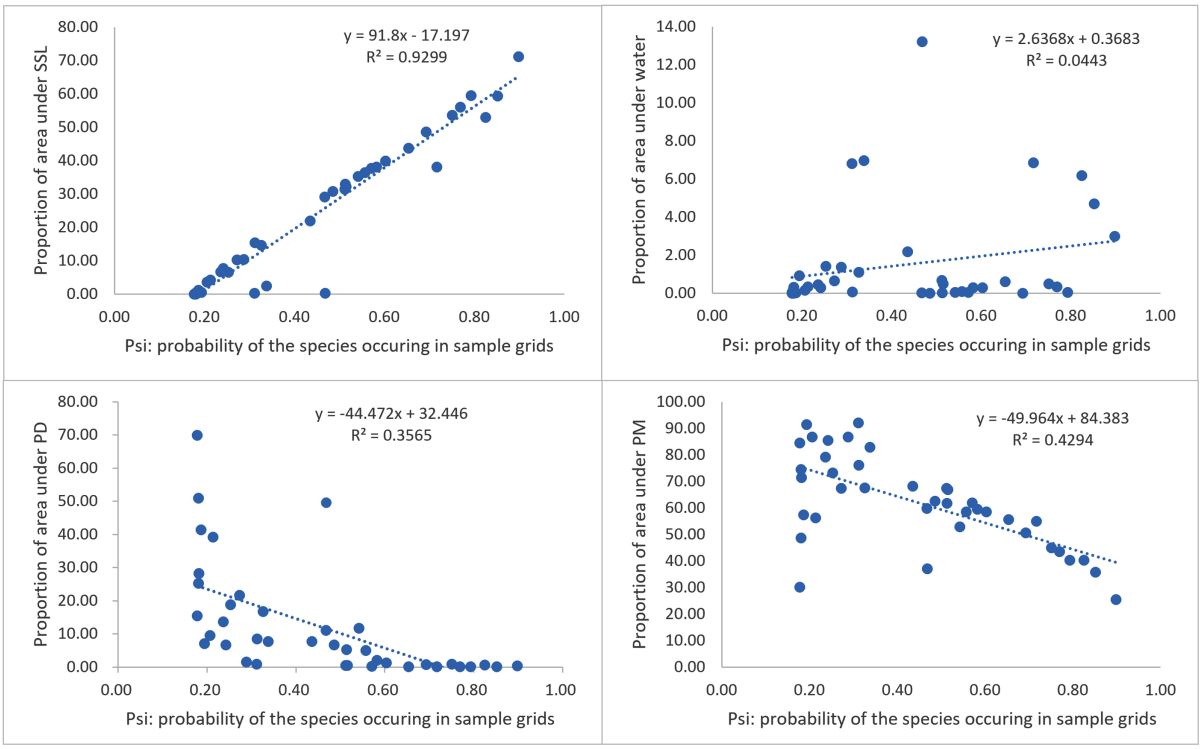


Figure 3. Plotted individual site estimates of occupancy probability (Ψ) averaged across the top models and plotted against different habitat type.

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Table 4. Top models ranked by AIC_c explaining den-site selection by desert fox *Vulpes vulpes pusilla* at micro-habitat scale.

Models	K	AIC_c	ΔAIC_c	*Wi*
Grass_cov.+Shrub_dens.+Herb_cov.	3	74.49	0.00	0.65
Bare_cov.+Vissibility	2	77.18	2.70	0.17
Bare_cov.+Grass_cov._Rodent_abun.	3	77.94	3.46	0.12
Grass_cov.	1	81.08	6.59	0.02
Grasss_cov.+Rodent_abun.	2	82.55	8.06	0.01
Grass_cov.+Shrub_dens.+Visibility	3	82.57	8.09	0.01
Grass_cover+Visibility	2	83.13	8.64	0.01
Grass_cov.+Rodent_abun.+Visibility	3	84.56	10.07	0.00
Rodent_abun.	1	96.50	22.01	0.00
Rodent_abun.+Shrub_den.	2	98.03	23.55	0.00

fox *Vulpes chama* in Kalahari rangelands. The cape fox selects open rangelands with low shrub cover, and an increase in woody vegetation has a negative impact on their abundance and distribution (Blaum et al. 2007).

The high degree of selection for open habitat has also been seen in other fox species as well as sub-species of red foxes that inhabit arid and semi-arid ecosystems. In Israel's Judaean desert, the Blanford's fox, *Vulpes cana* has been shown to occupy open dry creek-bed habitat and avoid surrounding dense vegetation cover (Geffen et al. 1992). Similarly, the Indian fox, *Vulpes bengalensis*, selected for open grassland habitats, even in human-dominated landscapes (Vanak and Gompper 2010a).

Although desert foxes seem to avoid thick vegetation at the landscape scale, at scale of the den site, they selected areas having higher vegetation cover than the surrounding open flats. This is similar to what is seen in several other species of open habitat foxes such as the swift fox, *Vulpes velox* (Uresk et al. 2003), kit fox, *Vulpes macrotis* (Arjo et al. 2003) and the Indian fox *V. bengalensis* (Punjabi et al. 2013). At the broader scale, desert fox dens were located in areas that were closer to water sources, as this is a strongly limited resource. Red foxes (*V. vulpes*) in the arid areas of North Africa show similar behavior in making dens close to agriculture lands because of water availability (Dell'Arte and Leonardi 2008).

The dietary habits of the Indian desert fox, with a high dependence on plant matter, including halophilic vegetation, show an adaptation to this hot semi-arid ecosystem. According to optimal diet theory, a predator includes more diversity of prey items in their diet in low-productivity habitats (Schoener 1971, Krebs 1980). In more productive systems, red foxes tend to have a diet consisting mainly of small mammals (Jędrzejewski and Jędrzejewska 1992, Kidawa and Kowalczyk 2011). For the Indian desert fox, invertebrates and plants were the most frequently occurring food item in all scats. Both arthropods and plant material such as fruits and succulent leaves are water-rich food items. The high concentration of insects and plant material in the diet helps species to gain much-required water and essential nutrients to survive in the desert climate (Williams et al. 2002). A similar kind of insect and plant-based diet was observed in other desert inhabiting species such as the Blanford's fox, *Vulpes cana* in Israel (Geffen et al. 2006), fennec fox *V. zerda* in Algeria (Brahmi et al. 2012), *V. ruppelli sabea* in Saudi Arabia (Lenain et al. 2004) and in other desert inhabiting red foxes such as *V. v. arabica* from Saudi Arabia (Lenain et al. 2004) and *V. vulpes* from Tunisia (Karssene et al. 2019).

Though small mammals were rare in the diet of Indian desert fox, their energetic contribution is likely much higher than any of the other food item (Mukherjee et al. 2004). This is seen in the diet of fennec fox in southern Algeria, where insects occurred more frequently, but biomass consumed was dominated by rodents (Brahmi et al. 2012). Rodents have been reported to be an important part of diet in the cape fox *Vulpes chama* in South Africa, with an estimated consumption of 11 rodents/day (Klare et al. 2014). However, the low occurrence of rodents in our dietary analysis could either be due to lower availability of rodents in these saline habitats or lower predation success due to the additional cover provided by *P. juliflora* (Kotler et al. 1988, Jayadevan et al. 2018, Norbury and Overmeire 2019). We also observed waterfowl remains at several den sites, particularly during winter when large numbers of migratory waterfowl visit the Banni. Similar predation on waterfowl by the red fox has also been recorded in Minnesota (Sargeant 1972).

Although our study is one of the first to document occupancy of the Indian desert fox, the lack of sufficient seasonal representation, both in the occupancy and diet analysis remains a key limitation. For example, during the monsoon season, much of the low-lying areas where we observed dens are partially submerged, and it is likely that foxes use higher ground, which may have a higher *P. juliflora* cover. The presence of the desert fox may also be affected by the other co-predators such as the golden jackal and domestic dog (Vanak and Gompper 2010b, Gompper et al. 2016). Despite these limitations however, the study provides some basic information about the ecology of the desert fox in an arid environment. Given the rapid spread of *P. juliflora* across the arid north-western region of India, the structural modifications to the habitat may have a deleterious impact on this highly habitat specialized sub-species of the red fox

Table 5. Parameter estimates (betas) from the top model used at microhabitat scale.

Variable	β	exp(coef)	SE(coef)	Z	p
Grass_cov.	1.19	3.29	0.29	4.16	< 0.0001
Shrub_den.	0.21	1.23	0.25	0.84	> 0.05
Herb_cov.	0.89	2.43	0.30	2.97	< 0.001

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Table 6. Frequency of occurrence (FO) and relative occurrence (RO) for each prey item in scat samples (n = 80) of Indian desert fox (broader category shown in bold letters).

Prey item	FO %	RO %
Small mammals	**28.75**	**5.20**
Rodentia	22.5	3.74
Erinaceinae	8.75	1.46
Birds	**40**	**6.65**
Reptiles	**15**	**3.33**
U. hardwickii	10	1.66
Other reptiles	10	1.66
Invertebrate	**100**	**53.43**
Coleoptera	91.25	15.18
Isoptera	82.5	13.72
Arachnida	22.5	3.74
Orthoptera	87.5	14.55
Hymenoptera	28.75	4.78
Odonata	5	0.83
Diptera	1.25	0.21
Crustacean	2.5	0.42
Plant material	**87.5**	**31.39**
Sueda sp.	48.75	8.11
P. juliflora	30	4.99
Grass roots	25	4.16
Grass/leaves	65	10.81
UIF	11.25	1.87
Ziziphus sp.	1.25	0.21
Cucurbitaceae	7.5	1.25

in India. This preliminary information can support future research on interspecific interaction and resource partitioning among Indian desert fox and sympatric species, and how these relationships are affected by changes in habitat type due to invasive species.

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