A WHISTLE AMONGST GROWLS:
DHOLES IN A MULTI PREDATOR SYSTEM IN DRY DECIDUOUS FORESTS OF INDIA

Dissertation Submitted to Saurashtra University, Rajkot
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in Wildlife Science

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"The wild dog is a bundle of contradictions;
Tribal hunter gatherers welcome them as providers;
To the ignorant they are drones living off the fat of the land;
To scientists they are predators, not parasites, and play an important role in the ecosystem;
And to dog lovers they remain a puzzle."

-E.C. Davidar, Whispers From The Wild

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CERTIFICATE

This is to certify that **Ms. Pallavi Ghaskadbi** of Wildlife Institute of India has carried out an original research titled ***"A whistle amongst growls: Dholes in a multi predator system in dry deciduous forests of India"*** in partial fulfilment of her ***"Master in Wildlife Science"*** from ***Saurashtra University***, Rajkot. This study was carried out under our supervision at the **Wildlife Institute of India** from December 2014 to May 2015. We also certify that this work has not been submitted for any other degree to any other university.

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SUMMARY

Background

The study of carnivores has evolved greatly since the time of Mech (1966) and Schaller (1967, 1972), from comprehensive monographs to statistically robust models. As the book Carnivore Ecology and Conservation (Boitani & Powell 2012) identifies correctly, carnivore guilds, resource partitioning, niches, competition, intra-guild predation and mutualism are only narrowly understood, if at all. A significant amount of research has proved that there is a positive correlation between habitat heterogeneity/diversity and animal species diversity owing to the availability of more exploitable niches (Tews et al. 2004). On a spatial scale for free ranging large carnivores, a place like the Tadoba- Andhari Tiger Reserve has a low habitat heterogeneity (Fig. 1), however, it shows a variety of species of both predators and prey in a small area. Studying the prey- predator interactions in such a system would lead to a better insight into large carnivore ecology. Not many studies on niche partitioning of sympatric carnivores have considered the interactions of social predators like Dholes or the Asiatic Wild dog (*Cuon alpinus*, Pallas 1811) with other solitary predators in India.

Dholes are highly elusive social carnivores. Apart from the natural history, social and reproductive behaviour of the Dhole which had been documented by A.J.T. Johnsingh (1992), no work has been undertaken to study the behavioural ecology of the Dhole. In contrast with the African Wild dog which enjoys much more attention of researchers and biologists, the Dhole has clearly not been a favourite. Being a social carnivore, there is a complex and dynamic fission and fusion of packs amongst Dholes. However, there is a grave lack of information on the pack dynamics of the Dhole. I attempted to conduct experiments to study one of the fundamental factors of social behaviour which is individual recognition.

Methods

A basic understanding of sympatric carnivore ecology with asymmetric competition enables us to hypothesize that in order to coexist and not just co-occur, there must be a niche segregation on at least one of the three axes: space,

time and/or diet. To understand how three large sympatric predators co-occur in space and in time, camera trapping was carried out and carnivore scats were analysed to complement the activity data with an idea of the actual consumption of prey species. Temporal activity overlaps were derived by using kernel density estimates whereas multiple response permutation procedure test was used to study the space use of the animals. Diet analysis was carried out following Mukherjee et al. (1994) to study prey biomass, prey selectivity and diet overlap amongst carnivores. I conducted scat translocation experiments to study whether Dholes demonstrate the Neighbour-Stranger Discrimination (NSD) phenomenon like many other social animals (Packer 2010). To understand the pack dynamics and the basic behavioural ecology of the Dholes, a preliminary ethogram of all observed behaviours was compiled. Digital videos of Dholes shot during the field observations were analysed frame by frame for this purpose.

Significant findings

All the sympatric predators were found to co-occur in the small area of TATR. There was a similar space use pattern observed for all three carnivores, however there was no strong spatial segregation/overlap pattern found except that the Dholes and leopards showed a significant segregation and avoidance of each other's space. There was a significant overlap between the temporal activity pattern of the tiger and the leopard. Both tiger and the Dhole showed a bimodal, crepuscular activity pattern but the peaks were different suggesting that the tigers were more active during the dusk whereas Dholes during the dawn. The diet analysis indicated that there was no significant difference in the prey species consumed by the predators. However, it indicated that they were consumed differently. This simply means that the major prey species of the tiger, leopard and dhole, though remained more or less similar, the proportions in which the prey were taken were different.

After analysing a total of 427 minutes of digital videos for behavioural data (3394 events recorded in 1654 snapshots of ten seconds each), a preliminary ethogram of Dholes was compiled. The frequency and the activity budgets of the Dholes were also calculated. The scat translocation experiments were successful and it was observed that the Dholes investigated stranger scats for longer duration than their own or the neighbours'. It also seemed that the sex and hierarchical position of an individual determined how they responded to the scats. However, further trials would be required to draw strong inferences from these experiments.

Significance of the study

The short term study was insightful on many accounts. Predator-prey interactions are more often than not, site-specific. This happens to be one of the first studies of sympatric carnivores from TATR. An ethogram of Dhole behaviour was compiled for the first time which sets stage for an even more comprehensive ethogram and study of Dhole behavioural ecology in the future. Through this study, I described, two important scent marking behaviours which were not reported before for the Dholes: '*hind bounce*' and '*hind scrub*'. Dholes are categorised as Endangered by the IUCN and face a great threat from habitat loss, disease and human prejudices. A better understanding of this species is required for its conservation before we lose this species without even unravelling the enigma that it is!

CHAPTER I
INTRODUCTION

1.1. Introduction:

Carnivore ecology emphasizes on an integrated approach to study predators without neglecting the interactions it would have with other members of the guild. Hence, a comprehensive understanding of intra guild community interactions is crucial while studying any predator species. Competition between large predators may be either exploitative or by interference (Linnell 2000). Interference competition between the tiger, leopard and the Dhole has not been well documented in India though there have been records of tiger hunting Dholes or vice versa. This is primarily because co-existing sympatric species are bound to segregate based on their individual niches either temporarily, spatially, based on dietary niches or some form of character displacement (Brown 1956; Hutchinson 1959; Pianka 1978). Exploitative competition between these three carnivores has been studied in the southern Indian forests (Johnsingh 1992; Karanth & Sunquist 1995; Venkataraman 1995); in Central India (Acharya 2007; Edgaonkar 2008; Majumder 2011) and also the North East (Selvan et al. 2013). However, the mechanisms underlying the patterns of segregation or overlap between predators are seldom addressed. Basic information about interactions between predators and their prey incorporating the ecology of the prey is still incomplete and also very site-specific. Habitat heterogeneity leads to availability of more niches to be occupied. A variety of niches would be conducive for more species to colonize and thrive in a particular habitat. However, TATR seems to have a relatively low level of habitat heterogeneity but a large number of predators and prey making this a highly competitive system.

1.2. Rationale of the study:

The Asiatic wild dog, *Cuon alpinus*, also known as the Dhole, is an endangered species of dogs found in much of South and South-East Asia. In spite of belonging to the most alluring Order - Carnivora and being an animal of a considerable body size, Dholes have been moderately studied in India. These social carnivores are unique in many aspects from other predators found in the Indian forests. Dholes are social predators like the wolves but, unlike wolves, they are a predominantly forest-dwelling species sharing their habitat with other top predators (Krishnan 1972; Acharya 2004; Acharya 2007). Zoogeographically, Dholes seem to be the most widespread canid of South East Asian region ranging from around 500 N from the Sanghalien Amurland and the Altai mountains to roughly 700 E covering the whole of continental Asia and are also found on the islands of Sumatra and Java (Acharya 2007).

Throughout their range in India, the Dholes are sympatric with other large carnivores like the tiger, *Panthera tigris*, and leopard, *Panthera pardus*. Carnivore ecology emphasizes on the influence of other members of a guild while studying the ecology of a single predator. Hence, a comprehensive understanding of intra guild community interactions is crucial while studying a single predator species. Competition between large predators may be either exploitative or by interference (Linnell 2000). Interference competition has not been documented in the three large predators in India though there have been odd photographic records of tiger hunting a Dhole. Exploitative competition studies between these three carnivores have been mainly from the Southern (Johnsingh 1992; Karanth & Sunquist 1995; Venkataraman 1995); a few from Central India (Acharya 2004; Acharya 2007; Majumder 2011) and also the North East (Selvan 2013). However, there is no published data available from the dry deciduous forests of the Tadoba-Andhari Tiger Reserve.

Co-existing sympatric species are bound to segregate based on their individual niches either temporarily, spatially, based on dietary niches or some form of character displacement (Brown 1956; Hutchinson 1959; Pianka 1974). A recent study has proved that the accessible prey spectrum of Dholes overlaps with leopards and tigers in Asia (Hayward et al. 2014). However the mechanisms underlying these patterns are seldom addressed.

The TATR is a unique reserve in the sense that it has maintained stable populations of all three species and seems to be operating at the carrying capacity (Habib et al. 2014). Species can survive together if intra-specific competition is stronger than inter-specific competition. This means that each species will inhibit their population growth before they inhibit that of the competitor, leading to coexistence. Studying the inter-pack relationships in Dholes would lead to a better understanding of the intra-specific interactions within this species. In the milieu of intra-specific social interactions, individual recognition is important primarily for maintaining territories, competition, hierarchy and parental care. Empirical studies in the past on the response of solitary and territorial animals to their neighbours as compared to the responses towards strangers demonstrate the "dear enemy" effect. First described by Fisher through his study on sociality in birds, the dear enemy effect illustrates the intensity of aggression of an individual towards a familiar neighbour is far less than towards a floater or a stranger in order to reduce the energy costs of actively defending the territory constantly. However, there have been studies that prove otherwise. This is known as the threat level hypothesis or the "nasty neighbour" effect. It may seem obvious to hypothesize that social animals demonstrate the nasty neighbour effect based on our understanding of group living. A group would encounter the neighbour frequently and may be under a constant threat whereas a stranger group would not pose a threat as 'strangers' in this aspect would be mostly refer to one or few dispersing individuals and not the entire group. In either of these cases, recognition between individuals and groups (Neighbour-Stranger Discrimination) is a key factor. Such complex behaviour has not been extensively studied in social carnivores and not at all explored in social canids. This study, therefore, aims to provide new insights into inter-pack relationships in Dholes as well as supplement the earlier studies on the food habits and spatio-temporal patterns thereby contributing a piece in the intriguing puzzle of Dhole ecology.

1.3. Hypotheses:

Based on the literature review and a priori data at hand, I hypothesized the following:

- ***The spatio-temporal activity pattern and dietary niche of the three carnivores do not overlap throughout the TATR landscape.***
- ***The activity peaks of predators are co-related to the activity peaks of the prey.***
- ***Dhole packs individually recognise other Dhole packs as neighbours or as strangers***

1.4. Key research questions:

- ***How do Dholes, tiger and leopards segregate themselves in terms of food, space and time?***
- ***Are neighbouring Dhole packs able recognize and distinguish between neighbours and strangers?***

1.5. Current status of research in the subject area:

The approach to studying community ecology was significantly modified ever since the concept of niche was popularized by Joseph Grinnell (1917, 1924), Elton (1927) and Gause (1936). Since then, the niche concept was used to study inter-specific competition and resource partitioning (Wuenscher 1969; MacArthur 1967; Pianka 1973, 1974; Carothers 1984). Empirical work has been done on co-existence of sympatric carnivores based chiefly on three aspects: space, time and diet (Johnsingh 1992; Karanth & Sunquist 1995; Acharya 2007; Wang 2009; Ramesh 2011; Hayward et al. 2014). Most of the studies from India have studied the interactions between the two large cats- the tiger, *Panthera tigris,* and the leopard, *Panthera pardus*. A moderate amount of literature is also available on the interactions between these two large predators and the Dhole *Cuon alpinus*. The presence of a social carnivore like the Dhole has a significant effect on the ecology of the two large cats (Johnsingh 1992; Karanth 1995; Acharya 2007; Ramesh 2011; Hayward et al. 2014). The studies describing activity patterns of these carnivores in a system have seldom addressed the cause or the process behind the observed patterns. Animals dedicate most of their active time to food acquisition (Suselbeek et al. 2000) implying that a complete understanding of the activity pattern of predators would be one which encompasses an understanding of the prey activity pattern as well. The focus of studying temporal activity patterns of predators is fast shifting from comparing individual time distributions to estimate the extent of overlap of activity amongst predators and between predator and prey (Rideout & Linkie 2009; Linkie & Rideout 2011; Rowcliffe et al. 2014).

The dietary analysis methods of animals have undergone a significant change. Though, till date, scats are analyzed for studying the food habits, molecular methods are being used to reliably identify the prey from the scats. Radio-telemetry studies of collared animals can generate large data sets of kill observations in order to study their prey via direct sightings. However, microscopically identifying undigested remains of the prey is still the most logistically sound and fairly reliable method to study the diet of a predator. To make it more robust, it may be complimented with other methods as well.

As behavioural science evolves, the emphasis on statistics and the interpretation is increasing rather than data acquisition (Boitani & Fuller 2000). However, at the beginning of a study of the behavioural ecology of a species, a fundamental understanding of the behavioural repertoire is essential. For this purpose, an ethogram is compiled which is a comprehensive inventory of behaviours. Carnivores tend to actively protect and defend a particular area for at least some part of their life cycle and thus they are said to be 'territorial' (Gittleman 1989). A territory holder has an exclusive access to all the resources in that particular area. Territories may be classified based on the resources being defended and may be single or a multipurpose territory. Often territories are based on food and water resources or access to mates (MacDonald 1983; Gittleman 1989). Dholes are territorial social carnivores (Johnsingh 1992; Acharya 2004, 2007; Venkatraman 1995; Majumder 2011) with mutually exclusive core ranges but overlapping buffer areas. Dhole packs are dynamic and may show fission-fusion of packs based on seasonality (Johnsingh 1992; Acharya 2004). Individual recognition of conspecifics is an important phenomenon in the study of social behaviour and is studied in many species like insects, reptiles, birds as well as mammals (Falls 1982; Breed 1983; Vander Meer 1998; Hurst 2001; Brennan 2006; Carazo 2008; Parker 2010). Based on individual recognition, it had been demonstrated that animals can distinguish between neighbours and strangers. This is known as the "familiarity hypothesis" (Bartlett et al. 1984) or neighbour-stranger discrimination (NSD). This was later challenged by the "threat level hypothesis" which suggested that it is not how familiar an animal is to another but the perceived threat which facilitates the distinction between conspecifics (Temeles 1994). These two hypotheses were then used to comprehend the "dear enemy" effect (Fisher 1954). The dear enemy effect explains that the aggression showed by individuals towards their neighbours is less than that shown towards strangers or "unfamiliar" individuals. However it was proved that some species like the banded mongoose which is a social carnivore, the dear enemy effect was replaced by the "nasty neighbour" effect which is exactly opposite to former hypothesis (Muller et al*.* 2007; Carazo et al. 2008; Newey et al. 2010). The rationale behind this hypothesis in case of social animals is that, unfamiliar individuals would not pose much of a threat as it is unlikely that the entire group of unfamiliar individuals or "strangers" would displace another far off territory under normal ecological conditions. However, there is a constant threat from the neighbours. Thus, quantifying threats would enable us to understand individual recognition in a more robust fashion and there have been attempts to do so (Muller et al. 2007; Schradin 2010). It would, therefore, be interesting to see whether and how Dhole packs can distinguish other packs as neighbours or strangers, if certain conditions are simulated. This would help us better understand social living in canids and behavioural ecology of Dholes. Considering the fact that eventually we may need to manage our wildlife actively in PAs, a thorough understanding of species biology would be crucial.

1.6. Study area:

The Tadoba Andhari Tiger Reserve (20°04’53” to 20°25’51”N and 79°13’13” to 79°33’34” E) is a 625.40 km^2 protected area located in the Chandrapur district of the state of Maharashtra, India. Tadoba-Andhari Tiger Reserve (TATR) is considered as one of the potential source populations for tigers in Central India. It maintains connectivity to the adjoining forest areas such as Indravati Tiger Reserve in the south-east through the forests of Chandrapur - Gadchiroli districts which further connects to Kanha National Park in north-west through the forests of Navegaon National Park and Nagzira Wildlife Sanctuary and Pench National Park in the north through the forests of Bor and Umred-Karhandla Wildlife Sanctuaries. All these forests also have remnant Dhole populations of the Central Indian Landscape.

The TATR comprises of the Tadoba National Park spread over an area of 116.55km^2 and the Andhari Wildlife Sanctuary spread over 508.85 km^2 (ref. Fig. 1a)- d)). Irai in the western half and Andhari in the eastern half are the two major rivers flow across the Reserve. The area is mostly undulating and hilly in the northern part of the Park whereas it is plain in southern part. It has a subtropical climate with three distinct seasons- summer, monsoon and winter. The Reserve receives southwest monsoons and rainfall persists from June to Spetember. This biodiverse region include 41 species of mammals, more than 195 species of birds, 111 species of butterflies and 30 species of reptiles (Tiple 2010; Nagendra et al. 2006).

The intensive study area can be characterized as southern tropical dry deciduous forest (Champion & Seth 1968). Teak, *Tectona grandis*, dominates most of the forest area. Other commonly found tree species found in the study area include Ain *Terminalia alata*, Mahua *Madhuca indica*, Tendu *Diospyros melanoxylon*, Dhaoda *Anogeissus latifolia*, Jamun *Syzygium cumini*, Palas *Butea monosperma*, Shalmali *Bombax ceiba*, Karu *Sterculia urens*, Kusum *Schleicheria oleosa* and Ber, *Zizyphus* spp. Bamboo *Dendrocalamus strictus,* is also widespread throughout the forest.

The tiger *Panthera tigris*, leopard *Panthera pardus* and the Dhole *Cuon alpinus* are the large carnivores found in the study area. Other carnivores include sloth bear *Melursus ursinus*, jungle cat *Felis chaus*, palm civet *Paradoxurus hermaphroditus*, small Indian civet *Viverricula indica*, ruddy mongoose *Herpestes smithii*, common mongoose *Herpestes edwardsi* and ratel *Mellivora capensis*. The chital *Axis axis*, sambar *Cervus unicolor*, nilgai *Bosephalus tragocamelus*, gaur *Bos gaurus*, wild pig *Sus scrofa*, chausinga *Tetracerus quadricornis*, Barking deer *Muntjacus muntjak*, the common langur *Semnopithecus entellus*, black-naped hare *Lepus nigricollis* and Indian porcupine *Hystrix indica* form the potential prey base of the carnivores in Tadoba Andhari Tiger Reserve.

The Reserve has 3 villages in the core and 79 villages (Dhanwatey et al. 2013) in the buffer zone. The buffer zone is composed of villages, tourist facilities and croplands. Cattle are grazed in buffer forests and firewood and fodder are harvested from forests near villages, leading to degradation in these areas (Nagendra et al. 2006).

...the Dhole and the Tiger in TATR

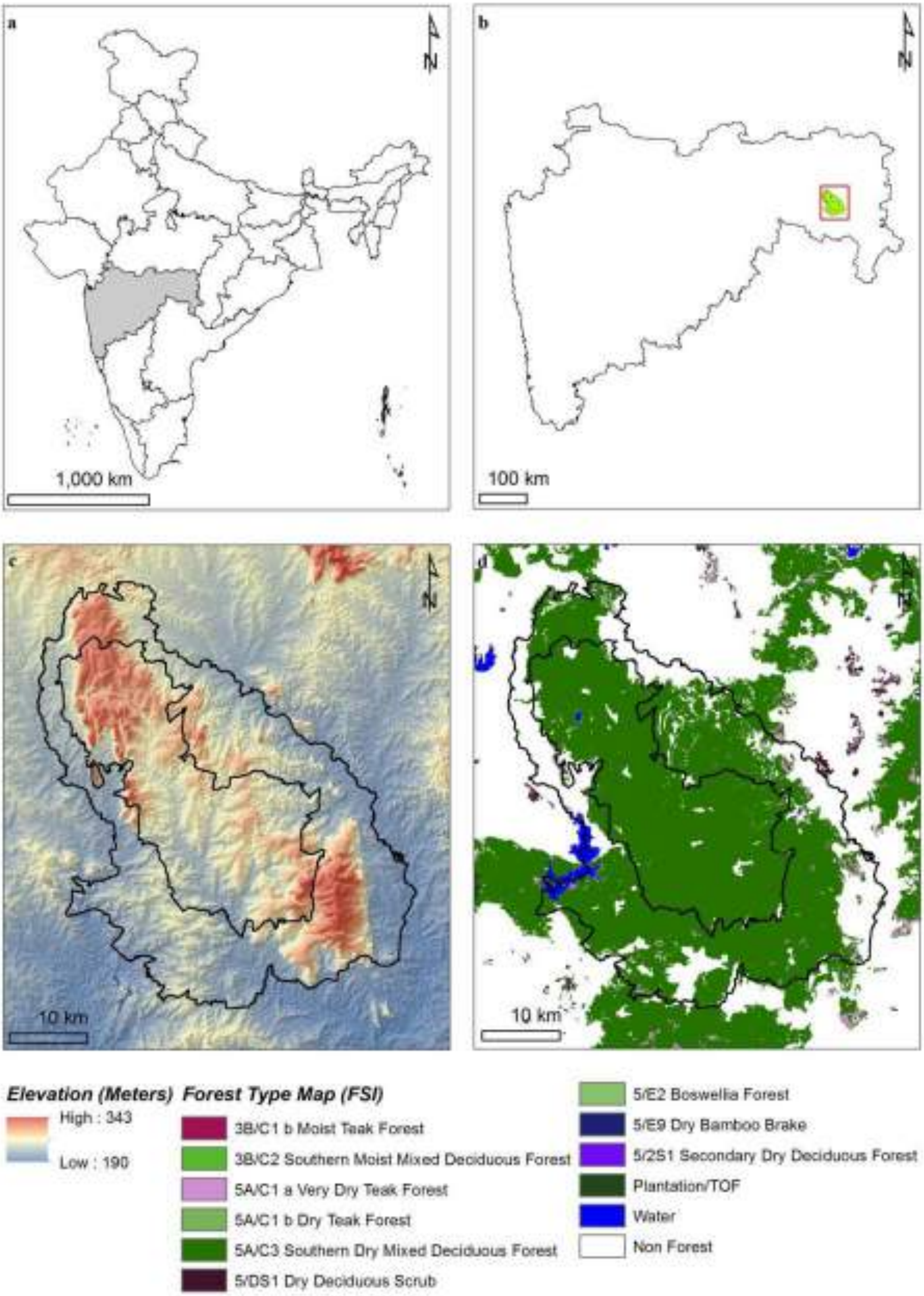


Figure 1: Maps 1 a) and b) showing the location of the study area in the state of Maharashtra, India. Maps 1 c) and d) depict the topography and vegetation of the study area respectively

CHAPTER II
THE CIRCUS OF CO-EXISTENCE

RESOURCE PARTITIONING BETWEEN TIGER, LEOPARD AND THE DHOLE

'Wonderful and admirable as most instincts are, yet they cannot be considered as absolutely perfect: there is a constant struggle going on throughout nature between the instinct of the one to escape its enemy and of the other to secure its prey'
Charles Darwin (I883)

2.1. Introduction:

Over the years, a constant evolutionary arms race between the prey and predator has shaped their adaptations or traits in a system (Matter & Mannan 2005; Eriksen et al. 2011). Exploitative as well as interference competition has been studied extensively on the basis of three axes- temporal, spatial and diet partitioning (Carothers & Jaksic 1984). On an evolutionary scale, traits such as activity patterns have been shaped for both prey as well as predators, however, these may be flexible to a certain extent depending on the site-specific environmental conditions (Monterroso et al. 2013). Activity time for an animal is a tradeoff between risk of starvation and predation risk (Lima 1988; Bednekoff 2007). Depending on the intensity of competition among predators and predator-prey interactions, activity peaks may be dynamic (Lima 1988) and site-specific conditions 'can override the endogenous regulation of an animals' circadian clock' (Monterroso et al. 2013). Furthermore, the presence of multiple predators in a system can influence behavioural decisions of both the prey as well as amongst predators themselves to optimize their activity times. Fundamentally, animals move in search of resources like food, mates or refuges which, to a great level, are interdependent. However, on an individual level, most activity of animals is dedicated to foraging or rather acquisition of food (Suselbeek et al*.* 2014). Thus it makes sense to study the activity patterns of prey and predators both spatially and temporally complimenting it with an understanding of their actual diet through scat analysis. Camera traps have been used widely to study population densities and spatial ecology of various animals but there have been only few comparative studies of activity patterns between the three large sympatric carnivores with respect to their prey in India (Ramesh et al. 2012).

"...from the least to the greatest in zoological progression, the stomach sways the world; the data supplied by food are chief among all the documents in life"
Fabre, The Glow Worm and Other Beetles (1913)

The dietary profiles of carnivores have been predominantly studied by examining the scats for undigested recognizable parts of prey like hair (Koppikar & Sabnis 1976; Putman 1984). Although scats may not be the true representation of the diet of a carnivore, it is nevertheless, a snapshot of the types of prey consumed. This method also has an advantage over other techniques such as gut content analysis (Smuts 1979), spoor tracking (Mills & Mills 1978) or direct observation of feeding (Schaller 1972; FitzGibbon & Fanshawe 1989) because of the relative ease of obtaining samples and the non-invasive nature of the sampling procedure (Andheria et al*.* 2007). Furthermore, complimenting the activity pattern data of predators and their prey with the dietary profiles would lead to a better understanding of the mechanism of co-existence.

2.2. Methods

Field and Laboratory methods

Temporal activity pattern and spatial segregation:

In order to study the temporal activity and the space use among three carnivores and their prey, camera trapping was carried out. Typically, camera traps record the date and time of a photograph which can be used to study these patterns of interest. Camera trap data were collected between January and April 2015 as a part of research on sympatric large carnivores – tiger, leopard and Dhole. Intensive camera trapping was done in TATR with camera traps deployed in 1.4 x 1.4 sq. km grids. Camera stations were placed along roads, trails or stream-beds to maximize photo-captures. Camera trapping was done for 40 days at the beginning of the summer season. The mean inter-trap distance between a two camera trap stations was 1 km. Each station comprised a pair of passive white flash cameras (Cuddeback Attack Model 1149 or the Moultrie Game Spy D55) to maximize capture probability. Camera traps were active throughout the day and night for the entire duration of trapping sessions.

Collection of scats for Dietary Analysis:

Scats were collected opportunistically as well as actively by searching for them along forest roads and animal trails in the study area. Identification and differentiation of tiger and leopard scats was based on associated tracks or sign and only those scats which could be identified correctly were analyzed further. The Dhole scats were easy to identify as they were deposited mainly at junctions or across the roads. Communal defecation sites (Johnsingh 1983) and the typical scent of these scats made it even easier to correctly identify the Dhole scats.

Analytical Methods

Temporal activity pattern:

In order to study the temporal pattern of the three predators and their prey, the temporal data was analyzed in the statistical software R (version 3.0.1) (R Development Core Team 2013 http://www.R-project.org) and Microsoft Excel 2013. I used the package 'overlap' which estimates the coefficient of temporal overlap non-parametrically using kernel density estimates, following the approach of Linkie and Rideout (2009). In the package 'overlap', data are regarded as a random sample from the underlying distribution that describes the probability of a photograph being taken within any particular interval of the day. The probability density function of this distribution is then referred as the activity pattern, which assumes that the animal is equally likely to be photographed at all times when it is active (Ridout & Linkie 2009). It is a two step process. In the first step, each activity pattern is estimated non-parametrically, using kernel density estimation (Fernandez-Duran 2004). The kernel density estimates used a bandwidth parameter, which is selected following the procedure developed by Taylor (2008). For the second step, a measure of overlap between the two estimated distributions was calculated. Ridout and Linkie (2009) reviewed several alternative measures of overlap between two probability distributions, favouring the coefficient of overlapping, Δ (Weitzman 1970), which ranges from 0 (no overlap, e.g. one species entirely diurnal, the other entirely nocturnal) to 1 (complete overlap). This is defined as the area under the curve that is formed by taking the minimum of the two density functions at each time point. A useful interpretation of the coefficient of overlapping is that for any time period during the day the proportion of activity that occurs during that period differs between the two distributions by $<1-\Delta$. 1000 bootstrap samples are used to derive the confidence intervals.

Program Oriana 4.0 (Kovach Computing Services, Wales, UK) was used to plot the mean activity of large carnivores and their prey on a 24 hour circular distribution scale. Oriana analyses orientations and other circular data. It calculates a variety of statistics necessary for working with data measured in degrees, time of day or other circular scales and graphs the data in a number of different ways. The data available from last year's camera trap sampling in the same area during the same season were compared to test if there was a significant difference in the temporal patterns. Per hour captures of the three carnivores were plotted in the form of a rose diagram. Hours with the greater number of captures showed higher activity peaks. Oriana calculates basic statistics such as the circular mean and median, various measures of circular dispersion such as mean vector length (r), concentration and circular variance and standard deviation, along with confidence intervals for the mean.

Space use:

To account for spatial overlap between large carnivores, a multiple response permutation procedure (MRPP) test was performed. MRPP is a nonparametric procedure for testing the hypothesis of no difference between two or more groups of entities. In this case, it would translate as null hypothesis is that there is no spatial segregation between two species. The weighted mean within group distance is calculated as the first step of the analysis.
The weighted mean within group distance (δ) is given by the following formula:

$$\boldsymbol{\delta = \sum_{i=1}^{g} C_1 \, x_1}$$

for g groups where C is a weight that depends on the number of items in a group.

The test statistic T is the difference between the observed and the expected deltas divided by the square root of variance in delta. It is calculated as

$$\mathbf{T=(\delta\text{-}m_{\delta})/s_{\delta}}$$

where m_{δ} and s_{δ} are the mean and standard deviation of δ under the null hypothesis.

The p value is useful for evaluating how likely it is that an observed difference is due to chance, but a description of the effect size is required which is independent of the sample size. This is provided by the chance corrected within-group agreement (A).

$$\text{A}= \mathbf{1} - \frac{\textbf{\textit{Observed}}\ \boldsymbol{\delta}}{\textbf{Expected}\ \boldsymbol{\delta}}$$

The agreement statistics A describes within group homogeneity, compared to the random expectation. When all items are identical within groups, then the observed δ = 0 and A=1, the highest possible value for A. If heterogeneity within groups equals expectation by chance, then A=0. Statistical significance may result even when the "effect size" (A) is small if the sample size is large. In such cases, the ecological significance of the result should be considered and not just the statistical significance. Data was analyzed using the software Blossom Statistical Package.

To test whether animals are avoiding each other, a simple species interaction factor was calculated in Microsoft Excel 2007. The following formula was used,

SIF= Probability of co-occurrence for Group A/ Probability of co-occurrence of Group B

The probability of 2 species occurring together at the same camera trap location was calculated from the number of camera traps where the species have occurred independently vs. together. This was then divided by the expected value of their co-occurrence. If the observed co-occurrence was more expected, the species were said to have no apparent avoidance towards each other ace and versa. The standard error estimator for proportion: **sqrt[p(1-p)/n]** and delta-variance method to combine SE's across the proportions was used.

The space use was graphically represented by generating weighted kernel density maps of camera trap captures at each location in GIS (Silverman 1986).

Diet analysis

All collected scat samples were dried and broken down and teased apart with forceps to collect the undigested contents in them. The prey remains included hair, claws and plant material. All the prey remains apart from hair were identified macroscopically. The hair samples were microscopically examined to identify the species based on the medullary pattern of the hair by comparing them with the reference collection of hair at the Wildlife Institute of India following a standard protocol (Mukherjee et al. 1994). In all 185 Dhole scats, 54 tiger scats and 11 leopard scats collected during field work were analyzed.

Table 1: Prey density of various prey species from Tadoba Andhari Tiger Reserve (TATR), Maharashtra, India (Habib et al., 2014)

Species	Individual density ± SE
Chital	5.10 ± 1.22
Sambar	4.68 ± 0.76
Nilgai	1.09 ± 0.36
Wild pig	5.42 ± 2.08
Gaur	2.03 ± 0.56
Barking deer	0.96 ± 0.23
Hare	1.70 ± 0.36

Prey biomass and number:

In order to estimate prey biomass and number, the percentage frequency of occurrence of all the major prey species was calculated. I used the density of prey estimated during the 2014 sampling session (Habib et al. 2014) (ref. Table 1) as the sampling was done in the same season The frequency of occurrence is biased towards smaller sized prey, since relatively more scats are produced for smaller prey than larger prey. To correct for this bias, relative frequencies of prey were converted to relative biomass consumed for tigers and leopards using an equation estimated for cheetahs (Wachter 2012), and for Dholes using an equation estimated for wolves (Jethwa & Jhala 2003). These regression equations estimate the number of field collectable scats for a given weight of prey biomass. The equations are given below:

$y = 0.38 + 0.020x$ (for Dhole) and
$y = 2.358(1\text{-}\exp(-0.075x)$ (for tigers and leopards) where,

the independent variable x is the average weight of the prey and the dependent variable y is the number of field collectable scats for that weight of prey. The dependent variable can then be converted into the relative biomass of prey consumed by multiplying it by the relative frequency of each prey species found in the scats. The relative number of each species consumed is obtained by dividing relative biomass by the average weight of the prey species. The weight of various prey species killed by tiger, leopard and Dhole was assumed to be similar to that used in previous research (Karanth & Sunquist 1995).

Dietary overlap:

The extent of dietary overlap between all three species was calculated by Pianka's Index (Pianka 1973). The Pianka index is a single numeric value on a 0 to 1 scale that summarizes the average pair wise niche overlap in an assemblage. Software EcoSim (Gotelli & Entsminger 2001) was used for null model analysis. These null model tests have wide applicability in both applied and basic ecology.

For species 1 with i = 1 to n resource categories, the proportional resource utilization p of resource state i by species 1 is defined such that:

$$\sum_{i=1}^{n} p\,i = 1.0$$

Niche overlap indices are always calculated by first dividing each entry in the utilization matrix by the corresponding row total, so that all entries are proportional utilization values (p) for each species. The Pianka niche overlap index O for the pair of species (1, 2) is calculated as

$$O_{12} = O_{12} = \frac{\sum_{i=1}^{x} p_{2i}\ p_{1i}}{\sqrt{\sum_{i=1}^{x}(p_{2i}{}^{2})(p_{1i}{}^{2})}}$$

EcoSim allows the user to incorporate additional data on the availability of resources. In nature, resources are not equally abundant (or usable) by all species. If this assumption is not true, the analysis will tend to over-estimate niche overlap because species will tend to use common resource states even if there is niche segregation. Assuming the resources are equally available would lead to a less robust inference if there are very common/ very rare resources. Hence a user-defined resource state was used which incorporated the density of prey as well.

Prey selection:

A prey is said to be 'selected' if it is consumed at frequencies more than is expected by chance. These expected frequencies are estimated from the densities of the prey species. I used the density of prey estimated during the 2014 sampling session (Habib et al. 2014) (ref. Table 1) as the sampling was done in the same season. Ivelev's selectivity index was used to estimate 'selectivity' of prey species by a predator (Ivelev 1961; Acharya et al. 2007; Majumder 2011).

A two-way ANOVA was performed to investigate if there is a difference between the occurrence of species of prey in the diet of three predators and the proportions of the species being harvested by the three carnivores. The two-way analysis of variance (ANOVA) examines the influence of two different categorical independent variables on one continuous dependent variable. It not only aims at assessing the main effect of each independent variable but also if there is any interaction between them.

2.3. Results

Activity Pattern:

An effort of 3420 trap nights resulted in 360 photographs of tiger, 113 photographs of leopard and 34 photographs of Dhole were obtained. Tiger showed bimodal peak activity; a smoother early morning peak and a steeper one at dusk, thus tending towards a typical crepuscular activity pattern. The Dhole showed a similar bimodal peak, however, it was smoother at dusk than at dawn which is exactly opposite to the tiger. The leopard was seen to be active throughout the day except for the hottest hours from noon till early evening. 55% of tiger captures were between 1800 hrs to 0600 hrs with peaks at dawn and dusk. The leopard was strongly nocturnal (72% captures between 1800 hrs to 0600 hrs) whereas the Dhole tending towards a crepuscular pattern of activity (41% captures between 1800 hrs to 0600 hrs). Amongst the prey species, sambar also had peaks at dawn and dusk with 66% captures from 1800 hrs to 0600 hrs similar to the temporal activity pattern of the tiger. Chital and wild pig showed 28% and 31% captures between 1800 hrs to 0600 hrs whereas the barking deer was fairly diurnal (39% captures between 1800 hrs and 0600 hrs) and the hare was strongly diurnal (99% captures between 1800 hrs and 0600 hrs) similar to the activity pattern of the leopard. (ref. Fig. 2 and 3)

The circular distribution of temporal pattern was plotted in Oriana to compare data of this season with the last season's data (Habib et al. 2014). A significant shift was seen in the temporal pattern of the tiger from a highly nocturnal activity peak to a more crepuscular pattern. This could probably be due to the coinciding activity peaks of the sambar which is a major prey species for the tiger. The Dhole did not show much difference in the temporal activity. The leopard did show a shift in the activity peak from dusk in 2014 to dawn in 2015 and seems to be avoiding the activity peak of both the tiger and Dhole (Fig. 4).

From the kernel density estimators, the sambar and gaur were observed to have a high degree (>0.8) of overlap with the tiger as indicated by the estimated overlap coefficients in Table 2. The Dhole showed a high coefficient of overlap with the wild pig and barking deer [0.78 (0.66-0.87) and 0.70 (0.49-0.82) respectively]. The leopard and the tiger had a high coefficient of overlap 0.80 (0.73-0.88) (ref Fig. 5a to e).

a)

b)

c)

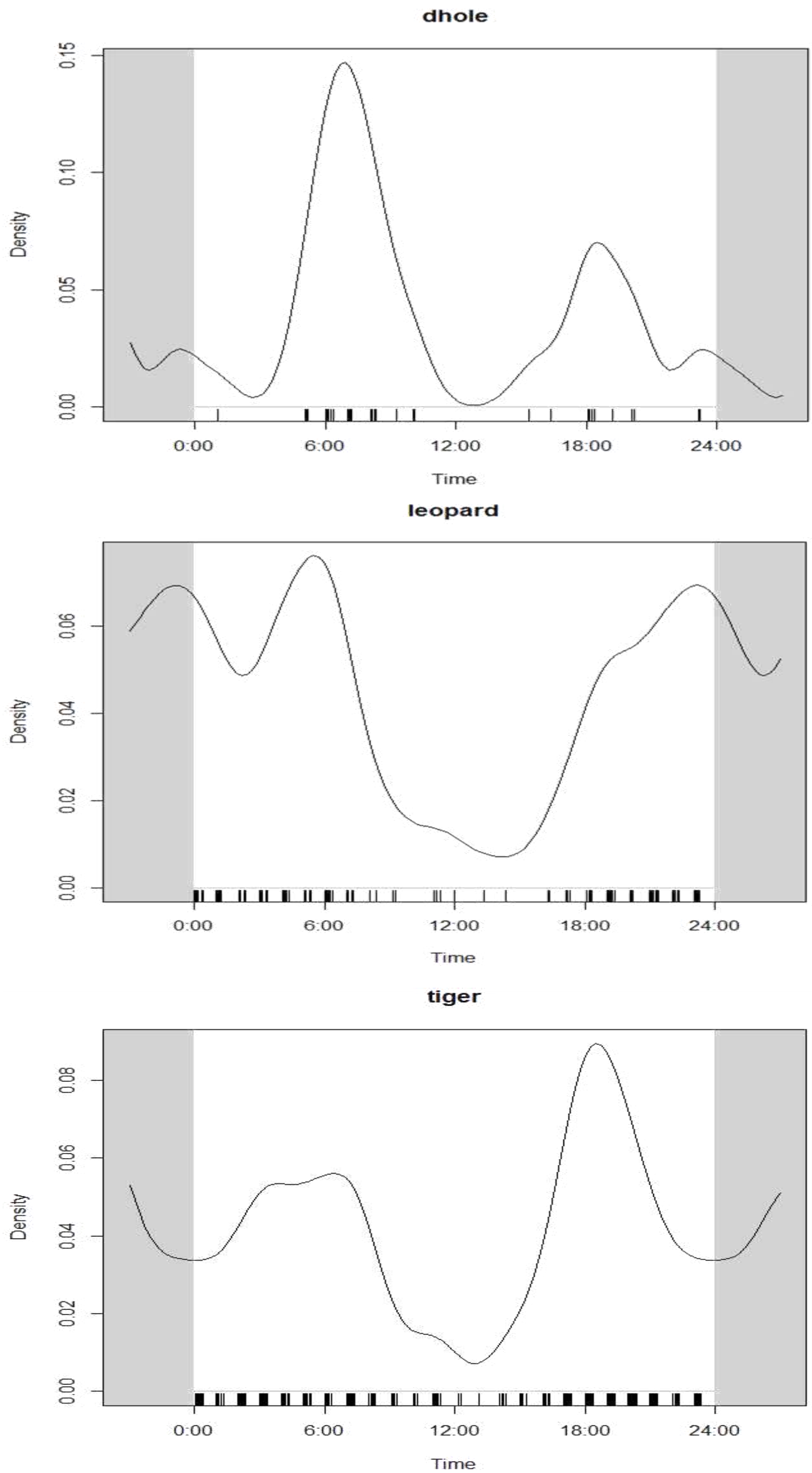


Figure 2: Kernel density estimates of daily temporal activity patterns of (a) Dhole, (b) tiger and (c) leopard - sympatric carnivores in TATR

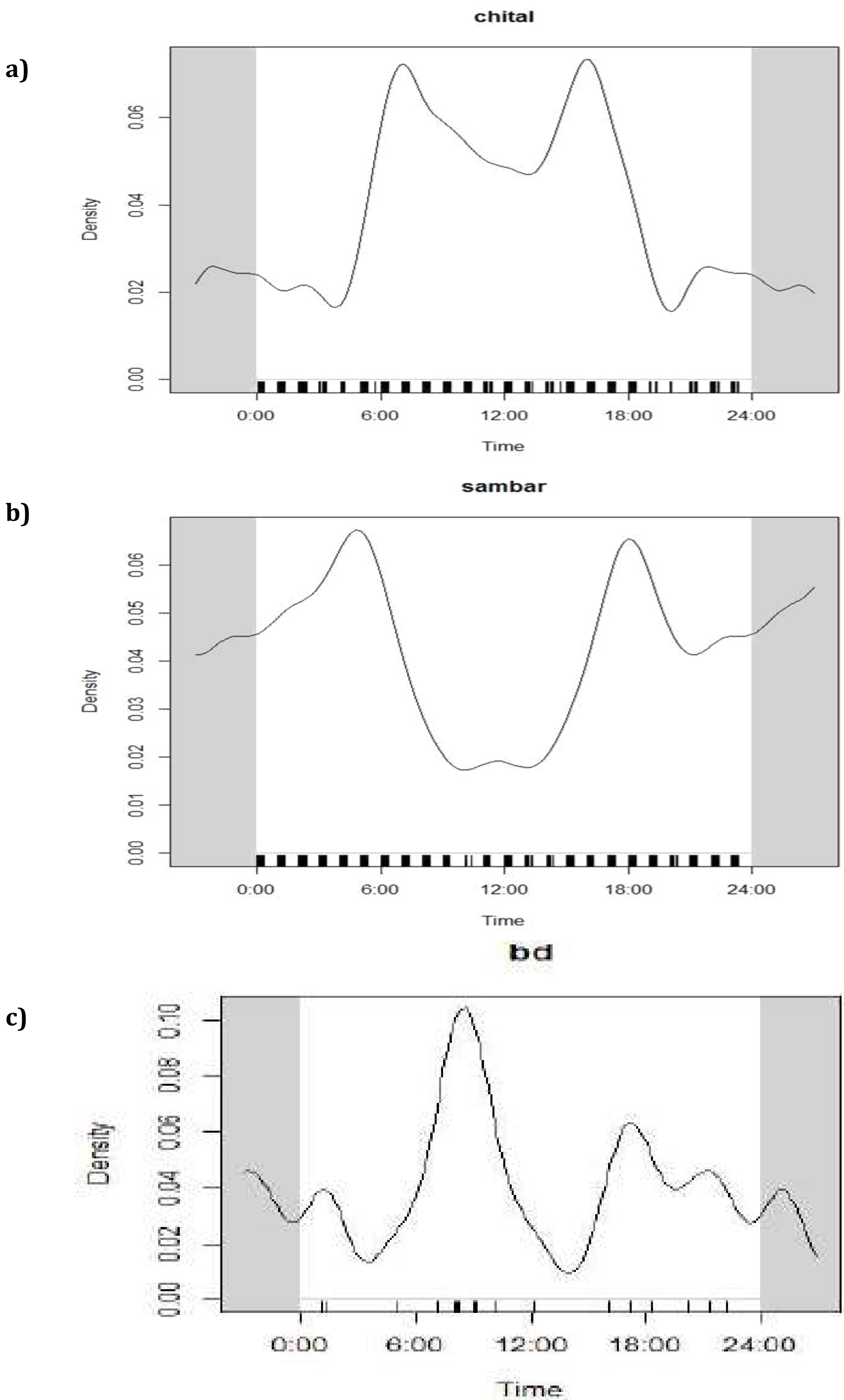


Figure 3: Kernel density estimates of daily temporal activity patterns of major prey species namely, (a) chital, (b) sambar and (c) barking deer in TATR

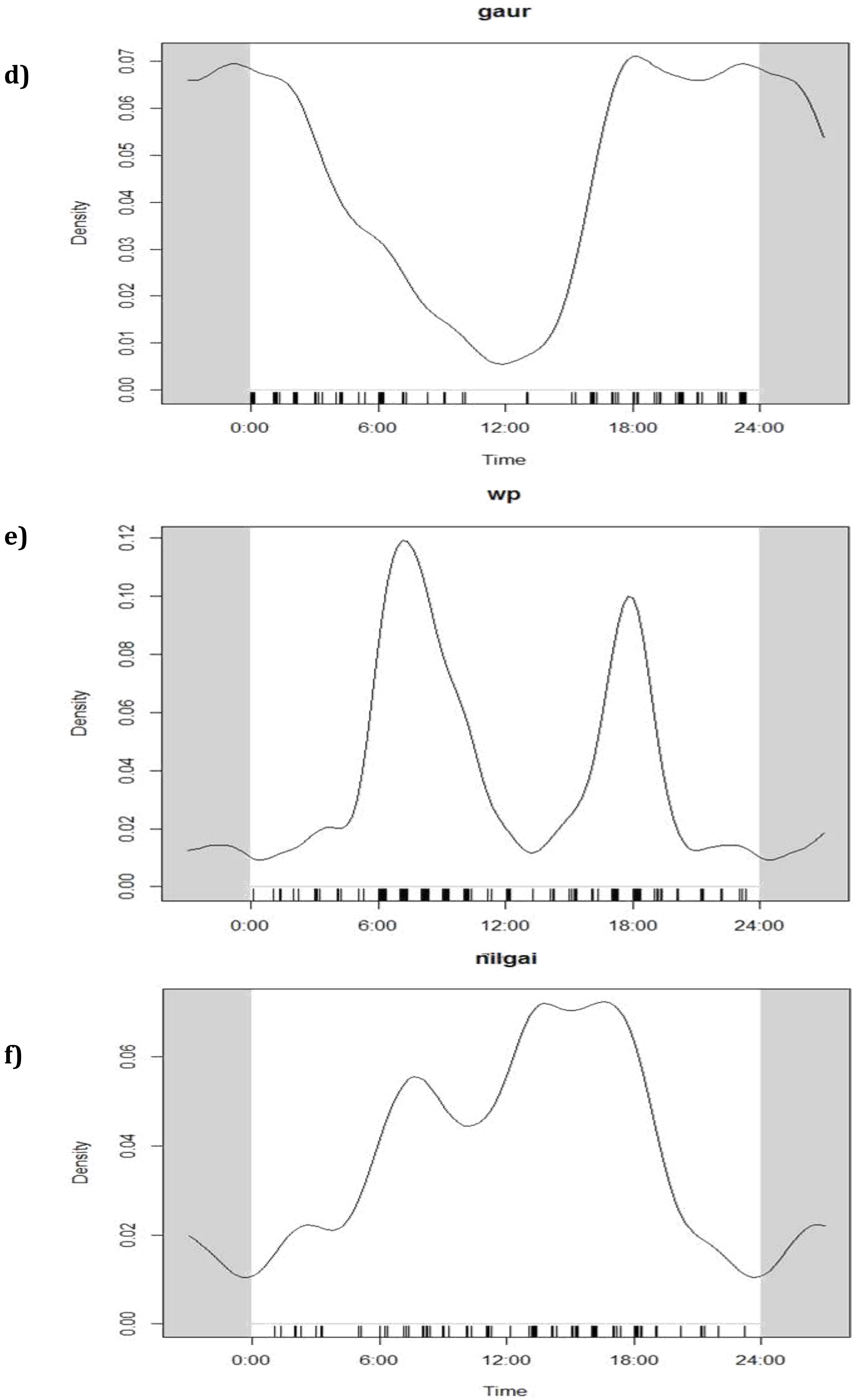


Figure 3: Kernel density estimates of daily temporal activity patterns of major prey species namely, (d) gaur, (e) wild pig and (f) nilgai in TATR

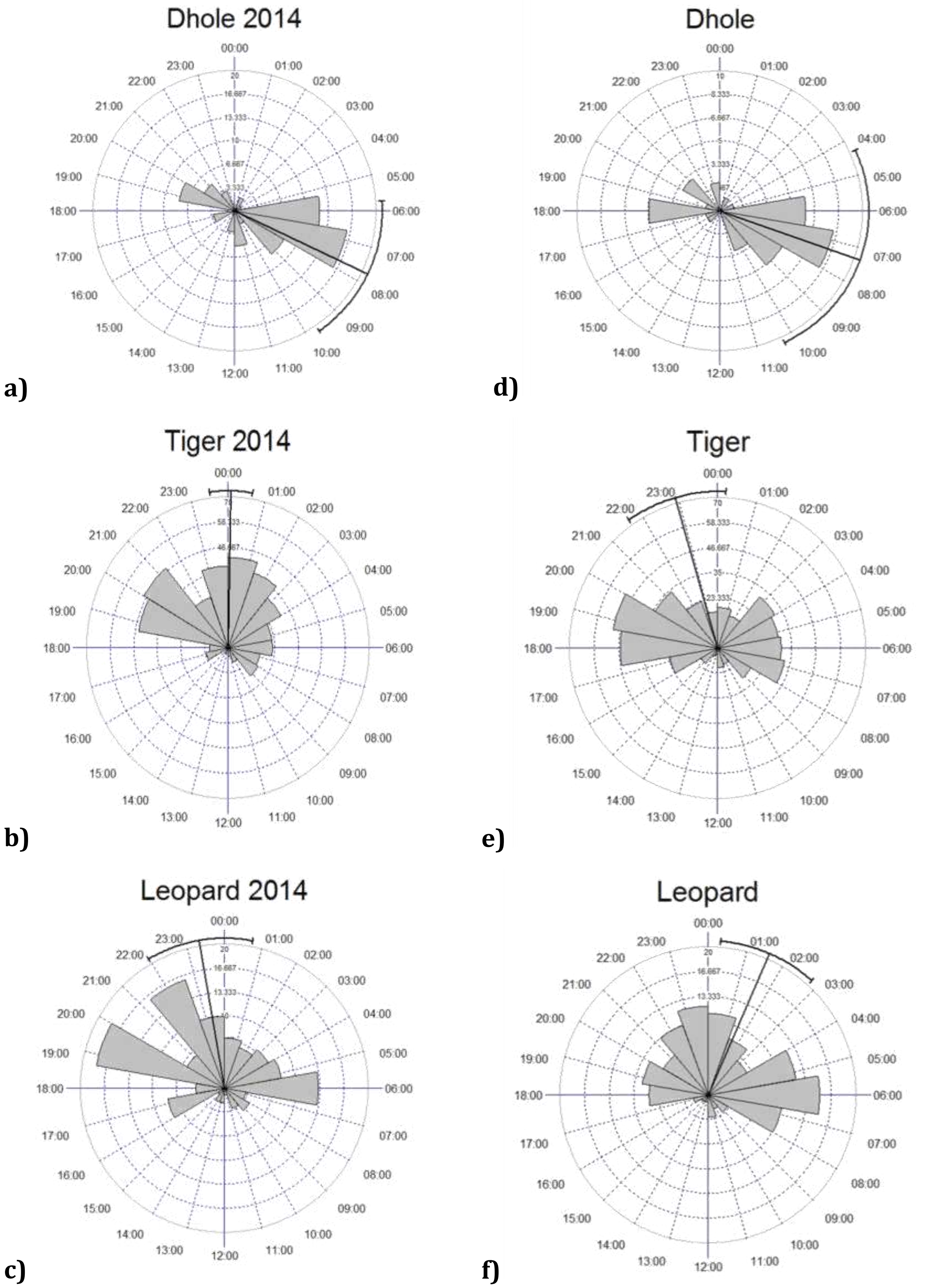
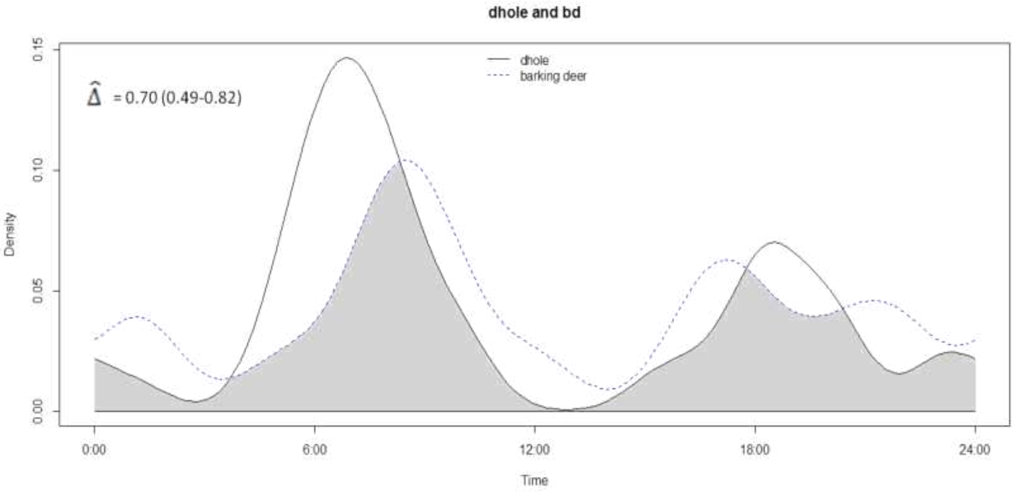


Figure 4: The temporal activity pattern of (a) Dhole, (b) tiger and (c) leopard respectively as observed in 2014 in TATR (Habib et al. 2014) and the temporal activity pattern of (e) the Dhole, (f) tiger and (g) leopard respectively as observed in 2015 in TATR

Table 2: Kernel density overlap co-efficient of the three predators with the prey species in TATR, India

Prey Species	Kernel density estimates of co- efficient of temporal overlap		
	Tiger	**Leopard**	**Dhole**
Sambar	0.87 (0.83-0.92)	0.84 (0.78-0.91)	0.62 (0.51-0.78)
Chital	0.64 (0.61-0.71)	0.56 (0.52-0.66)	0.63 (0.54-0.77)
Gaur	0.82 (0.75-0.88)	0.81 (0.71-0.89)	0.54 (0.40-0.70)
Wild Pig	0.66 (0.62-0.74)	0.53 (0.49-0.66)	0.78 (0.66-0.87)
Chausinga	0.44 (0.38-0.59)	0.41 (0.35-0.57)	0.62 (0.47-0.75)
Barking Deer	0.72 (0.51-0.85)	0.64 (0.51-0.67)	0.70 (0.49-0.82)
Nilgai	0.63 (0.57-0.74)	0.52 (0.47-0.66)	0.59 (0.48-0.74)
Porcupine	0.60 (0.56-0.69)	0.68 (0.62-0.78)	0.37 (0.29-0.56)
Hare	0.64 (0.60-0.75)	0.78 (0.70-0.87)	0.43 (0.35-0.61)
Tiger	-	0.80 (0.73-0.88)	0.66 (0.54-0.81)
Leopard	0.80 (0.73-0.88)	-	0.61 (0.49-0.77)
Dhole	0.66 (0.54-0.81)	0.61 (0.49-0.77)	-

i)



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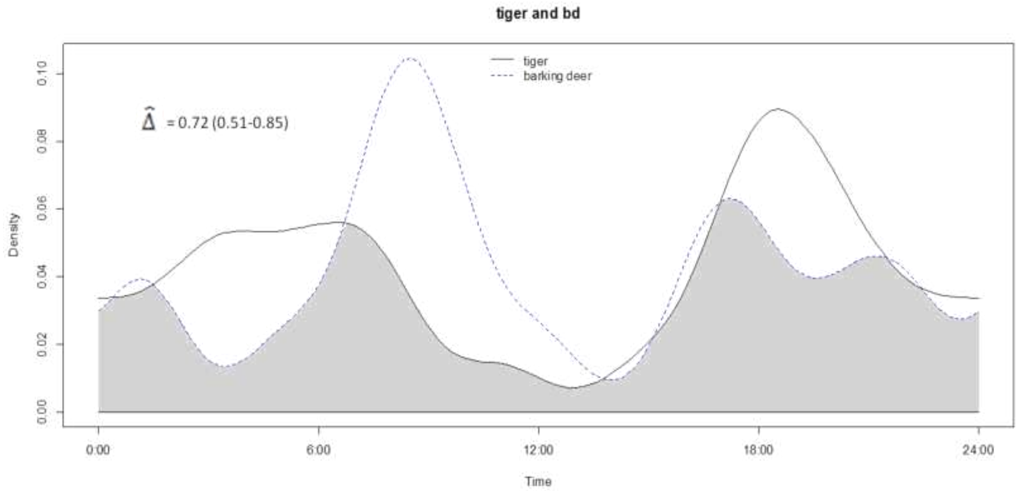

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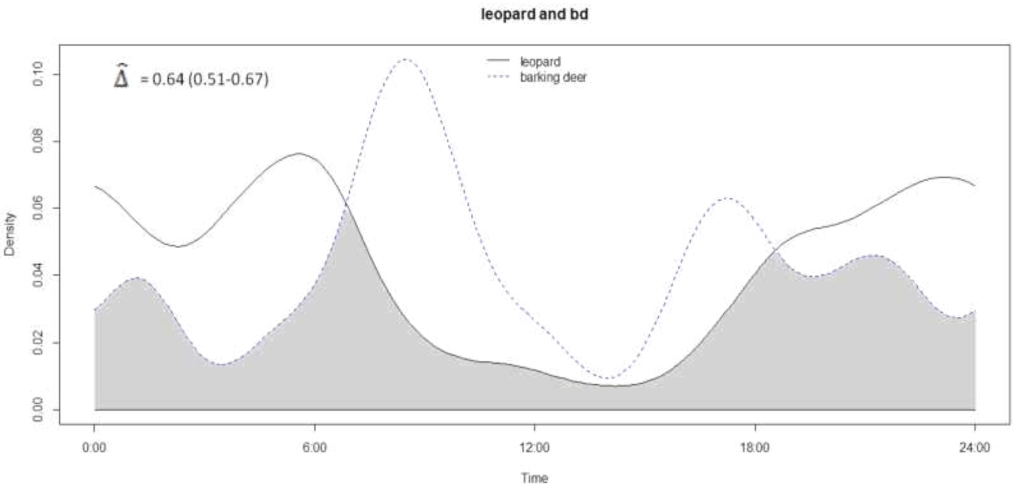


Figure 5a: Daily temporal activity patterns of (i) the Dhole, (ii) leopard, (iii) tiger vs. barking deer respectively in TATR, India. The lines represent the kernel density estimates based on individual photograph times. The overlap is shown by the shaded area in each plot. The coefficient of overlap is given with 95% bootstrap confidence interval in parentheses

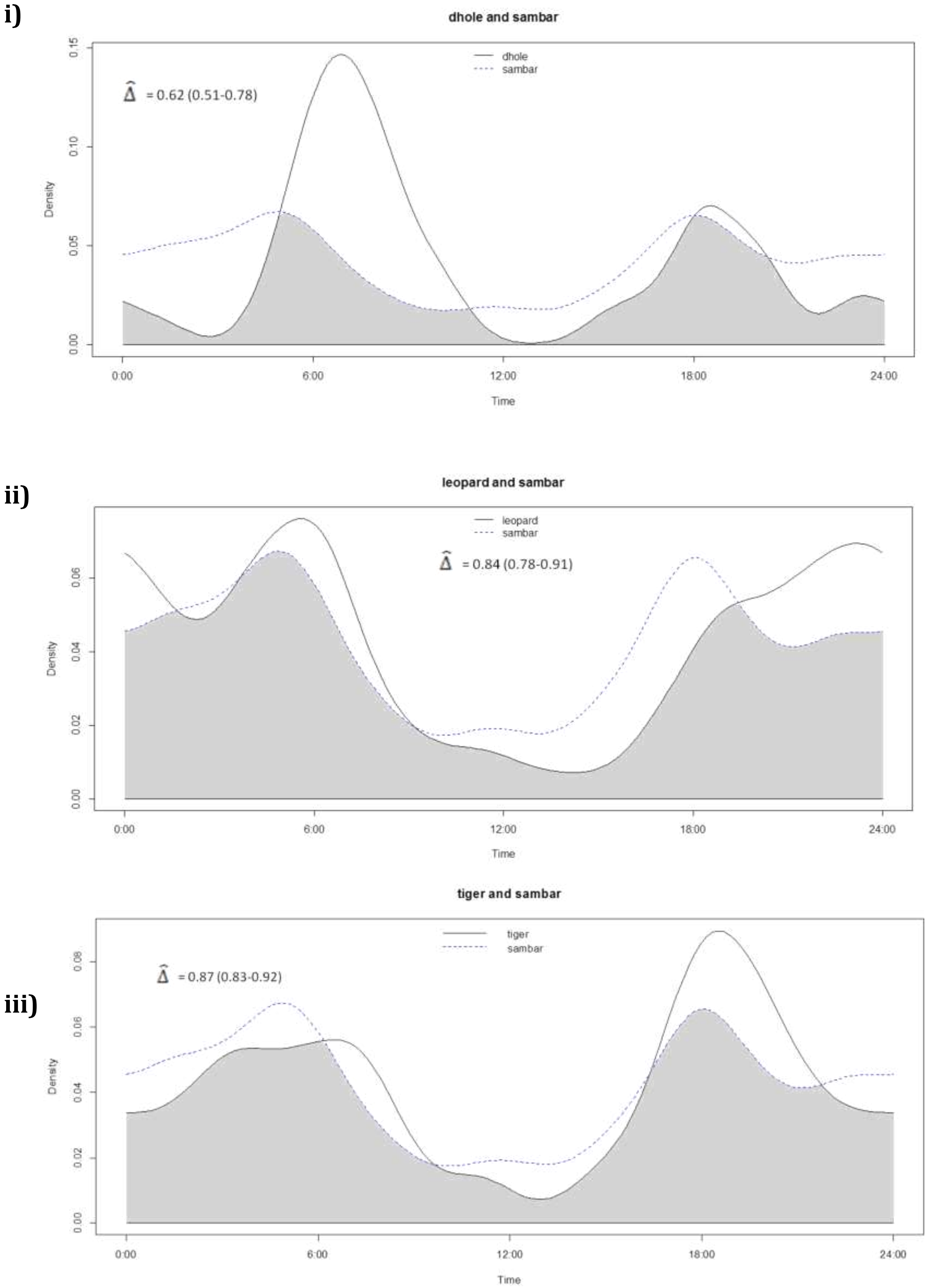


Figure 5b: Daily temporal activity patterns of the (i) Dhole, (ii) leopard, (iii) tiger vs. sambar respectively in TATR, India. The lines represent the kernel density estimates based on individual photograph times. The overlap is shown by the shaded area in each plot. The coefficient of overlap is given with 95% bootstrap confidence interval in parentheses

i)

ii)

iii)

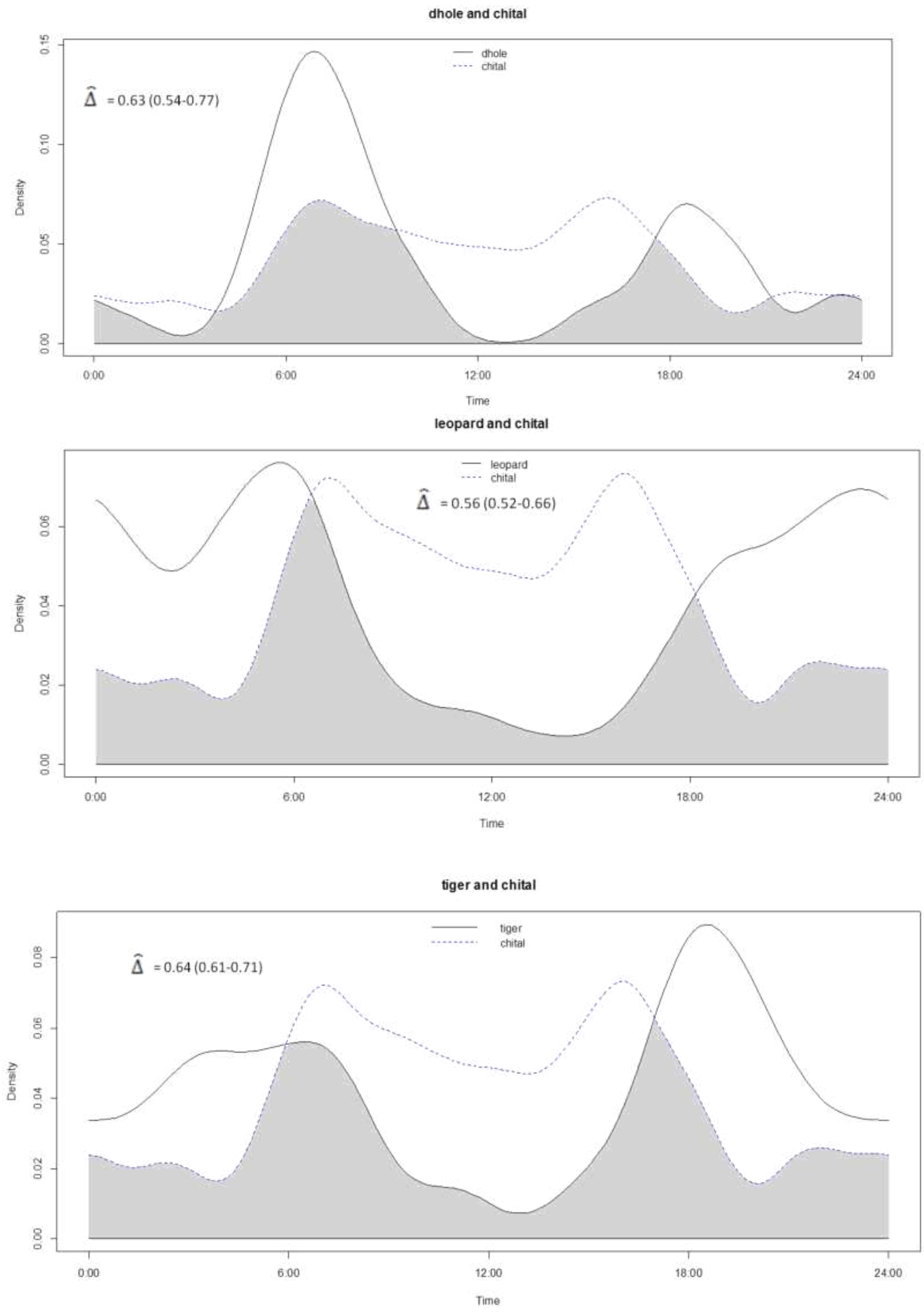


Figure 5c: Daily temporal activity patterns of (i) the Dhole, (ii) leopard, (iii) tiger vs. chital respectively in TATR, India. The lines represent the kernel density estimates based on individual photograph times. The overlap is shown by the shaded area in each plot. The coefficient of overlap is given with 95% bootstrap confidence interval in parentheses

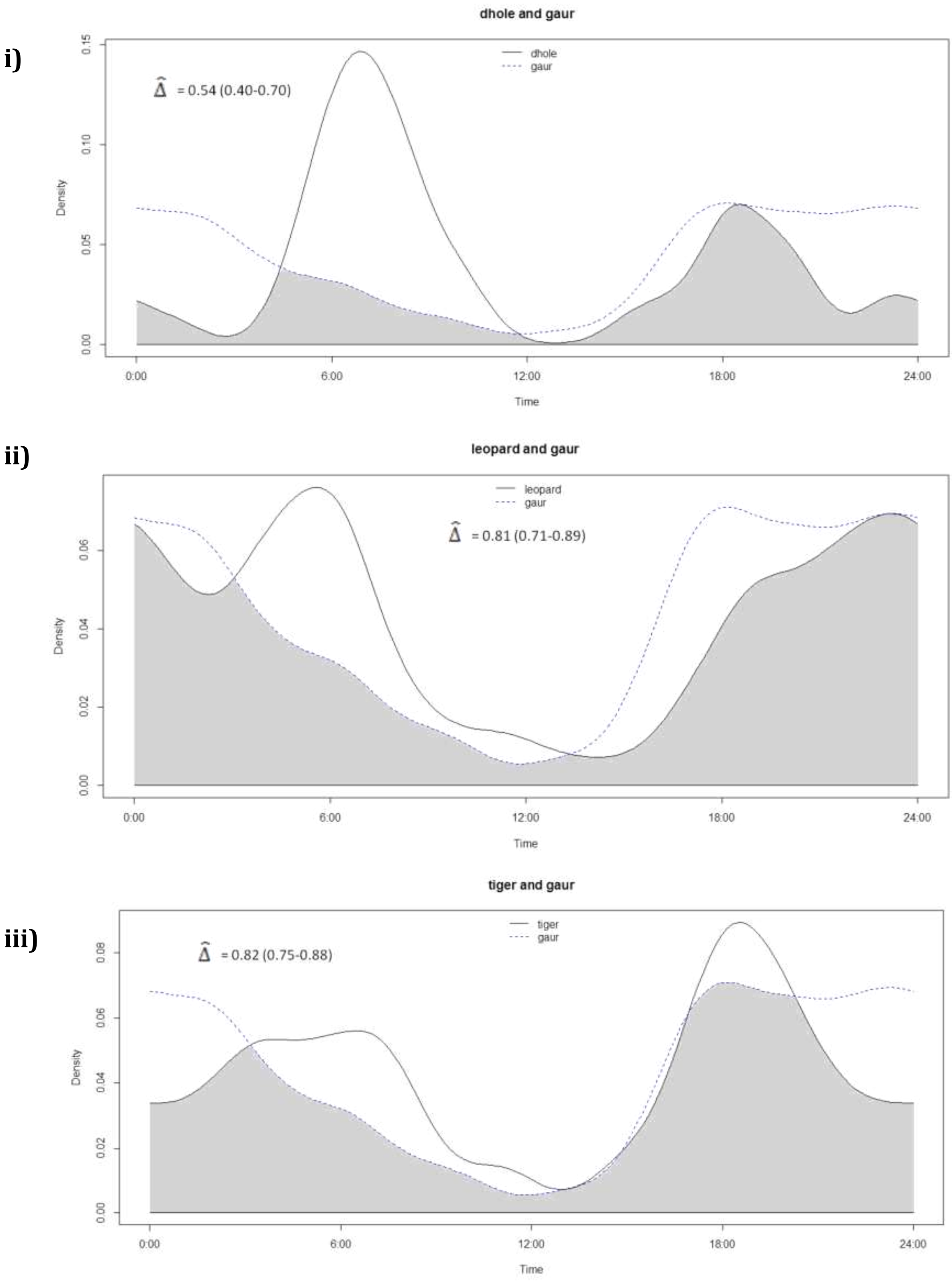
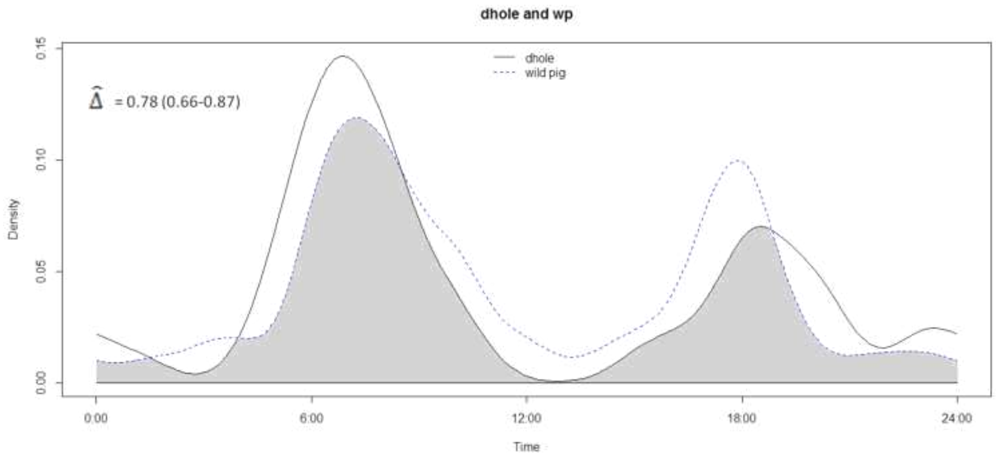


Figure 5d: Daily temporal activity patterns of (i) the Dhole, (ii) leopard, (iii) tiger vs. gaur respectively in TATR, India. The lines represent the kernel density estimates based on individual photograph times. The overlap is shown by the shaded area in each plot. The coefficient of overlap is given with 95% bootstrap confidence interval in parentheses

i)



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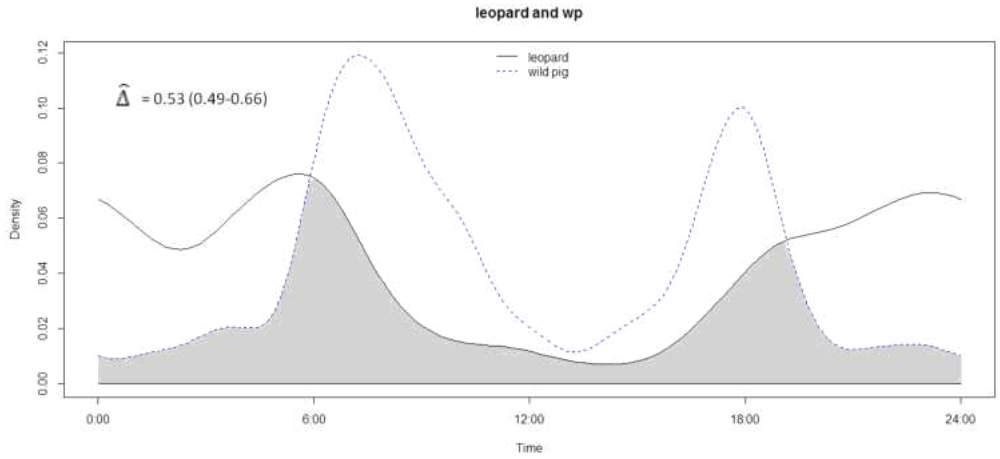

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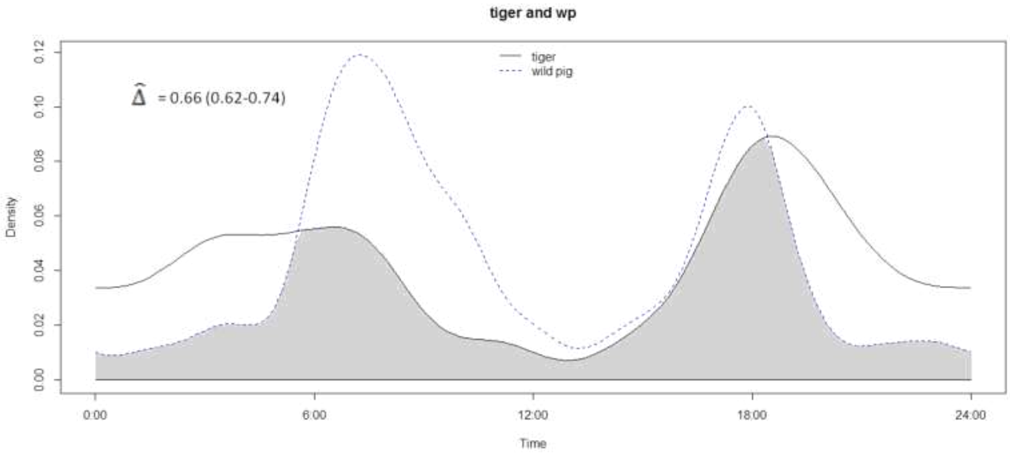

Figure 5e: Daily temporal activity patterns of (i) the Dhole, (ii) leopard, (iii) tiger vs. wild pig respectively in TATR, India. The lines represent the kernel density estimates based on individual photograph times. The overlap is shown by the shaded area in each plot. The coefficient of overlap is given with 95% bootstrap confidence interval in parentheses.

Spatial Activity Pattern

Comparisons between tigers and Dholes show that we cannot reject the null hypothesis (T=-0.46, *p*=0.22, A=0) (ref. Table 3.1 and 3.2) that there is no difference between the groups being compared. Therefore, a significant p value for the interaction between tiger and Dholes suggests that there is no difference in the space use. In contrast to this, the null hypothesis is rejected in the case of leopard and tiger (T=-9.11, p=8.27E-05, A=0.01) (ref. Table 3.2). In the case of comparison between Dhole and leopard as well, the null hypothesis is rejected (T=-3.50, p=0.01, A=0.02) (ref. Table 3.2). However, the A values or the effect size is very low for all the groups. This signifies that there is a co-occurrence of all the three predators and we cannot infer much from the above test as it involves only the presence absence data and not the weight of a point. To understand the spatial pattern better, kernel density maps were generated. Based on the kernel density estimate of the number of species specific photographs at each camera trap location, the three sympatric carnivores show different hotspots of spatial activity (Figure 6). In light of the kernel density maps, the results obtained from the MRPP test need to be interpreted with caution.

To further test whether there is a spatial segregation of particular areas by a predator due to the other, a simple species interaction factor was calculated which is basically the probability of capturing a particular species at a location w.r.t. the probability of capturing another species at the same location (ref. Table 4). This clearly signifies that the leopard and the Dhole are avoiding each other but there is less intense pattern seen between the leopard and the tiger; whereas there seems to be a very weak spatial segregation between the tiger and the dhole.

Table 3.1: Average within-group distance calculated from Euclidean distance matrix. The average within-group distance is used as the test statistic

Species	Average within group distance
Tiger	1.48
Leopard	1.71
Dhole	1.19
Average	1.46

Table 3.2: Summary statistics for MRPP: Results are given comparing across all groups as well as multiple pair wise comparisons

	δ under null hypothesis				T	P	A
	Observed	**Expected**	**Variance**	**Skewness**			
Tiger-Leopard-Dhole	1.52	1.54	8.86E-06	-1.61	7.15	0.0001	0.02

	δ under null hypothesis				T	P	A
	Observed	**Expected**	**Variance**	**Skewness**			
Tiger-Leopard	1.52	1.54	5.09E-06	-2.31	-9.11	8.27E-05	0.01
Tiger-Dhole	1.54	1.54	7.25E-06	-2.2	-0.46	0.22	0
Dhole-Leopard	1.50	1.53	5.42E-05	-2.21	-3.50	0.12	0.02

Table 4: Species Interaction Factor (SIF) calculated as the ratio of observed to expected probabilities of occurrence of Species 1 (X1) and Species 2 (X2) occurring together

	No. of captures	p(X1)	P(X2)	p(X1X2)) Expected	(X1X2) Observed	SIF	SE
Tiger	113	0.95	0.46	0.44	0.41	0.94	±0.14
Leopard	55						
Tiger-Leopard	49						
Leopard	55	0.46	0.17	0.08	0.04	0.54	±0.27
Dhole	20						
Leopard-Dhole	5						
Tiger	113	0.95	0.17	0.16	0.17	1.05	±0.30
Dhole	20						
Tiger-Dhole	20						

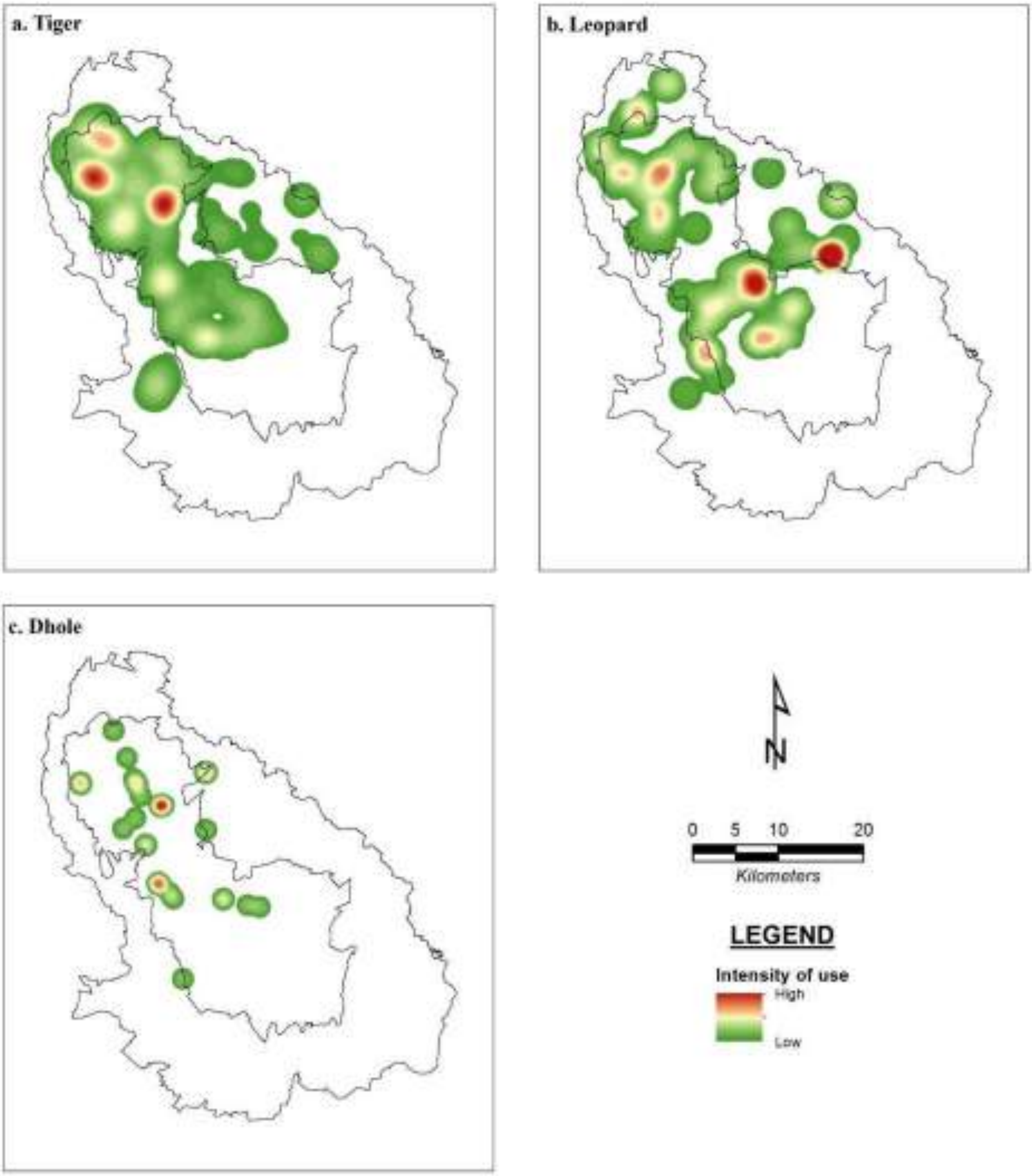

Figure 6: Kernel density maps showing intensity of use of the three predators a) tiger, b) leopard and c) Dhole

Diet analysis

Relative occurrence and biomass consumed:

A total of 54 tiger scats, 11 leopard scats and 185 Dhole scats were collected during the field work that could be analyzed. Avoidance of trails regularly utilized by the tiger and the Dholes by the leopards could be one reason of low detection of leopard scats. The major prey species found in the tiger scats were sambar (42.10%), chital (15.78%) and gaur (8.77%). The major prey species found in the scats of Dhole were sambar (42.66), chital (28.0) and barking deer (10.66). Since the sample size for leopards was low (n=11), strong inferences could not be drawn for the leopard diet. 7.14% of the tiger scats contained double prey items whereas 45% of the leopard scats contained double prey items. 21.62% scats of Dholes contained double prey items and 0.54% contained 3 prey items. The high occurrence of double prey items in the leopard diet is because the leopard was seen to prey on smaller species like rodents and hare. About 5.4% of tiger scats and 27.02% of Dhole scats contained varying amounts of bamboo leaves. The frequency of occurrence, relative biomass and estimates of relative number of individuals of prey consumed by the three sympatric carnivores based on the analyses are presented in Table 6.

Two-way Analysis of Variance (ANOVA) with predator and prey items showed that there was no significant difference (F= 0.03; df= 2; p=0.9717) in the occurrence of the major prey species in the diet of the three large carnivores at TATR. However, the magnitude at which they were harvested showed a significant variation (F= 3.24; df = 7; p=0.03) (ref. Table 5).

Table 5: Analysis of variance of diet between and amongst predators and prey in TATR, India

Source of Variation	*SS*	*df*	*MS*	*F*	*p-value*
Predators	5.270973	2	2.635486	0.028731	0.97173491
Prey	2082.214	7	297.4592	3.242783	0.029034095
Error	1284.214	14	91.72959		
Total	3371.7	23			

Table 6: Frequency of occurrence (A), relative biomass consumed (D) and relative number of prey individuals consumed (E) by tiger, Dhole and leopard, based on 54, 185 and 11 scats respectively

Predator	Prey	X kg	A %	Y	D%	E%
Tiger	Chital	55	15.78	36.61	16.52	19.36
	Sambar	212	42.10	99.27	44.80	13.62
	Barking Deer	20	0.00	0.00	0.00	0.00
	Hare	3	0.00	0.00	0.00	0.00
	Gaur	287	8.77	20.68	9.33	2.10
	Nilgai	212	3.50	8.25	3.72	1.13
	Langur	8	1.75	1.86	0.84	6.77
	Wild pig	38	22.80	50.65	22.86	38.77
Dhole	Chital	55	28.00	34.10	30.18	6.39
	Sambar	70	42.66	63.61	56.29	9.36
	Barking Deer	20	10.66	6.19	5.48	3.19
	Hare	3	1.33	0.36	0.32	1.24
	Gaur	75	0.88	1.39	1.23	0.19
	Nilgai	70	1.33	1.98	1.76	0.29
	Langur	8	1.33	0.48	0.43	0.62
	Wild Pig	31	0.00	0.00	0.00	0.00
Leopard	Chital	48	12.50	28.67	16.63	7.42
	Sambar	62	12.50	29.19	16.94	5.85
	Barking Deer	20	6.25	11.45	6.64	7.11
	Hare	3	6.25	2.97	1.72	12.30
	Gaur	85	12.50	29.42	17.07	4.30
	Nilgai	62	12.50	29.19	16.94	5.85
	Langur	8	12.50	13.30	7.71	20.66
	Wild Pig	37	12.50	27.64	16.03	9.28

Prey selection:

Prey selectivity was estimated by comparing the available densities of prey to the actual biomass consumed. The results indicate that the Dhole killed sambar (0.90) and chital (0.75) more than available, hence strongly preferred and hardly consumed the wild pig (-1). The tiger consumed wild pig (0.45) and chital (0.17) more than expected by sheer chance and were thus, preferred over other prey. Sambar which is considered to be the primary diet of the tiger (Johnsingh & Negi 2003) was not harvested more than its availability, however it was the principal prey of the tiger. The leopard seems to prefer, barking deer (0.6) and langur (0.49) (ref. Fig.7).

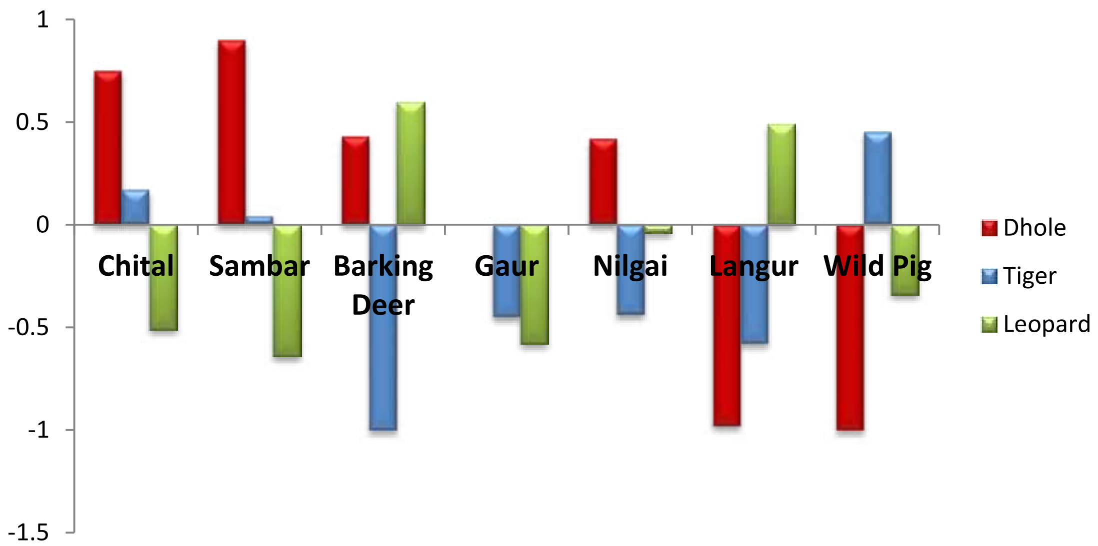

Figure 7: Ivelev's index of prey preference by tiger, leopard and Dhole in TATR, India

Observed kills:

Kills made by the three carnivores were recorded opportunistically. For identifying the predators, direct and indirect signs (pugmarks, tracks, known refuge areas of the collared tigers) were used. Sex and age class was recorded for each kill. The sample size was too low to make a strong inference due to the short duration of my study; nonetheless, the presented data may give some idea of the prey being consumed and be useful for interpreting the other data on diet analysis (ref. Fig.8).

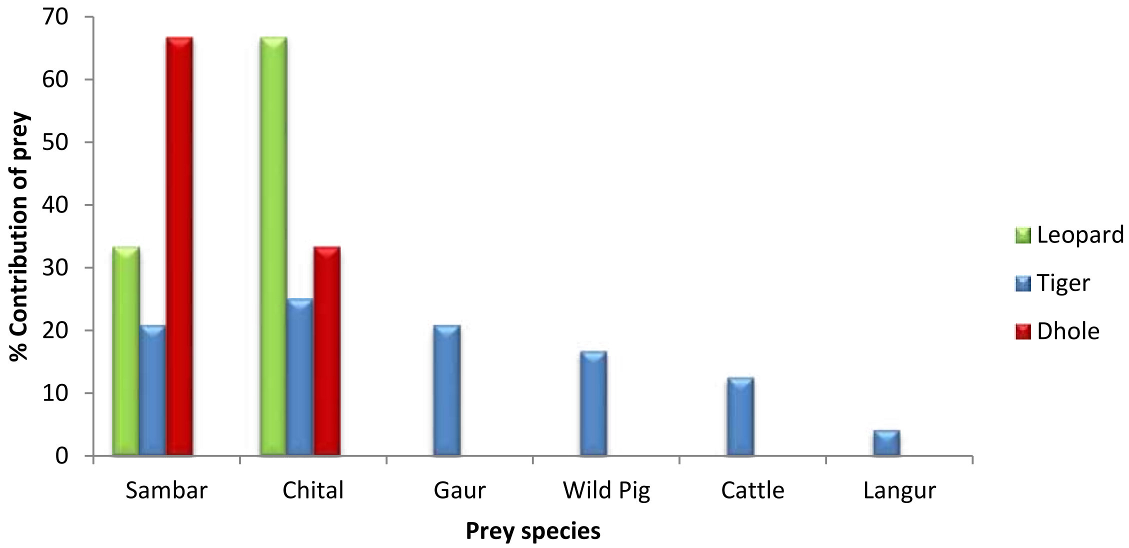

Figure 8: Percent contribution of prey taken by tiger, leopard and Dhole based on field observations in TATR, India

Diet overlap:

A variety of diet overlap indices are used in field measurements of ecological niche separation (Pianka 1973). Pianka's index was used for measuring diet overlap between predators. This index ranges in value from 0 (indicating no overlap between two predator species) to 1.0 (complete overlap). The overlap indices for the three predators were 0.61 between tiger and leopard, 0.80 between tiger and Dhole and 0.46 between leopard and Dhole. This suggests that the diet of tiger and dhole, in terms of the prey species shows a strong similarity in the diet. Leopard and tiger show a less similarity whereas the leopard and the Dhole show dissimilarity in the dietary niche.

2.4. Discussion

Prey animals optimize the balance between food acquisition and predator avoidance by concentrating their foraging activity at times of relatively low predation risk to a certain level (Whitham & Mathis 2000). In a system where more than a single predator operates, co-predators may segregate themselves based on their peak activity times. The results suggest that the peak activity time of the tiger has a strong overlap with the sambar and a significant overlap with chital which also happen to be two of the tiger's major prey species in the Reserve based on the results of the diet analysis. The wild pig is one of the major prey selected by the tiger according to the dietary analysis and shows a significant overlap of activity times as well. The leopard showed a nocturnal activity pattern which strongly overlapped with sambar and hare. According to the diet analysis of the leopard, hare and barking deer were preferred prey species. Although, sambar was not seen as the preferred prey species, its activity peak overlapped strongly with that of the leopard. This could be an artifact of sampling as the sample size for leopard scats was very low. The activity peaks of the Dhole, overlapped strongly with the wild pig and the barking deer. According to the dietary analysis however, wild pig was not preferred. Sambar, chital and the barking deer were preferred by the Dhole. Although the Dhole is a pack hunter, it is risky for a pack to take down a prey like the wild pig as any injury to a pack member would bring down the chances of the pack to hunt efficiently in future and hence it seems to be hardly consumed. Although the density of the wild pig (5.42) was higher than that of both the sambar and chital it was consumed less by the predators as it is very difficult to take down owing to its sheer strength and low centre of gravity (Hayward et al. 2012, 2014).

The spatial analysis results indicate a co-occurrence of tiger, leopard and Dhole. The leopards and Dholes seem to strongly segregate in space however no such significant interaction was observed between the other carnivores. Owing to a large number of tigers in the Reserve and a small area, the three carnivores cannot avoid each other spatially but might do so on temporal and dietary axes to reduce competition. Also, interference competition is operating in the Reserve as there have been observations of tigers chasing Dholes and even hunting the pups, Dholes treeing leopards and tigers avoiding the areas when a pack of Dholes is spotted at a distance. There have been instances of Dholes stealing a sambar carcass killed by a leopard and a tiger stealing sambar fawn carcass from a pack of Dholes. The diet analysis also indicates that bamboo, which is a dominant species in the Reserve, is consumed by all three predators. On a number of occasions, the Dhole scats had very little mass and only undigested bamboo leaves entangled and binding the scat. This is usually done as self medication to tackle the parasitic load and could also be due to some deficiencies. The scat would be further examined to study the parasitic load. Remains of a sloth bear, which is a large bodied omnivore in the Reserve, were also found in one of the tiger scats. At the time of my study, there were around 20 tiger cubs in the Reserve. Tigresses with grown up cubs were seen taking down large prey like the gaur. The Dhole packs were observed to be not more than 5 adult individuals although a pack of nine adults was reported. At relatively smaller pack sizes as compared to the South Indian forests, the Dholes in the Reserve were observed to take down mainly the fawns of Sambar and Chital. It was also observed that the leopard, similar to the leopard in the savannahs of Africa, dragged its kill to a tree or a vantage point probably to safeguard the kill from the co-predators. All three predators were seen to scavenge at kills once it had been abandoned by the primary predator. Interestingly, the Reserve has no specialist scavengers except the Long-billed crows. The Ruddy mongoose has been observed scavenging on old carcasses whereas the three large predators themselves scavenge if the quarry is not too old. Scavengers like Striped hyena, Golden jackal and vultures which were previously reported are no longer found in TATR.

CHAPTER III
THE CUON ENIGMA

BEHAVIOURAL ECOLOGY OF DHOLES IN TATR, INDIA

3.1. Introduction:

The first step in the study of animal behaviour is defining the behavioural patterns to be documented. Without pre-defined terms, there is no fixed meaning to a described behaviour and it would remain open to individual interpretation. Ethograms are an inventory of behaviours (Bekoff 1978) which serves as a reference material to describe animal behaviour. In order to study the finer intricacies of animal behaviour, designing ethograms is crucial as it determines the scope of analysis, often dictating the course of future research (Bekoff 1979; MacNulty et al. 2007). The Dhole or the Asiatic wild dog is a pack-hunting carnivore that ranges over much of South and South-East Asia. Previous work on the species was summarized by Johnsingh (1980), Fox (1984), Acharya (2007) and Hayward et al. (2014). Although this species has been fairly studied in the past, none of the studies published a standardized and complete ethogram of the Dhole. Apart from wolves, coyotes, red fox and the singing bush dog there are no detailed behavioural repertoires of the approximately 35 canid species (Ewer 1973, Way et al. 2006). This study describes a broad scale ethogram of the Dhole and sets stage for a detailed behavioural repertoire for the Dhole in the future.

To study complex behaviours like inter pack relationships, one needs to first study the basic behaviour of a Dhole and of a single pack. The ability to discriminate between neighbours and strangers has rarely been tested in group-living species. Inter-pack individual recognition is important primarily for maintaining territories, competition, hierarchy and parental care. Such complex behaviour has not been extensively studied in social carnivores and not at all explored in social canids. One of the objectives of my study was to provide new insights into inter-pack relationships in Dholes by performing scat translocation experiments.

3.2. Methods

Field Methods:

Behavioural data were collected opportunistically in the form of videos. A Canon Powershot SX 50 was used for recording the behaviours of Dholes. Data collected by tourists, forest guards and guides in the time period of my study was also analyzed for studying the behaviour and to derive an ethogram. These videos were shot on different cameras, camcorders or mobile phones.

Scat Translocation Experiment:

Scats were collected and stored in a cool, dry place to keep them from drying or getting infested with fungus. In separate trials, each group was presented with excreta collected from three different donor groups: a neighbouring group, a non-neighbouring group ('strangers') and the group itself ('own group'). The "neighbour" packs were identified by field observations over two months to ensure the right scats were used for the experiments. Only samples with known pack identity of the excreting animal were used. The experiments were recorded for later analysis using a digital video camera.

The following response variables were evaluated:

- number of individuals vocalizing stressfully;
- number of individuals counter-marking; and
- number and duration of inspection bouts (nose within 1 cm of a sample)

The duration of inspection bouts (one individual inspecting one sample) was determined in software CowLog. Only responses of adults were included in the analyses presented here, with the assumption that younger individuals may not have learned to recognize neighbours yet.

Since there is very little information on the fission-fusion and pack dynamics of Dholes, identifying the stranger was vital. To ensure the use of right scats, samples from another pack situated at more than 200 kms apart were used for the experiment. The scats were placed on the ground from a vehicle. Getting down from a vehicle was avoided to place the scats on the ground when an individual was in front of the vehicle. After placing the scats, the vehicle was parked at a safe distance to give space to the animal to inspect the foreign object placed on the ground. To avoid observer bias, only I conducted the scat translocation experiments on the Dholes. The Dholes were habituated to humans due to the tourism in the Reserve and did not react to the observers during the experiments

Analytical Methods

Ethogram:

Video recordings are used to study behaviour because direct observation has a high risk of disturbing the observed subject. For constructing an ethogram as well as deriving an activity budget for behaviours, the videos were analyzed in a software called CowLog 2.0. CowLog 2.0 is an open source software for recording behaviours from digital videos. It tracks the time code from video files, and records the time with the coded behaviours to a data file. Further analysis was carried out in Microsoft Excel 2007. Focal animal sampling was done to study the behaviours of all the Dholes in a pack. To avoid bias, only I conducted analyzed the videos for activity budget of Dholes. In the ethogram, I categorized the behaviours into 6 parent categories which were further classified into sub categories related to the parent category. One of the parent categories was called named as “Other” which included behaviours which were recorded on rare occasions and did not fit into the already created parent categories. These included: Startle, sit on top of the other, running with an object in the mouth.

Frequency of Behaviour and Activity budget

The frequency of behaviour (of parent categories) was calculated based on the number of events that fall under a particular class of behaviours. Further analysis was carried out in Microsoft Excel 2007. In order to study the acitivity budget of the Dholes, the software CowLog was used. Time (in seconds) of each event was recorded in a particular class of behaviours. Further analysis was carried out in Microsoft Excel 2007.

Relative Activity Budget:

A relative activity budget was derived by calculating the proportion of time adult males, females and sub-adults spent performing various behaviours. Only those data were used where individuals could be correctly identified as adult male/female/sub-adult. The data was then standardized to match the scale for comparing the proportion of time spent.

3.3. Results:

The ethogram is presented in the Table 7. A total of 427 minutes of data was analyzed at different time periods of the day. 3394 events were recorded in 1654 snapshots of ten seconds each. The 6 parent categories were: Rest, Locomotion, Social behaviour, Scent Marking, Feeding and Other.

Table 7: A preliminary ethogram of Dhole behviour observed in TATR, India. The ethogram has 6 parent categories of behavioural events by pooling together fine scale behavioural events.

RESTING BEHAVIOUR	
Rest	Lying down with eyes open or closed.
Sphinx Rest	Lying on the belly with forelegs extended to the front, hind legs bent and resting close to the body on each respective side, or with the body twisted and both hind legs to one side. Head may or may not be lowered to rest on the forelegs or the ground.
Sit	Resting on the hocks and Ischia.
Stand	Assuming an upright position with the weight of the body on all four legs.
Observation Stand	Standing upright on the hind legs with front legs folded to observe an object of interest above eye level or to avoid obstruction like tall grass and view the object of interest.
LOCOMOTION	
Walk	Ambulatory gait; the slowest upright gait, in which three feet are supporting the body at all times, each paw lifting from the ground one at a time in a regular sequence.
Trot	A rhythmic two-beat gait in which the diagonally opposite feet strike the ground together.
Run	Move at a speed faster than a walk, never having both or all the feet on the ground at the same time.
Tail chase	The individual notices and tries to grab its own tail in its mouth by circling around.
Circle	To move around an object or another individual in a tight circle.
Gallop	A four beat gait, often with an extra period of suspension during which all four feet are off the ground. The hind feet strike almost in unison
Hunt-Approach	Travelling towards potential prey
Hunt-Watch	Assessing a group of prey to (probably) decide upon a strategy to take down the quary.
Hunt-Chase	To run after a prey (may be a group of animals or a single prey)
Hunt-Surround and eviscerate	Typical Dhole behaviour with the prey encircled followed by the pack members taking bites at the prey without necessarily killing it completely.
SCENT MARKING	
Autogroom	An act of maintenance in which an individual directs at its skin, coat or claws and will usually invlove licking, scratching, shaking
Sniffing	Investigating either an object or the air for olfactory cues.
Scent mark-Squat	To urinate on an object or place after investigating it. (SQU)
Scent mark-Raised leg	To urinate on an object or place with one hind leg raised. (RLU)
Scent mark-Handstand	To urinate on an object or place previously marked by another individual/s by balancing on the two fore legs.
Scent mark-Hind bounce	Sitting on hocks with anus touching the ground accompanied by sudden springing at the same place.

Scent mark-Hind scrubing	Scrubbing the buttocks across the ground to express anal glands.
Body rub	Rubbing body against an object, ground or conspecific.
Trail	To follow a ground scent, sniffing the ground, bushes and other vegetation, usually at a WALK or slow TROT.
FEEDING	
Eat	Act of ingestion of food items once prey was completely killed and Dholes are at rest.
Drink	Lapping up water with the tongue
SOCIAL BEHAVIOUR	
Amicable Dhole	Lick, paw or groom (allo-groom); often with a tail wag
Snarl	Expose canines usually with ears down and raised hackles
Submissive	Evade, cower, roll over with ears lowered
Sniff dog	Nose to any area of a con-specific
Solicit play	Bow, short charges with bouncing gait, swift and short charges with head lowered
Body slam	Throwing self at another con-specific in a non aggressive manner with tail wagging and open mouth. Accompanied often by bites.
Mount	The actor clasps the receiver with its forelegs around the flanks, or sometimes the back. Includes pelvic thrusting, and frequently is accompanied by hackle licking and hackle biting. Non-estrus clasping during play or to show dominance.

The Dholes were observed to vocalize while doing other activities. Hence it was not considered as a separate category for the ethogram. I compiled a short vocal repertorie for Dholes (ref. Table 8).

Table 8: A vocal repertoire of Dholes in TATR, India

Event	Definition
Whistle	Emit a clear, high-pitched sound by forcing air through the nose
Yelp	A short, sharp high pitch cry, especially of pain or alarm
Screech	High frequency cry
Bark	A typical dog bark (heard only when alarmed).
Chuckle	A low pitch, 5-note sound accompanied by screeching when threatened / alert / scared.

Frequency of behaviour

The results of plotting the percent of frequency of behaviour classes indicate that 41% of the events recorded were under the parent category 'Locomotion'. The next category was 'Resting' with 37% of the recorded events. Feeding, social behaviour, scent marking and other followed in that sequence (ref. Fig.9).

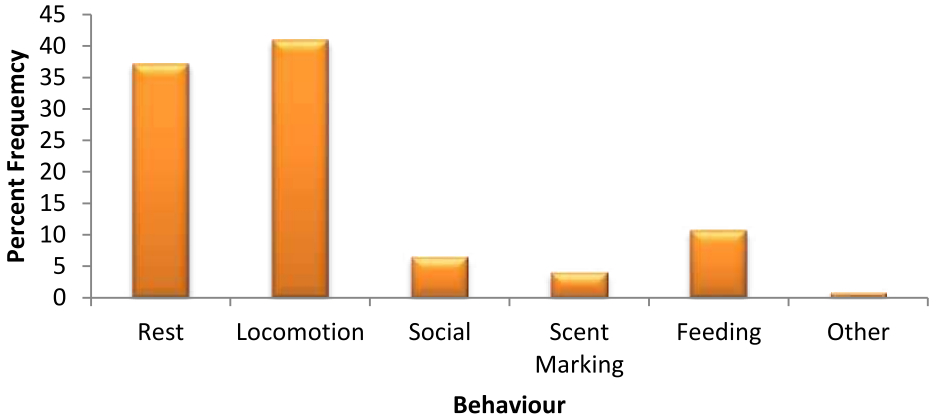

Figure 9: Percent frequency of behaviours; represented by 6 categories (Rest, Locomotion, Social Behaviour, Scent Marking, Feeding and Other) in TATR, India

Activity budget

The activity budget data graphically represented in Fig.10 showed a similar trend as the frequency table for locomotion and resting. This is probably because my observations were restricted to the da y hours when the Dholes are more active.

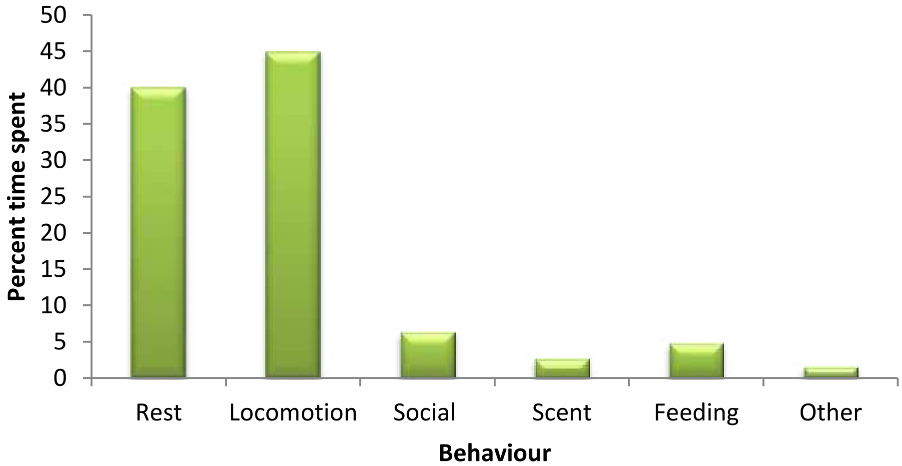

Figure 10: Percent time spent on each behavioural category; represented by 6 categories (Rest, Locomotion, Social Behaviour, Scent Marking, Feeding and Other) in TATR, India

Relative activity budget:

The relative activity budgets of males, females and sub adults were calculated. Fig.11 graphically represents the relative time spent by the alpha males, females and sub adults respectively on various behaviours. Chi-square test results suggest that there was no significant difference in the activity budgets of the males, females and the sub-adults ($\chi_2^{10} = 1.831; p = 2.2E - 16$). The acitivty budgets of pack living animals would not have much difference as they need to be together constantly.

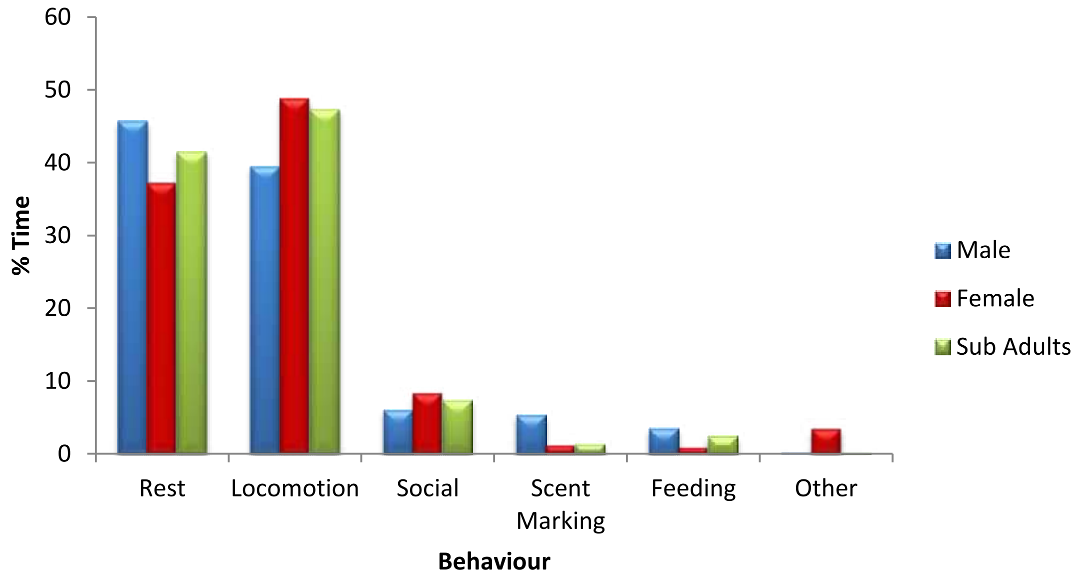

Figure 11: Percent time spent on each behavioural category by dominant Males (blue), dominant Females (red) and Sub-adults (green); represented by 6 categories (Rest, Locomotion, Social Behaviour, Scent Marking, Feeding and Other) in TATR, India

Scat Translocation Experiments:

With three control experiments where a recipient pack was presented with its own pack scat, one trial with the neighbour pack and two trials with stranger pack it was observed that the packs investigated non-neighboring or 'stranger' pack scent marks more intensively than either their own or their neighbors' scent marks.. This is in accordance with the results from a similar study on African wild dogs (Parker 2010). On one occasion where the pack members investigated their own pack scat for a longer duration than expected (ref. Table 9), could probably be because the pack was moving with pups and had to be more vigilant.

The sex and dominance status of individual wild dogs would probably influence how they investigate scent marks as reported in African wild dogs. This is because the benefit of excluding intruders may differ between dominant and subdominant group members, based upon potential breeding opportunities (Parker 2010). However, more trials would be needed to infer correctly whether or not the Dholes demonstrate the 'nasty neighbour' which was hypothesized.

Table 9: A summary of the scat trnslocation experiments carried out in TATR, India

Sr. No.	**Trial**	**No. of scats presented**	**No. of insepction bouts**	**Duration of inspection bouts (in secs.)**	**Relevant additional observations**
1.	Control 1 Dominant ♀	2	0	0	Did not react at all to the scats
2.	Control 2 Dominant ♂	1	1	4	-
3.	Control 3 Tadoba pack	1	2♂ 1♀ 3SA	13♂ 8♀ 10SA	Both the pups were also observed to sniff the scat.
4.	Neighbour Jamni adult ♂	1	1	7	Pre-occupied with a chital fawn that had been chased into the water
5.	Stranger 1 Lone ♀ at tadoba	1	3	16	Tail wag; but was to ward off flies sitting on wound
6.	Stranger 2 Lone ♀ at tadoba	3	3	32	Tail wag; but was to ward off flies sitting on wound

3.4. Discussion:

The study was set out to understand the behavioural ecology of the Dhole in TATR and compile an ethogram of the observed behaviours. The study also set to experimentally test if Dholes demonstrate NSD (Neighbour-Stranger Discrimination); however, owing to a small sample size, strong inferences could not be drawn from the experiments. The ethogram was compiled as a preliminary inventory of the observed behavioural events of Dholes. Since no standardized ethogram has been published for the Asiatic wild dog, it was an essential component of my study. During the period of my study, pups had started emerging from the dens and accompanied the adults from the end of the month of December till the last month of the study in April. However, this study does not include the behavioural activity of the pups. The Dholes are considered to be mainly diurnal in habit (Johnsingh 1972, Kawanishi & Sunquist 2008, Acharya et al. 2007, Majumder 2011) and all the observations made during the study, although confined from dawn to the end of dusk, comprehensively cover the peak activity times of the animal. I could not locate active dens during the period of my study and hence the nature of activity during the night hours remains to be studied and may well be added to the ethogram in the future. From the best of my knowledge, I would predict that there would be minimal activity during the night hours. For the purpose of this study, behavioural events were organized into 6 parent categories.

Resting:

The behavioural events like standing, observation stand, sitting, sphinx rest and lying down were recorded as a part of resting behaviour. The Dholes were commonly observed to rest at junctions or the sides of the forest paths for short periods after they had covered fairly long distances and scent marked. On two occasions I observed them resting at length near a stream under dense canopy cover during the hot, late morning hours of the day. They were also observed to rest after killing a large prey animal like an adult chital or sambar. The observation stand was an act of standing erect on the hind legs with the forelegs in mid-air. This act was observed when the Dholes moved fast and had to assess the surroundings promptly.

Locomotion:

The events like walking, running, trotting, tail chase, circle and galloping were recorded under the parent category 'locomotion'. The events of hunt and observation stand were also recorded under locomotion. Following MacNulty et al 2007, 'hunt' was further broken down but modified according to the observations of Dhole hunts. The characteristic evisceration of prey by the Dholes which is basically disembowelling the prey was placed under this category as this event was a part of hunting and the animals were still not at rest (ref. Fig.12). 'Eat' was placed under the parent category 'feeding'. Based on my observations of successful and unsuccessful hunts (n=7), the hunting strategy of wild dogs was not as complex as reported earlier(refs). The dominant male did lead the hunt on almost all the occasions as reported earlier and chased the prey; usually towards the other pack members. However, other than this observation, the individual roles seem to not be fixed. The other members of the pack seemed to assume roles based on the need of a particular hunt. The prey was eviscerated before it was completely killed as previously reported.

Figure 12: A typical hunt scene where the prey is eviscerated even before it is completely killed by the Dholes

Social Behaviour:

Amicable Dhole, snarl, submissive, sniff dog, solicit play, body slam and mount were events placed under the parent category 'social'. Physical contact seems to be an extremely crucial factor for maintaining the pack bond. The dominant male and female were observed to be highly social, frequently body slamming or rolling over each other. The sub adults were observed to be more amicable towards each other than with the adults owing probably to the hierarchy in a pack. However, the Dhole packs did not exhibit strong hierarchy and agonistic events were rare. The Dholes were observed chasing each other and relaying on a couple of occasions. Previous literature has reported this behaviour and interpreted it as a practice ritual before or after hunts. However, I did not find any such association between relays and hunts. On one occasion the dominant male was seen to play with the pups for 6 seconds before he walked away. The dominant female was observed to solicit play by taking bites at the flanks and moving away from the dominant male on one occasion. The male was not aggressive and circled around the female trying to avoid the bites. This was very similar to observed evisceration and could be a hunt practice session.

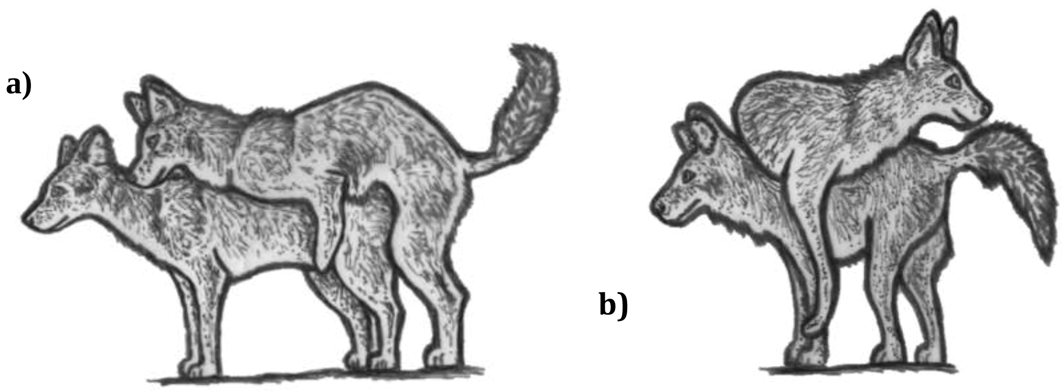

Figure 13: Illustrations depicting a) the classic mount and b) front mount in Dholes

Mating was observed on one occasion (ref. Fig.13a). The dominant male mounted the female several times. As reported by Fox (1984), the wild dogs did not exhibit a copulation knot, however contradictory to his observations; they did not lie next to each other after the act of mating. I observed them drinking water after mating before they galloped away into the undergrowth. During the act of mating, the sub-dominant female was constantly trying to interrupt mating. The male did not react aggressively towards the sub-dominant female but the dominant female showed aggression in the form of snarls and also chased away the other female on two occasions. The dominant female solicited mating in the breaks by being overly amicable. On one occasion, the female mounted the male and on another occasion the male mounted the female the other way – front mount (ref. Fig.13b).

Scent Marking Behaviour:

Scent-marking is the application by an animal of faeces, urine, or cutaneous gland secretions to features in its environment (Macdonald 1980). Scent marking may have various important functions among social carnivores. Hierarchy assertion and maintenance, territory maintenance, status of health of individuals, may be few of them. Territory ownership and maintenance by scent marking has been studied in Grey wolves (Peters & Mech, 1975). Whether Dhole packs maintain their territories by scent marking is not evident from my observations. However, I did observe a significant overlap of territories among neighbouring Dhole packs.

Path junctions and crossroads where 2 or more trails converged seemed to be scent marking posts and were strongly and regularly marked. Scent marking was also seen across main roads. As observed in the African wild dogs (Johnson 1973), dominant males tend to scent-mark more frequently than other age/sex categories. The dominant males and females of the packs were observed to have a scent marking ritual where they over marked or cross marked (next to the each other) taking turns. However, most of the times the dominant males were observed to end this short but evident ritual by a raised leg urination event. I also observed that the females almost compulsively marked over the male on several occasions even though she was seen resting or doing other activities when the male started the scent marking ritual. On two occasions, the Dholes were seen to cross mark over tiger scent posts by rubbing their body on the ground next to the scent post tree or by squat urinating.

Johnsingh (1972) mentions two studies on African wild dogs (Kellar 1973 & Van Leawick 1971) and his observation of one dhole from Kanha which state that the dogs were observed to balance on their forelegs while urinating to scent mark over their pack members' scent marking. I observed this behaviour on 4 occassions in which both the males and females were seen balancing on their forelegs while scent marking probably to accurately mark the same spot as the conspecific. I also observed two scent marking behaviours which were not reported for wild dogs before. The characteristic erratic bouncing of the dog over grass or ground was observed on several occasions. I termed this behavioural act as the '***hind bounce***' **(appropriate terminology still being worked out)**. This is probably done to smear the secretions of the anal glands onto the substrate. Another act was termed as **'*hind scrub*'**. It is very similar to a common practice to express the anal glands in domestic dogs called ***scooting***which is done when the animal is in discomfort or diseased. Every time the dog defecates, some amount of secretion is supposed to be excreted along with the faeces which lunbricates the anal tract. However, at times this does not happen naturally and the anal glands get saturated causing discomfort to the dogs (personal communication Capt. Dr. Nigam, Veterinary Doctor, Wildlife Institute of India). Pet dogs are taken to vets to manually express these glands; however, for the Dholes, thie hind scrub seems to have an important function for scent marking as it was usually seen in association with other scent marking events and healthy individuals (ususally the dominant male) were observed doing this. Body rubbing was seen as a common way of scent marking. Dominant males were seen rubbing their bodies against the dominant females which could probably also signify mate guarding (ref. Figs.14a to e).

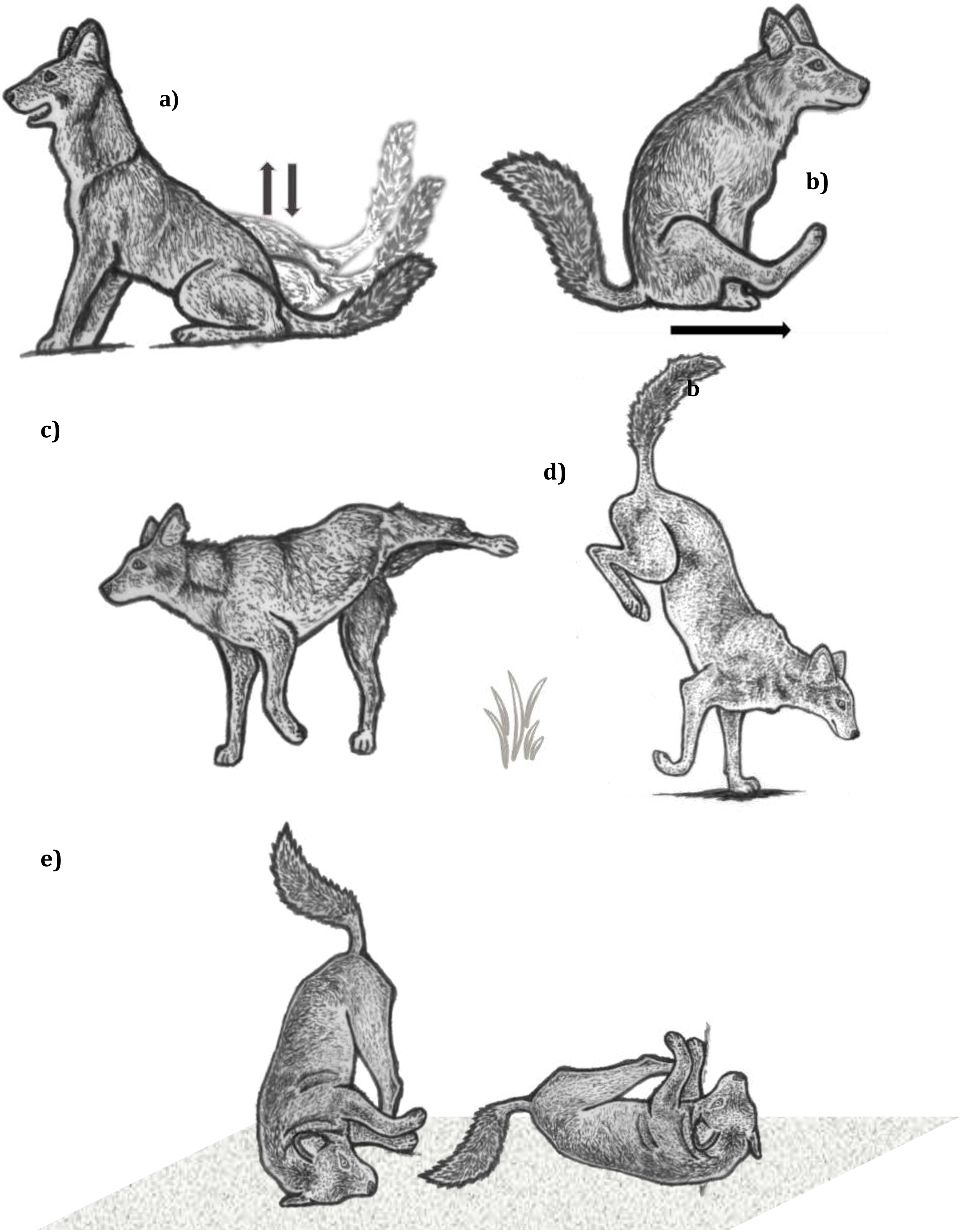

Figure 14: Illustrations depicting the scent making behaviours of Dholes: a) Hind bounce b) Hind scrubbing c) Raised Leg Urination d) Handstand urination e) Body rub

Feeding:

'Eat' and 'drink' were the two events placed under the parent category 'feeding'. The fawn kills were completely devoured in a matter of minutes while bigger prey was consumed at leisure. I also observed some amount of aggression between pack members when the kill was small and had to be shared. On one occasion the dominant female was observed walking away from the other pack members with a chital fawn kill in her mouth while the dominant male and the sub adult fed on parts which separated from the main kill. For larger kills, the alpha males did feed the last as reported earlier (Wild Dog Diaries, National Geographic), however, he was observed eviscerating while taking down the kill. For larger kills, the pack members took turns to feed but no particular pattern was consistent other than the alpha male feeding towards the end. The breeding female was observed to regurgitate food for the pups. On one occasion, a sub adult Dhole was seen to carry the liver of a chital to approximately 2 month old pups which later, fed on the organ. Organ meat being more nutritive in nature may be fed to pups in the initial stages of their lives. Dholes were observed to be extremely alert while eating and drinking water probably due to the competition amongst other predators.

Other Behaviour:

Behaviours which were not routinely observed and as a result not fitting in any parent category of the ethogram were clubbed under 'Other'. For example, on one occasion a sub- adult was observed sitting on top of the dominant male (ref. Fig. 15).

Figure 15: Illustration depicting a behavioural event placed in the category 'other' which shows a sub-adult sitting on the dominant male

Dholes in a Multipredator System

This is the first study to understand the status of Dholes in TATR. To cope with the intense inter-specific competition, the Dholes have adapted their activity patterns with respect to tigers and leopards which are the other co-predators in the system. Although direct confrontation is avoided as far as possible, there are occasions when the tigers have chased or even killed the Dholes (ref. Fig.16). On one occasion, three wild dogs walked into a tigress which had spotted them and was in a stalking position. Members of the Canidae are known to have a highly developed sense of olfaction. How and why they did not spot the extremely apparent approaching tigress either visually or by the scent was inexplicable. As in the case with the African wild dog, interference competition with larger carnivores must be an important force shaping the behavior, number, and distribution of dholes (Creel & Creel 1996, 1997).

Figure 16: A tigress with a Dhole pup kill in the mouth, TATR, India

Pack Dynamincs:

According to the long term tiger monitoring project report, the Dhole population is estimated to be in the range of 42-45 (Habib et al. 2014). The mean group size of **3.6** Dholes recorded during this study was much smaller than that of Dholes in the Southern India but close to the group sizes reported from elsewhere in central India (ref. Table 10).

Table 10: Average pack size of Dholes reported by other authors from studies across India

Location	Mean pack size	Reference
Pench Tiger Reserve	7.5	Acharya 2007
Pench Tiger Reserve	3.5	Majumder et al. 2011
Mudumalai Tiger Reserve	14.5	Ramesh et al. 2012a
Pakke Tiger Reserve	2.5	Selvan et al. 2013b
Tadoba- Andhari Tiger Reserve	6.18	Habib et al. 2014

To test whether Dholes demonstrate NSD, scat translocation experiments were conducted. However, more trials would be needed to draw inferences about the responses of Dholes. A high degree of overlap between territories was evident based on field observations over time. Since the Dholes are not individually recognizable, the fission- fusion between the packs can only be well studied if the individuals are marked using tags or radio-collared. A pack of 4 members seen in December had only 3 individuals from the month of February. Whether the individual died or joined another group was impossible to say as the individual was without apparent differentiable markings (wounds, cuts, etc). Locals have reported the sightings of pups almost every year around the period of November-April. However, there is no understanding of where the pups go the pack size seems to be more or less constant by the next breeding season.

3.5. Conservation:

According to my observations, the pup mortality is high in the Reserve. One pack was observed to have 4 pups in the month of January but the same pack had only two survivors by the end of March. Some of the Dholes in the population seem to be diseased (sarcoptic mange) but this needs to be clinically tested to ascertain what exactly they are suffering from and whether this is a threat to their population. The pups seem to be more susceptible to this skin condition probably due to a weaker immune system. Whether predation by co-predators, disease or natural selection is the cause of mortality of pups needs to be studied in further detail. TATR is a source population of tigers and has been proved to be important for tiger conservation. No conservation measures specifically focused on Dholes have been reported in India. However, Project Tiger could potentially maintain Dhole prey bases in areas where tigers and Dholes coexist. Main threats to the species include ongoing habitat loss and probably disease transfer from domestic dogs. There have been captures of feral dogs in camera trap pictures which may be a potential threat to spread various diseases.

3.6. Suggestions and Solutions:

Raising awareness about the species within local communities, as well as with the national government and international organisations to help people understand the species better is the one major solution to conserve Dhole in India. Assessing the level of conflict between Dhole and people throughout their range, and implementing measures to reduce it is one way of dealing with the hostile attitudes of people towards the species. There is a pressing need to ensure protection of the forest habitat from further loss and fragmentation.

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