The Company Canids Confront: Resource Partitioning in Sympatric Carnivores in an Arid Ecosystem

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Declaration

This thesis entitled "The company canids confront: Resource partitioning in sympatric carnivores in an arid ecosystem" is a presentation of my original research work. Wherever contributions of others are involved, every effort is made to indicate this clearly, with due reference to the literature, and acknowledgement of collaborative research and discussions. The work was done under the guidance of Dr. Abi Tamim Vanak at the National Centre for Biological Sciences - Tata Institute of Fundamental Research, Bangalore, India.

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In my capacity as supervisor of the candidate's thesis, I certify the above statements are true to the best of my knowledge.

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Certificate

I certify that the thesis entitled "The company canids confront: Resource partitioning in sympatric carnivores in an arid ecosystem" comprises original research work carried out by Kadambari Devarajan at the National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, under the guidance of Dr. Abi Tamim Vanak during the period September 2014 - June 2015 for the degree of Master of Science in Wildlife Biology and Conservation of the Tata Institute of Fundamental Research. The results presented in this thesis have not been submitted previously to this or any other university for a Master of Science degree, or any other degree.

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Summary

Canids are the most successful family of carnivores in the world and several species may occur sympatrically in a region. This study attempts to understand how intra-guild competition and habitat factors influence the occurrence and resource use of multiple species in a region. The mechanisms behind the partitioning of space, time, habitat, and diet by different species forms the focus of this study. This study was carried out in the Banni grasslands in the Kutch district of Gujarat between September 2014 and March 2015. The region harbours sizeable populations of four sympatric species of canids, namely: the desert fox (*Vulpes vulpes pusilla*), Indian fox (*Vulpes bengalensis*), golden jackal (*Canis aureus*), and domestic dog (*Canis lupus familiaris*). All four species are free-ranging and the latter two are human-subsidized to varying extents in the region.

The entire landscape was divided into grids based on the home-ranges of the organisms studied. Camera trap and track plot surveys were done systematically in these grids following a chequerboard design. At each camera trap location, several environmental and habitat variables were measured, in addition to the presence of each of the canid species. The camera traps and track plots were employed to determine the occurrence of each of the species, directly through videos and indirectly through signs (primarily pugmarks), in order to understand habitat, spatial, and temporal partitioning between them. Scat samples for the wild canids were collected opportunistically and analyzed to understand dietary partitioning between the species.

The results indicate complex interactions between the study species. For instance, from occupancy analysis, there appears to be noticeable spatial partitioning between desert foxes and the other canids. However, golden jackals and dogs seem to share the same space. There also appears to be some overlap between jackal and Indian fox occurrence. In addition, desert foxes avoided areas where dogs were present and for most part appeared to avoid areas that had any of the other species.

When considering the habitat features, broad patterns that emerge indicate that dogs prefer areas with *Prosopis* while desert foxes were most likely to be found in areas with *Suaeda*. Jackals, however, were spread across the landscape and using almost all landcover types considered, with a slight preference for areas having a combination of vegetation types alongside *Prosopis*. Indian foxes appear to have an affinity for areas with grasses and sedges. Indian foxes overlapped significantly with jackals in terms of habitat use, but seemed to have a stronger preference for areas with sedges and grasses. This pattern also extends to the soil types found in the corresponding habitats for each species, wherein the presence of desert foxes correlated with soils having high salinity. These patterns also matched those of proximity to human habitation, with dogs most likely to be found in and around areas of human presence and desert foxes found the farthest from villages.

The results of scat analysis for the wild canids indicate a considerable overlap in animal matter, with the notable exception that jackals have a larger dietary repertoire and had more mammals larger than rodents, such as hedgehogs and hare. However, there seems to be considerable partitioning between the species in the plant matter comprising their diets respectively. Jackals consumed more *Prosopis*, Indian foxes more grasses, and desert foxes primarily fed on *Suaeda*, and this pattern matches the land cover types in areas with the highest probability of occurrence for each of the species.

As for temporal partitioning, both fox species were active at the same time, and none of the wild canids were active when dogs, which seem predominantly diurnal, were about. Jackals were crepuscular as well as nocturnal, while both foxes were mostly nocturnal.

Overall, there was some spatial and considerable habitat overlap between the jackal and Indian fox, for whom dietary partitioning and to a lesser extent temporal partitioning seemed to operate. However, there appears to be noticeable temporal, spatial and habitat partitioning between dogs and desert foxes.

This study has resulted in essential baseline information on the occurrence and distribution patterns of multiple canids in a landscape that is human-dominated and is also modified by invasive plants, in addition to increasing our understanding of how human-subsidized canids affect other canids as competitors. It also provides insights on how interference competition, habitat type and quality, and human presence affect the distribution and landscape use of several sympatric canids.

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Introduction

Wild canids are the most widely distributed of carnivores and are found in all continents with the exception of Antarctica [Gittleman, 1997; Sillero-zubiri et al., 2004]. Along their distributions, sympatric canids occur in high densities [Sillero-zubiri et al., 2004]. This seems to be a common trend in the distribution of wild canids, but is especially true if human-subsidized, commensal or feral species, such as the domestic dog (*Canis lupus familiaris*), are included. Such sympatry in the occurrence of canids is seen not only across their distributions at a continental scale, but also at more local scales [Gittleman, 1997].

As a consequence of human induced habitat loss, competing species are forced into smaller areas, thereby increasing the frequency of negative interactions. Within Indian ecosystems, the Indian fox has been shown to suffer from interference competition with the domestic dog [Vanak and Gompper, 2010a]. A complete understanding of the habitat requirements for each species and how the species uses the landscape is an essential component of wildlife management.

In a typical ecosystem, almost globally, no more than three species of canids occur sympatrically [Gittleman, 1997; Kamler et al., 2004, 2012]. Moreover, there is usually either a minimum weight difference between them or massive character displacement, such as in the case of some parts of sub-Saharan Africa with the cape fox, bat-eared fox and the black-backed jackal [Kamler et al., 2012]. However, the canid assemblage in Kutch has species which have a significant overlap in their dietary niches. Also, by adding the dog, we have four species, which is very rarely seen. This assemblage becomes more complex when the now rarely seen wolf is added.

Typically, in systems with multiple sympatric species, there is resource partitioning of some kind occurring - habitat, spatial, temporal, and/or dietary [Gompper and Vanak, 2008; Kamler et al., 2012]. Frequently, dietary partitioning is a consequence of one of the others [Vanak and Gompper, 2009a]. Here, I would like to understand the kind of resource partitioning that is taking place in the context of the distribution of each species relative to the other canid species.

This study broadly aims to understand (1) how multiple competing carnivore species interact over space and time, and (2) the mechanisms leading to their co-existence. Here, I compare patterns of habitat use, as well as spatial, temporal, and dietary segregation of four species of canids found in the study area.

Multiple canids inhabiting the same area were studied at the same time using camera trap surveys using an occupancy framework. Spatial and temporal partitioning were observed using the camera trap data. GPS locations for these species were also overlaid onto detailed vegetation maps and prey species distribution maps to help define habitat specific characteristics of these relationships.

In order to understand how resources are partitioned by the species, the entire landscape was divided into grids based on the home-ranges of the organisms studied. Camera trap and track plot surveys were done systematically in these grids following a chequerboard design. At each camera trap location, several environmental and habitat variables were measured, in addition to the presence of each of the canid species. The camera traps and track plots were employed to determine the occurrence of each of the species, directly through videos and indirectly through signs (primarily pugmarks), in order to understand habitat, spatial, and temporal partitioning between them.

To understand dietary partitioning, scat for all the wild canids was opportunistically collected near known den locations or at camera trap locations. For scat collected at camera trap locations during the sampling period for that site, the scat was linked to the species in the process of defecating as recorded by the corresponding camera trap.

Additionally, dog population estimation was done at specific villages using photographic capture-recapture. Statistical and mathematical models were used to estimate the influence of the habitat and environmental variables, as well as presence of the other species, on the co-occurrence of a given species.

This study provides crucial information on how sympatric species partition resources, and also shows how dogs, which are human-subsidized predators, are avoided by all the wild canids studied here. The results of my study will provide valuable information on habitat selection that can be used to improve conservation management practices, especially outside protected areas. Understanding the factors that influence population dynamics is crucial to the development of conservation strategies that will ensure the survival of these species. The same strategies can be extended to other taxa.

The Company Canids Confront: Resource Partitioning in Sympatric Carnivores in an Arid Ecosystem

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Running Title : Resource partitioning in sympatric carnivores

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1 Introduction

Canids are mammalian carnivores belonging to the Family *Canidae* and Order *Carnivora*. They include foxes, wolves, jackals, coyotes, wild dogs as well as domestic dogs. The family is divided into two tribes, namely (1) *Canini* which includes species related to wolves and (2) *Vulpini* which are related to foxes.

In terms of distribution, canids are the most successful family of carnivores in the world, and often occur in human-dominated areas. It is not uncommon to find multiple species of canids in the same area [Sillero-zubiri et al., 2004]. Such sympatry in the occurrence of canids is seen not only in their distributions at a continental scale, but also at more local scales. Within carnivore communities, interference competition is emerging as a factor that could directly impact species distributions and community composition [Linnell and Strand, 2000; Palomares and Caro, 1999]. Such interference competition manifests both directly and indirectly through (1) intraguild predation, where the kill is consumed, and (2) interspecific or intraguild competitive killing, where there is no consumption of the kill.

Interference competition in carnivore assemblages may be either (1) symmetrical, where both species affect each other antagonistically, or (2) asymmetrical, where only one species has an agonistic effect on the other. Thus, such interactions are thought to be behavioral responses to exploitative competition [Peterson, 1995] since species that are sympatric are at a disadvantage due to the sharing of resources, based on the extent of overlap.

Since multi-species carnivore assemblages are seen almost globally, interference competition is now accepted as a crucial factor in the distribution and composition of mammalian communities [Crooks and Soulé, 1999; Estes et al., 2011; Ripple et al., 2014; Ritchie and Johnson, 2009; Ritchie et al., 2012; Terborgh, 2010]. A number of studies have established that a "landscape of fear" exists not just in prey-predator interactions but even in intra-guild interactions. In the latter case, as is true for carnivores, dominance is typically based on size [Palomares and Caro, 1999; Peterson, 1995]. However, there is considerable debate on such a model involving "top down control" exerted by large carnivores [Roemer et al., 2009]. This is because interactions between carnivores can vary significantly with resource availability or prey abundance, environmental conditions, and the community composition, in addition to anthropogenic factors [Elmhagen and Rushton, 2007; Ritchie and Johnson, 2009]. Newsome and Ripple [2015] suggest that studies at multiple spatial scales (local, regional, and continental) need to be made [Newsome and Ripple, 2015]. This is a concern since understanding carnivore interactions require spatial scales large enough to incorporate their abundances and complete geographic range, especially in the case of sympatric carnivores. On the other hand, there could also be completely different patterns emerging due to competition at a local or regional scale.

This has given rise to the notion of "species-scapes", which has been defined as a "spatial plane of species interactions that combines with resources and habitat structure to drive species distributions" [Fisher et al., 2013]. While there have been a number of habitat selection studies ranging across taxa and landscapes, there have been just a handful, if at all, that have tried to understand species coexistence (or conversely, species segregation), which is emerging as an important and yet over-looked measure in such studies.

This study examined a species-scape with multiple canids. The different intra-guild competitors interact with each other in many ways and at multiple levels - individual, population, and species. They have either completely or partially overlapping homeranges, but there is differential habitat use between the species [Aiyadurai and Jhala, 2006; Gompper and Vanak, 2008; Jhala and Moehlman, 2004].

Here, I focus on a guild of sympatric canids, namely, golden jackals (*Canis aureus*), Indian fox (*Vulpes bengalensis*), desert fox (*Vulpes vulpes pusilla*), and free-ranging dogs (*Canis lupus familiaris*) in the Kutch district of Gujarat in India (Figure 1). Wolves are also seen in Kutch albeit extremely rarely in recent years. Since wolf sightings (both direct and indirect) were so infrequent, they could not be included in the study. In this study, I propose to understand the drivers of the existence of multiple, sympatric, intra-guild carnivores in an area, by understanding how the species partition resources.

It is important to know the scales at which different ecological and anthropogenic factors affect the distribution and habitat use at a landscape level, for conservation and management in heterogeneous landscapes. For instance, invasives such as *Lantana camara* [Wilson et al., 2013] and *Prosopis juliflora* have differential impacts on different species that could operate at different scales. How such an invasive (*Prosopis* in this case) would affect the distribution and habitat use of an assemblage of species would have crucial management implications.

Photo: Abi Tamim Vanak		Common Name Scientific Name Distribution Diet	 Indian Fox or Bengal Fox Vulpes bengalensis Most parts of India except the Himalayan range, Indus river valley, and wet forests Rodents, reptiles, invertebrates, small birds, fruits
Photo: Kalyan Varma		Common Name Scientific Name Distribution Diet	 Desert Fox or White-footed Fox Vulpes vulpes pusilla Northwestern India (arid regions of Gujarat and Rajasthan) Rodents, reptiles, invertebrates
	e e e e e e e e e e e e e e e e e e e	Common Name Scientific Name Distribution Diet	 : Golden Jackal : Canis aureus : Most parts of India except the Himalayan range and Indus river valley : Rodents, reptiles, invertebrates, small birds, and fruits
	T	Common Name : Scientific Name : Distribution : Diet :	Domestic Dog <i>Canis lupus familiaris</i> Throughout India Rodents, reptiles, invertebrates, small birds, fruits, grain

Figure 1: The guild of canid species considered in this study.

In a typical ecosystem, almost globally, no more than three species of canids occur sympatrically [Gittleman, 1997; Kamler et al., 2004, 2012]. Moreover, there is usually either a minimum weight difference between them or massive character displacement, such as in the case of some parts of sub-Saharan Africa with the cape fox, bat-eared fox and the black-backed jackal [Kamler et al., 2012]. However, the canid assemblage in Kutch, has species which have a significant overlap in their dietary niches [Aiyadurai and Jhala, 2006; Jhala and Moehlman, 2004; Vanak and Gompper, 2009a]. Also, by adding the dog, we have four species, which is very rarely observed (Figure 1). Typically, in systems with multiple sympatric species, there is resource partitioning of some kind occurring - habitat, spatial, temporal, and/or dietary [Gompper and Vanak, 2008; Kamler et al., 2012]. Frequently, dietary partitioning is a consequence of one of the others [Vanak and Gompper, 2009a]. Here, I would like to understand the kind of resource partitioning that is taking place in the context of the distribution of each species relative to the other canid species.

Moreover, there are lacunae in the quantitative information available on the densities, habitat use, dispersal, disease, and ranging patterns of the golden jackal [Aiyadurai and Jhala, 2006; Jhala and Moehlman, 2004], while almost no information is available on the ecology of the desert fox. Here, I would like to establish baseline data on the distribution and habitat use of all all three canids mentioned, as well as consider free-ranging dogs so as to understand the relative influences of each on the other.

I hypothesize that competition and anthropogenic change impact the distribution and landscape use of the canids in tangible ways (Table 1). Examining the differential habitat use of the different species in a heterogeneous landscape is fundamental to understanding the ecology of the species individually and as an assemblage. This is also essential for conservation and management planning.

2 Materials and Methods

2.1 Ethics Statement

The study was conducted inside and outside protected areas in Gujarat and research permits to carry out ecological research required for the study were obtained from competent authorities, namely, the Office of the Chief Wildlife Warden, Gujarat, and the Gujarat Biodiversity Board. Since the methods used were non-invasive and protected species were not sampled, animal ethics committee approval was not required. No human subjects and/or tissue were involved in this study.

2.2 Study Area

This study was conducted in the Banni grasslands which lie in the Kutch district of Gujarat in north-west India (Figure 2) between September 2014 and March 2015. Spread over an area of 2500 km^2 , the Banni grasslands are considered the largest tropical grassland in Asia and the largest natural grassland in the Indian sub-continent. It is a mosaic of seasonal grassland patches and arid desert patches which frequently involve salt pans.

Also called the Banni Grasslands Reserve, the region is currently a legally protected area, having been classified as a Protected or Reserve Forest in 1955, according to the nomenclature described by the Indian Forest Act, 1927. However, since then the status of the region has been mired in ambiguity since the actual transfer of the land from the Revenue Department to the Forest Department had not been completed. The grasslands are primarily inhabited by pastoralist communities and the region has a very high density of livestock.





Figure 2: A map of the study area in the Banni grasslands with some villages and adjoining regions, with the inset maps showing location of Banni in the Kacchch district of Gujarat state in India. *Map courtesy: K-Link Foundation, India.*

The region has a high faunal diversity. Among mammals, apart from the four canids mentioned, some of the other carnivores than can be found in the Banni grasslands include the desert cat, caracal, jungle cat, and striped hyena. While the Indian wolf has been an integral part of the carnivore assemblage historically, the species is very rarely seen in the region in recent years and hence was excluded from this study.

2.3 Survey Design

Camera traps and track plots [Sarmento et al., 2010; Zielinski and Kucera, 1995] were used to determine the occurrence of each of the species, directly (photographs) and indirectly (pug-marks), in order to understand habitat, spatial, and temporal partitioning between them. (Figure 3)

A grid-based sampling approach having a nested design was used by superimposing a grid over the entire study area of 2500 km^2 in the Banni grasslands (Figure 4). Each cell of the grid measured 4 km^2 .

The cell size was determined by the largest home range amongst the study species which was assumed to be $4 \ km^2$. The home range of the golden jackal is highly variable across its distribution and could be anywhere from $1 \ km^2$ to $20 \ km^2$ [Jhala and Moehlman, 2004]. It has been taken to be $4 \ km^2$ for the purpose of this study. The home range of the Indian fox is between 1.6 and $3 \ km^2$ [Vanak and Gompper, 2007, 2010a,b]. Since little is known about the ecology of the desert fox, we are assuming a home range of about $4 \ km^2$ considering that it is intermediate in size relative to the jackal and Indian fox. This factor helps in meeting the assumption that the canids do not move in and out of the cell during the days of survey.

This grid-based chequerboard design for sampling resulted in 296 grids of 4 km^2 each. Thus, across the landscape, 296 sites were sampled for the occupancy modeling, while a further 379 sites were taken as unsampled sites, giving a total of 675 sites for which the probability of occurrence estimates for each species were obtained (Figure 5).



Figure 3: The components involved in the study design.



Figure 4: The chequerboard grid-based sampling study design employed.

Banni Sampling Design



Figure 5: A map of the study area in the Banni grasslands depicting the sampling design employed. The large gaps in sampling can be attributed to the presence of water bodies at some of the sites and due to an inability to obtain permission to set up camera traps at the rest.

2.3.1 Camera Trap Survey

The entire Banni grassland landscape, which is about $2500 \ km^2$, was divided into $16 \ km^2$ cells, resulting in 78 cells by employing a chequerboard approach in a systematic sampling framework. Of these 78 cells, it was possible to set up camera traps in 74. Within each cell, four camera trap locations were set up in a nested design, thereby increasing the spatial coverage. In total, there were 296 such camera trap locations across the landscape. Each camera trap location, thus, corresponds to a single site. Each camera trap was operated for four consecutive nights ensuring four temporal replicates for modeling the detection probability.

The cameras use passive infrared sensors that are triggered when an object warmer than the ambient temperature moves in front of the sensor. The Moultrie M990i No-Glow Game Camera with motion sensors were used for this study. Thirty two of these cameras were deployed in the field at any given time during the study. Since all cameras were from the same manufacturer, and belonged to the same model, any bias introduced from mixing camera trap types was avoided. In the absence of any sturdy trees on which camera traps can be securely mounted in the study area, custom camera trap mounts or stands were used.

In order to maximise detection if a species was present, a drop of lure (Cross Breed Food Lure from Kishel's Scents, USA) was used for every camera trap. While this is considered an 'active system' method, lures are not as strong incentives as bait and hence do not introduce any associated bias into the study [Garrote et al., 2012; Gerber et al., 2012].

Typically, it took about eight days to finish 4-8 grids, and a minimum of five days per grid (from setting up to retrieval), resulting in a total of about 150 days of effort for completing camera trapping. With 296 camera trap locations ('sites'), and each camera trap having four temporal replicates, this design resulted in 1184 days of camera trapping, in total. The camera trap survey resulted in a total of 6221 videos during the duration of the study.

2.3.2 Track Plot Survey

Track plot surveys were done in order to detect indirect signs of prey species as well as the target canids. Four track plots with an approximate radius of 1 m were set up in front of every camera trap. The track plots provided a two-pronged mechanism for maximising detection of the species, since lure was applied to every track plot as well as ensuring that indirect signs were obtained in the event of camera-related problems.

2.3.3 Covariates Measured

A number of covariates were measured in each cell (Table 1). The covariates were measured once per cell, irrespective of temporal replicates for camera trapping. All measurements were made within a radius of 10 *m* for each site. The remotely-sensed covariates were primarily obtained from maps provided by the K-Link Foundation and Sahjeevan. These include the Banni extent, village locations, waterbody locations, roads, and vegetation (Figure 6).



Vegetation Map of the Banni Grasslands with Villages, Panchayat Roads, and Water Bodies

Figure 6: A map of the study area in the Banni grasslands depicting vegetation cover, roads, villages and water bodies.

2.3.4 Dog Population Estimation

The estimation of dog populations at each village was done through the photographic capturerecapture method [Belsare and Gompper, 2013]. For the spatial and habitat partitioning, data from this as well as any captures in the camera traps were used. The dog populations at the village level obtained (Table 2) were used in the occupancy modeling as well, where the distance to each village was weighted by the estimated dog population for the corresponding village.

The demographic data for the villages in Banni were obtained from Sahjeevan. While designing the photographic capture-recapture study, the 48 villages for which data was available were divided into four classes based on the size of the village, which was decided by the number of households in each village. Incidentally, the division of villages into the corresponding size classes, in this case, resulted in roughly the same number of villages per size class.

Covariata	Sourco	Expected Relationship				
Covariate	Source	Dog	Jackal	Indian Fox	Desert Fox	
Distance to Village	RS	+ve	+ve	-ve	-ve	
Distance to Road	RS	+ve	+ve	-ve	-ve	
Distance to Water	RS	-ve	+ve	+ve	+ve	
	Gb	+ve Prosopis	+ve Prosopis	+ve Prosopis	-ve Prosopis	
Vagatation Type		-ve Suaeda	+ve Suaeda	+ve Suaeda	+ve Suaeda	
vegetation Type		-ve Grass	-ve Grass	+ve Grass	+ve Grass	
		-ve Sedge	+ve Sedge	+ve Sedge	-ve Sedge	
Soil Type	Gb	-ve Saline	-ve Saline	+ve Saline	+ve Saline	
Prey Burrows	Gb	-ve	-ve	+ve	+ve	
		-	+ve Dog	-ve Dog	-ve Dog	
Other Canida	Gb		-	+ve Jackal	-ve Jackal	
				-		
				-ve Desert Fox	-	

Table 1: Covariates used in habitat selection models and expected relationship with site use for study species. (*RS – Remotely Sensed; Gb – Ground-based*)

Using the statistical package R, four villages from each size class were chosen randomly. The resulting 16 villages were sampled for dogs using the photographic capture-recapture method, along with one randomly chosen additional village, for a total sample size of 17. This is assumed as a reasonable sample size since 30% of the total villages were covered.

Based on this study design, dogs were photographed to the extent possible from both flanks, everyday for four days consecutively at every village. This was done at the same time of the day for each village, in the mornings for two days and in the evening for two days, based on the period of maximum dog activity. From the photographs and the observations made in the field, individual dogs were identified for each village. This data was fed into the program PRES-ENCE in order to obtain an estimate of the dog population at each village that was sampled.

A regression was run on the dog populations estimated through the program PRESENCE to find the line that best fits the data (Figure 7). This is listed as "A" or Actual in Table 2. Data from two of the villages sampled were discarded in the regression for a better fit, since they emerged as outliers, probably due their unusually high tourist influx. Based on this, given the number of households for unsampled villages, an estimate of dog populations was obtained, as an extrapolation of the results from the sampled villages. This is mentioned as "E" or *Extrapolated* in Table 2.

Village	No. of Households	Dog Population	Comment
Arendavali	70	10	А
Berdo	160	11	Е
Bhagadiya	200	13	Е
Bhirandiyara	830	45	А
Bhitara Mota	281	17	Е
Bhitara Nana	245	16	Е
Bhojardo	150	6	А
Burkal	50	6	Е
Chachivandh	72	9	А
Chachla	40	4	А
Dadhdhar Moti	207	14	Е
Dadhdhar Nani	141	10	Е
Dedhiya Mota	103	8	Е
Dedhiva Nana	0	3	Е
Dhordo	125	9	E
Dumado	270	18	A
Gorevali	250	16	E
Haiinir	85	42	A
Hodka	225	50	Δ
Inouka	15	<u> </u>	F
Jarmariyandh	10	8	
Karanwali	10	8	F
Karad	10	5	
Kilalou Laivara	42	3	E
Laivara	0	3	E
	80	/	E
Lakharavandh	130	10	E
Luna Mota	70	15	A
Luna Nana	225	15	E
Madan	41	5	E
Misriyado	339	20	E
Mithidi	117	9	E
Neri	45	5	E
Pannavari	35	5	E
Patgar	40	5	E
Reldi	120	4	A
Saadai	150	10	Α
Sarada Mota	306	22	А
Sarada Nana	331	20	E
Sargu	152	13	А
Shiniyado	50	6	Е
Thikriyado	91	8	Е
Udai	140	8	А
Udhma	25	1	Α
Udo	102	8	Е
Vad	50	6	Е
Vadli	40	5	Е
Vagura	92	8	Е

Table 2: Estimates of dog population through photographic capture-recapture for each village in Banni. (A – Actual; E – Extrapolated) 16 16



Figure 7: Population estimates of dogs based on photographic capture-recapture at sampled villages.

2.3.5 Scat Collection

Scat for each of the wild canids was collected opportunistically throughout the landscape for the duration of the study. Scat was collected only at known den locations that had been identified accurately at the species level, or from locations where camera traps and trackplots had been set up. In the latter case, the scat was collected only when the camera trap was present at the site and the species was recorded in the process of defecating in front of the camera trap during the sampling duration. The collection was done using standard methods, directly into an air-tight polythene bag, and the details associated with each sample were written directly on the bag.

This collected scat was than washed and cleaned with detergent soap, and gently pulverized by hand so that there were no chunks or lumps found. The samples were then desiccated in an oven such that there was no or very little moisture left. These dried samples were then analysed under a microscope and the components listed categorically as either present or not for each sample, in order to understand the diet of the species.

3 Analysis

3.1 Software

A bulk of the statistical modeling was implemented in the statistical package R version 3.2.0 (2015-04-16; The R Foundation for Statistical Computing) [R Core Team, 2012], which was also used for cleaning the data from the different components of the study. This was run in the integrated development environment (IDE) RStudio version 0.98.1103 [RStudio Team, 2014]. The package *ggplot2* [Wickham, 2009] available for R [Wickham and Chang, 2009] was used for a majority of the data visualization used in this manuscript. The package *unmarked* [Fiske and Chandler, 2011] available for R was used for the occupancy analysis.

Python version 2.7.6 [Van Rossum et al., 2007] was used for cleaning the data as well as for some of the GIS processing. The Python libraries *pandas* [McKinney, 2012] and *numpy* [Oliphant, 2007] were used for some of the data cleaning and processing done in the analysis. The program PRESENCE [Hines, 2006], invoked using Wine version 1.6.2-Oubuntu4 [Amstadt and Johnson, 1994], was used for the photographic capture-recapture analysis.

QGIS version 2.0.1-Dufour [Team, 2013] was used for all the GIS analysis, and for cleaning as well as operating on remotely-sensed data. The SAGA (System for Automated Geoscientific Analyses) algorithm provider version 2.1.0 [Conrad, 2005], invoked within QGIS, was used to obtain from the polygon data available (such as a vegetation or soil), the corresponding data for a sampled point or series of points. In this study, this method was used to obtain the vegetation present at each camera trap site location from the remotely-sensed vegetation map created by the K-Link Foundation.

All maps were created using the Map Composer available with QGIS. The extent of Banni, the panchayat boundaries, village locations, waterbody locations, vegetation, and roadways data created by the K-Link Foundation and available with Sahjeevan were used as remotely-sensed data for this study.

A software package named ViXeN (View eXtract aNnotate media) [Ramachandran and Devarajan, 2015] was designed and developed explicitly to handle the large volumes of data generated by the camera trap survey in this study. ViXeN is a simple tool to facilitate easily viewing, adding, and annotating metadata associated with media. It can be thought of as a special, customizable file browser with which one may view and edit metadata associated with media files like videos, images and audio. This was used to process approximately 6500 videos that were generated during the course of this study.

Data was entered into LibreOffice Calc (version 4.2.7.2), which was also used for some cleaning and processing of the data. The manuscript has been written in LATEX with the TeXlive distribution version 2013.20140215-1, using the editor Kile version 2.1.3, with a style template that was custom built for this thesis. All analysis for this study has been done with free and open source software to the extent possible, running entirely on the Ubuntu 14.04.2 LTS (Trusty Tahr), the Debian-based Linux operating system.

3.2 Estimating Occupancy

A number of models using different combinations of covariates were run as part of the occupancy analysis using the package *unmarked* [Fiske and Chandler, 2011] in the R programming language [R Core Team, 2012]. The occupancy analysis was done iteratively based on data obtained from the camera traps.

For the analysis, it was assumed that the occupancy of the larger canids is not affected by the smaller canids, but that the smaller canids are more likely to be affected by the larger ones. The iterative process started with the dogs and the results of the occupancy analysis for the dogs was used for the jackals, and results from both of these used for the desert fox, and the results of all the mentioned species were used for the Indian fox. This final occupancy is represented by ψ for the species and indicates the probability of site use across the landscape for each species.

Table 3 lists the top models that best explain the probability of site use (ψ). This occupancy analysis used the single season site occupancy model [MacKenzie et al., 2002]. When using the *unmarked* library [Fiske and Chandler, 2011] in R for occupancy analysis, the input data required involves detection histories, site-specific covariates, and sample-specific or observation-level covariates.

It was assumed that the site-specific covariates do not change over time and the observationspecific covariates do not vary between sites. Additionally, for this study, there were no major observation-specific covariates. The site covariates were examined for autocorrelation using Pearson's correlation coefficient and those that were not highly correlated with each other were used in the models in various combinations for the occupancy analysis. The process of model selection was rooted in information theoretic approaches [Anderson and Burnham, 2002; Burnham and Anderson, 2004], wherein the null model was compared with a number of ecologically plausible candidate models for each species individually (Table 3).

The parameters used in the traditional single season site occupancy model (SSDM) are:

- ψ The probability of site use by each species.
- *p* The detection probability of each species conditional on the presence of that species at the site, i.e. the site is occupied, Probability (detection | presence). It is also the proportion of sites where the species was present and detected.

For a site *i*, site occupancy (or 'species occurrence'), say Z_i , can be defined as a binary site variable such that $Z_i = 1$ if *i* is occupied by the species and $Z_i = 0$ if not. The latter state could arise if either the species was truly absent from site *i* or if the species may have been present but went undetected during the study.

The probability that the site was occupied can then be defined as

$$\psi = \Pr(Z_i = 1)$$

Thus, to estimate the number of sites occupied as well as the factors associated with any changes in ψ , the SSDM involves a sampling design wherein a sample of M sites are visited to record a binary response Y_{ij} . If a species is detected, then Y = 1 and Y = 0 otherwise.

This design typically involves multiple visits or replicates, say $J = j \forall j \ge 1$, within a single season. A false absence in such a case occurs when a species is undetected (i.e. Y = 0) even if it is actually present in the site (i.e. Z = 1). In order to account for such false absences, the detection probability, p, is used.

Some of the assumptions for this analysis are:

- The occupancy state, Z_i at a site remains constant throughout the season.
- The repeated visits or replicates, *J*, are independent for each site.

In this case, I have used a total of four temporal replicates for each site, i.e. $J = \{1, 2, 3, 4\}$, for sampled sites, $M = \{1, 2, ..., 296\}$, and the set of all sites, $N = \{1, 2, ..., 675\}$, such that $M \subset N$.

Thus, for site i = 1, 2, ..., M and replicate $j = 1, 2, ..., J_i$,

$$Z_i \sim \text{Bernoulli}(\psi)$$
, and
 $Y_{ij} \mid Z_i \sim \text{Bernoulli}(Z_i p)$

Also, given that m_i is a vector of site-level covariates and β is a vector of corresponding occupancy parameters, the relationship between these and the occupancy variable ψ is:

$$m_i^T \beta = \text{logit}(\psi_i)$$

The corresponding parameters for detection can be modeled by:

$$o_{ij}^T \gamma = \text{logit}(p_{ij})$$

where o_{ij} is a vector of the observation-specific covariates and γ is the vector of the detection parameters corresponding to them.

Thus, the intercepts β and γ can be obtained by:

$$\beta = \log\left(\frac{p}{p-1}\right)$$

$$\gamma = \log\left(\frac{\psi}{1-\psi}\right)$$

For each species considered in this study, for one of the top models chosen from those listed in Table 3, the corresponding β estimates for each the intercept of the model as well as for each parameter of the model are found in Table 4.

Additionally, it is possible to draw inferences for the unsampled sites in the occupancy modelling approach. This is typically done based on the covariates information, by using the *logit* function shown above. I used the model selection paradigm in the package *unmarked* to obtain the site-specific estimates of ψ for each species from the candidate models for the sampled sites (296). This was then extended to all the sites in the landscape (675) using the *logit* link function described for the selected model and the parameters used in that model. These occupancy estimates for all 675 sites in the landscape were used for the GIS analysis for spatial and habitat partitioning for each species. The empirical Bayes estimate of the number of sites occupied in this study was also obtained using the *unmarked* package in R (Table 5).

Model averaging was not implemented for the models for any of the species. This is because either the best model had minimal variables or involved nested parameters. Model averaging is typically used to make inferences from multiple non-nested models wherein the models have different covariate structures. For models with nested parameters, the model with just a few more parameters having a lower \triangle AIC score is not necessarily the best model since it has 'uninformative' parameters [Arnold, 2010].

4 Results

4.1 Spatial Partitioning

The occupancy estimates obtained were used for understanding spatial partitioning between the species. From Table 5, the näive occupancy estimates for each species can be obtained. Thus, Indian foxes occupied approximately 9% of the sites or a total of 58 out of 675 sites, including the unsampled sites. Similarly, golden jackals had a näive occupancy of about 23% with a total of 156 sites out of 675 sampled and unsampled sites. Desert foxes occupied 11% of the sites, or 75 out of the total 675 sites. And finally, dogs had an occupancy of 8% based on the camera trapping data, or 53 out of 675 sites in the landscape.

Species	Model	nPars	AIC	△AIC	AIC_{wt}	$\sum \mathbf{W} \mathbf{t}$
	p(.) ψ (people+road)	4	162.83	0.00	0.962	0.96
	p(.) ψ (DP+PA+PGOV+	8	169.29	6.46	0.038	1.00
Dog	SSL+SSP+WB)					
	$\mathbf{p}(.)\Psi(\mathbf{dogOcc})$	3	569.46	0.00	0.74	0.74
Colden Isolal	p(.) ψ (DP+PA+PGOV+	8	572.61	3.15	0.15	0.89
Golden Jackar	SSL+SSP+WB)					
	p(.) ψ (people+	5	573.30	3.84	0.11	1.00
	road)					
	p(.) Ψ(DP+PA+PGOV+	8	293.52	0.00	0.883	0.88
	SSL+SSP+WB)					
Desert Fox	p(.) ψ (dogOcc+	4	297.98	4.46	0.095	0.98
	jackalOcc)					
	p(.) ψ (people+	5	300.92	7.40	0.022	1.00
	road)					
	p(.) ψ(people+	5	293.92	0.00	0.43	0.43
	road)					
Indian East	p(.) ψ (dogOcc+	5	294.14	0.22	0.39	0.82
	jackalOcc+dfoxOcc)					
	p(.) ψ (DP+PA+PGOV+	8	295.66	1.74	0.18	1.00
	SSL+SSP+WB)					

Table 3: Models that best explain the probability of site use (ψ) with site level covariates in the Banni grasslands for all study species. Bold lettering indicates the model selected for further analysis. (*nPars - no. of parameters, AIC - Akaike Information Criterion, Wt - weight, road - distance to a point on the nearest road, people - distance to nearest village weighted by the number of households in the village, dogPop - distance to nearest village weighted by the estimated dog population for the village, dogOcc - occupancy estimate for dog, jackalOcc - occupancy estimate for jackal, ifoxOcc - occupancy estimate for Indian fox, dfoxOcc - occupancy estimate for desert fox, DP - Dense Prosopis, PA - Prosopis Aeluropus, PGOV - Prosopis Grass Other Vegetation, SSL - Suaeda Saline Land, SSP - Suaeda Sedge Prosopis, WB - Water Body)*

Species	Variable	$\beta_{intercept}$	SE	Z	$\mathbf{P}(> z)$
	(Intercept)	-1.0576	0.9473	-1.12	0.264
Dog	people	0.0576	0.0504	1.14	0.254
Dog	road	-18.5305	13.2854	-1.39	0.163
	(Intercept)	-0.0306	0.59	-0.0519	0.959
Golden Jackal	dogOcc	0.7259	1.66	0.4384	0.661
	(Intercept)	-0.4267	0.7927	-0.538	0.5904
Desert Fox	DP	-0.0069	0.0081	-0.847	0.3970
Desett FUX	PA	-0.0017	0.0034	-0.501	0.6160
	PGOV	-0.0228	0.0153	-1.494	0.1351
	SSL	0.0005	0.0016	0.309	0.7576
	SSP	0.0050	0.0077	0.651	0.5153
	WB	-0.0342	0.0172	-1.985	0.0472
	(Intercept)	-1.7042	0.4496	-3.7902	0.0002
Indian Fox	people	0.0202	0.0267	0.7589	0.4479
	road	-8.7955	8.0411	-1.0938	0.2740

Table 4: Individual and model selected β estimates.

Species	Estimated No. of Sites	No. of Sampled Sites
Dog	23	295
Golden Jackal	68	295
Desert Fox	28	253
Indian Fox	25	293

Table 5: Occupancy estimates for each species at the sampled sites.

When considering the gradient (ranging from 0 to 1) of the probability of occurrence for each site in the landscape, for each species, the pattern seen in Figure 8 is obtained. This map was obtained by overlaying the highest ψ values for each species on the map in order to compare the space use by all of them.



Figure 8: A map of the study area in the Banni grasslands with occupancy of the different canid species.

From Figure 8, one can see that dogs were typically found in and around villages, while desert foxes were the farthest from human habitation. Jackals and Indian foxes were at intermediate distances to human habitation, with considerable (almost complete, in fact) spatial overlap between them. Also, the probability of occurrence for the desert foxes seems to be low in areas where the occurrences of any of the other canids is high. Sites which have high ψ values for desert foxes did not overlap with any other species, typically. The pairwise comparison of occupancy for each species can be seen in the figures given in the **Appendix**.



Figure 9: Diagrammatic representation of the interaction between each species and the presence of the other three species in the area as understood from the occupancy models run for each species.

The relationship between the probabilities of occurrence for each species can be seen from Figure 9. From here, a directional positive interaction between the occupancy of jackals and dogs can be understood. On the other hand, desert foxes seem to be influenced negatively by both larger canids. Indian foxes seemed to be negatively influenced by desert foxes but not by jackals or dogs. Since the operative assumption was that larger carnivores are not influenced by the smaller ones, bi-directional interactions were not studied.

The broad patterns of distribution of each species as a function of their proximity to a village as well as the presence of the other species can be seen in Figure 10. This is the inferred distribution pattern of each species based on the occupancy analysis. The radius of the circles for each species are an approximate function of their respective populations in the area for the wild canids, and not the home ranges of the species.



Figure 10: Diagrammatic visualization of actual patterns of distribution of each species corresponding to proximity to villages.

For dogs, in the actual analysis, data from both the occupancy modeling (using the camera trap data) as well as the dog population estimates from the photographic capture-recapture method were used. The number of sites occupied does not change but an additional covariate in the form of distance to the nearest village weighted by the dog population that had been estimated for that village was used. Since there could be cross-correlation between distance to the nearest village and distance to the nearest village weighted by either the number of households for the village or the estimated dog population for it, I tried to include just one of them at a time in a model.

It can also be inferred from Figure 8 that while there is almost complete overlap between the Indian fox and the golden jackal, there is also a mild overlap between the sites with higher probabilities of occurrence for Indian fox and desert fox, as well as desert fox and golden jackal, although not much. This implies that there exist some pockets in the landscape where all three wild canids might be present. It must also be noted that there was negligible overlap between the presence of any of the canids and sites with high desert fox occurrence.

4.2 Habitat Partitioning

As explained earlier, from Figure 8 one can infer the co-occurrence of three out of four species in this study, namely, the Indian fox, golden jackal, and domestic dog. It was also seen that there was considerable spatial overlap between sites with jackals and dogs. From the same figure, it can be seen that the sites where the two foxes co-occur are all quite far from human habitation or villages, which is where dogs are predominantly absent.

They also seem to be at intermediate distances to waterbodies as well as roads as seen from the GIS analysis. From the vegetation data, it can be seen that these sites typically contain open *Prosopis juliflora* with *Suaeda*, sedges and a mix of other vegetation. A somewhat similar pattern emerges from Figures 11 and 12.



Figure 11: Barplot of normalized habitat use for all four species of canids.



Figure 12: Barplot of vegetation selectivity for all four species of canids.



Figure 13: Barplot of soil selectivity for all four species of canids.

From Figure 12, one can also clearly notice that both species of foxes were almost completely absent in areas with dense *Prosopis*. Golden jackals were the only study species found in all habitat types. Also, Indian fox and desert fox seem to show similar patterns of occurrence between the habitat types, although the former clearly show a higher correlation with the presence of grasses and sedges, while the latter seemingly has a clear affinity to highly saline areas. Where Indian foxes are present, they have a near complete spatial overlap with golden jackals, which also matches the extent of habitat overlap between the two.

Figure 13 compares the soil selectivity for all four species of canids. All species seem to have a preference for clayey soils, predominantly, with desert foxes and dogs also found in areas with sandy soils. As far as soil selectivity goes, golden jackals and dogs seem to overlap considerably, while Indian foxes overlap the least with the other species.



4.3 Temporal Partitioning

Figure 14: Hourly activity count for each of the study species.

The data for understanding the time when each species is active was obtained from the time stamps corresponding to the camera trap videos of each species. This data was extracted from the file information for the corresponding videos through the software ViXeN [Ramachandran and Devarajan, 2015] based on the presence of the species in the video. There appears to be considerable temporal partitioning between the wild canids and dogs (Figure 14).



Figure 15: Boxplot comparing the relationship between activity periods and temperature for each of the study species.

Golden jackals seem to be the most active of all the canids and were inactive only for a few hours in the afternoon, which appears to be the period of maximum activity for dogs according to the camera trap data. Indian foxes and desert foxes seem to be primarily nocturnal, while jackals were both crepuscular as well nocturnal, with some diurnal activity as well.

The temperature data was obtained from the camera traps as well. The camera traps used for the study are able to record the temperature and pressure at the location for each image or video, visible on the information strip found on the file. This data was entered from each file using the software package ViXeN [Ramachandran and Devarajan, 2015]. As expected, there is a correlation between the time at which the species is active and the corresponding temperature at that time (Figure 15). Dogs, being diurnal for most part seem to have the highest tolerance for high temperatures, while Indian foxes which were not diurnal had the least tolerance. Indian foxes also seemed to be most active at lower temperatures, while golden jackals were most active at intermediate temperatures. Desert foxes had the largest range of temperatures during which they are active, varying from intermediate to high. They seem more tolerant of higher temperatures and less tolerant of lower temperatures than Indian foxes.



4.4 Dietary Partitioning

Figure 16: Dietary composition as count of prey present in scats of Indian fox, desert fox, and golden jackal.

From Figure 16, we can see that broadly there seems to be some overlap between the diets of all three wild canids studied. A closer look indicates some distinct partitioning between the species. While all three seem to consume similar levels of coleopterans in their diet, jackals seem to be consuming significantly less isopterans and orthopterans than the foxes. The jackals also seem to consume less birds and reptiles, and more small mammals than the foxes. The difference between the species is even more marked when we focus on the plant matter. As far as plant matter is concerned, desert foxes seem to consume more *Suaeda*, jackals consume more *Prosopis*, and Indian fox scat indicate more grass matter in their diet.

5 Discussion

5.1 Choice of methods

Many prior studies involving carnivores on which capture-recapture (camera-trapping) studies cannot be done (such as wolves and other canids) involve the use of telemetry [Aarts et al., 2008; Burdett et al., 2007; Kamler et al., 2004, 2012; Vanak and Gompper, 2010a], which has now become the de-facto standard for assessing species-habitat relationships. Such radio-telemetry studies are ideal for examining their habitat use, selectivity and estimating home ranges of carnivore species. However, it was very difficult to obtain permission to radio-collar all species of interest given the timeframe of the study. Moreover, even in the event of permission being granted, the number of individuals of each species that can be radio-collared will be very low, not indicative of actual densities, and insufficient for the purposes of this study. Also, although reliable, these techniques are labor-intensive and often expensive [Hebblewhite and Haydon, 2010; Wilson and Delahay, 2001].

The application of robust non-invasive methods to estimate distribution and abundances of carnivores is increasingly being employed by researchers, particularly in habitats that are dense and in cases where animals are elusive [Hines et al., 2010; Karanth et al., 2006, 2011; Long et al., 2007, 2011; Vanak and Gompper, 2007]. A crucial limitation in using telemetry studies is that they involve physical capture of animals and inferences about species-habitat relationships are limited to few individuals. Recently developed occupancy models are considered robust for studies intended to identify areas of high use within larger areas [MacKenzie, 2006]. Moreover, the occupancy survey and modelling approach can explicitly account for imperfect detection

[MacKenzie, 2006; Mackenzie and Royle, 2005; MacKenzie et al., 2003; Mackenzie et al., 2004, 2005, 2009], the primary source of bias in wildlife studies [MacKenzie, 2006; Mackenzie and Royle, 2005; Mackenzie et al., 2005].

Occupancy estimation techniques allow for making assessments on spatial distribution of carnivores using detection – non-detection data, while explicitly addressing the issue of imperfect detection [MacKenzie et al., 2002; O'Connell et al., 2010; O'Connell Jr et al., 2006]. These methods are ideally suited for distribution studies of species occurring at low local densities or at large spatial scales [MacKenzie, 2006].

Spoor surveys are commonly used for monitoring wildlife across the globe. However, estimating changes in the distribution patterns and abundance of wildlife populations from such surveys involving indirect signs is not well established. As a reliable alternative, camera trap surveys are increasingly used for population studies.

This study is one of the first to utilize camera traps for estimating the distribution patterns of an entire guild of carnivores. Such a study designed for modeling multi-species occurrence is more efficient in terms of effort, time, funds, and personnel. Furthermore, modeling such guilds of organisms in a landscape provides a more comprehensive understanding of the system, as opposed to studying them individually, since inter-species interactions can be inferred as well.

5.2 **Resource Partitioning**

Prior research [Donadio and Buskirk, 2006; Elmhagen and Rushton, 2007; Fisher et al., 2013; Gompper and Vanak, 2008; Ritchie et al., 2012; Vanak, 2008; Vanak and Gompper, 2009a] indicate that diet, body size, predatory habits and taxonomic relationships emerge as important factors when trying to understand species coexistence. These studies indicate that body size differences have a direct correlation with the frequency of attack. They state that lethal interactions are less likely when the differences in body size are small or large. However, lethal interactions are more likely when the difference in body size is intermediate and may be related to an overlap in diets. This implies that generally one can expect more interactions between species within a family. The sub-lethal interactions result in "landscapes of fear".

Some of the studies that have involved looking at species coexistence include: bat-eared fox, cape fox, and black-backed jackals in South Africa [Kamler et al., 2012, 2013], dogs and jackals in Zimbabwe [Butler et al., 2004] Indian fox and domestic dog in India [Vanak, 2008; Vanak and Gompper, 2009a,b, 2010a,b], domestic dog and golden jackal in India [Aiyadurai and Jhala, 2006], wolf, coyote, and swift fox in Canada and North America [Atwood and Gese, 2008; Gese et al., 2012; Kitchen et al., 1999; Newsome and Ripple, 2015; Smith et al., 2003; Voigt and Earle, 1983], red and Arctic fox in Canada, North America, and Eurasia [Hersteinsson and Macdonald, 1992], crab-eating and pampas fox in Brazil [Faria-Corrêa et al., 2009]. It must be noted that almost all of these studies look at only two species at a time. Additionally, all of them involve species with considerable dietary niche separation. While human-subsidized carnivores are rarely considered, species-scapes are completely ignored.

The species considered in this study have two pairs belonging to the same genus: dogs and golden jackals (belonging to the genus *Canis*), Indian foxes and desert foxes (belonging to the genus *Vulpes*). From this study, we can see that there is clearly considerable spatial and temporal partitioning between desert foxes and the other three canid species. There is also some habitat partitioning between them. Having established this, we can now focus on the Indian fox, golden jackal and domestic dog, which seem to involve more complex interactions.

The spatial partitioning results indicate that the Indian fox, domestic dog, and golden jackal seem to co-occur in the landscape, with a considerable number of sites in which they can be found. Also, throughout the landscape, Indian fox presence overlapped considerably with golden jackal presence, although the latter appears to be present in more sites. Desert foxes do, however, also appear to be present mostly in areas without any of the other canids. This establishes that while all four species are sympatric at a broad scale, some canid species are sympatric at smaller scales as well.

We can now look at some of pairwise interactions between the wild canids to help tease apart the co-occurrence patterns at finer scales. There does not appear to be any major temporal partitioning between the Indian fox and the desert fox, although there is apparent dietary and habitat partitioning between the two. We can infer that, at local scales where the two species co-occur in a landscape, despite their similarity in size and even though they belong to the same genus (*Vulpes*), this partitioning in diet, habitat, and to a lesser extent time could be the reasons behind their coexistence, without one out-competing the other.

Between the desert fox and the jackal, there is conspicuous habitat, dietary, as well as temporal partitioning. If not for this partitioning of resources, there is a strong likelihood that the jackal could out-compete the desert fox with interference competition, due to its larger size as well as seemingly larger population sizes since more sites seem to have jackal presence. On the other hand, between the Indian fox and the golden jackal, there is conspicuous overlap in space and habitat. However, there appears to be clear dietary and temporal partitioning between the two, without which the Indian fox could again be out-competed by the jackal.

We can also see the effects of landscape and landuse change in areas with high human presence. For instance, while *Prosopis* is an invasive species in the region, it seems to have a differential effect on the presence of the different species. Desert foxes seem to have a negative correlation with the presence of *Prosopis*, while golden jackals seem to have a strongly positive correlation. This elucidates the complex dynamics between abiotic and biotic factors in ecological studies.

However, there emerges a strong negative correlation between the presence of dogs (which are human-subsidized, in the region and elsewhere) and some of the other canids. This raises important questions related to the management of landscapes with increasing human presence, and by extension, the presence of human-subsidized species such as dogs.

This study indicates the possible mechanisms by which an assemblage or guild of multiple sympatric species can co-occur. The results of this study also indicate the complex and intricate inter-relationships between species. Just focusing on one aspect of an interaction between species can be misleading. This could have management implications, in areas with species assemblages, as well as in landscapes with human-subsidized species.

Appendix



Figure 17: A map of the study area in the Banni grasslands with occupancy of the golden jackal and the Indian fox.



Figure 18: A map of the study area in the Banni grasslands with occupancy of the golden jackal and the dog.



Figure 19: A map of the study area in the Banni grasslands with occupancy of the desert fox and the dog.



Figure 20: A map of the study area in the Banni grasslands with occupancy of the Indian fox and the desert fox.

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