# ECOLOGY OF STRIPED HYENA (*Hyaena hyaena*) IN SARISKA TIGER RESERVE, RAJASTHAN

A THESIS
Submitted by
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For the award of the Degree of
**DOCTOR OF PHILOSOPHY**
**IN**
**WILDLIFE SCIENCE**

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**JUNE 2018**

Dedicated to all the solitary, social and not so social animals.....

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# Certificate

This is to certify that the thesis entitled **"Ecology of striped hyena (*Hyaena hyaena*) in Sariska Tiger Reserve, Rajasthan"** submitted for the award of degree of **Doctor of Philosophy** in Wildlife Science to Saurashtra University, Rajkot is a record of original and independent research work carried out by **Mr. Dibyendu Kumar Mandal** under our guidance. No part of this thesis has been submitted to any other university or institution for the award of any degree and it fulfils all the requirements laid down by Saurashtra University.

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I also certify that the Research work was appreciated by all who remain present and there was no comments made for this research work.

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**Dibyendu Kumar Mandal**

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Resource Dispersion Hypothesis (RDH) suggests that resource heterogeneity may allow animals to share space and form social groups at low costs. Co-operation may arise secondarily in these circumstances. RDH nullifies the significance of interaction to explain sociality. Thus, comparing degrees of sociality within less or intermediately social species such as striped hyena (*Hyaena hyaena*) effectively enhances our understanding of carnivore social evolution, rather than studying highly social species, because benefits may be consequence of grouping rather than the forces which initially fovoured it. However, the striped hyena has got relatively little research attention in spite of being a species with ecological and evolutionary significance due to their wide distribution and diverse sociality. Striped hyenas are behaviourally solitary scavengers and are known to form spatial groups (both polyandrous and polygynous) in the African systems. Conspecifics do not interact with each other in the African system. Striped hyenas are human tolerant and often found within proximity of urban centres and can survive on human organic waste generated at these sites. Arid regions of North-western India are important habitats for hyena persistence, which is among the most densely populated arid regions of the world both for humans as well as livestock. It might appear that their conservation status is secure due to their amazing ability to survive in the rapidly changing human dominated landscape. However, striped hyena often comes in conflict with humans due to their habit of livestock depredation, targeted retaliatory killing directed at other carnivores and road accidents. Although, India sustains significant proportion of striped hyena global population (20 – 25%) in diverse ecological settings, long term studies investigating their population dynamics,

resource utilization pattern, behaviour and sociality are rare. This study was conceived to fill gaps in our understanding of striped hyena population parameters, resource utilization and their sociality. Finally, the findings were synthesized to understand the processes shaping diverse sociality of striped hyenas across varying resources in a comparative context under the framework of RDH.

The present study was undertaken in Sariska Tiger Reserve (STR), a protected area situated in the semi-arid region of North-Western India. STR is an isolated system which has a sharp boundary with human habitations. Sariska has 29 villages inside the reserve and is surrounded by approximately 170 villages and a major city within three kilometres of its boundary. STR sustains comparatively high density of predators (leopard and striped hyena) and prey. STR is also beneficiary to India's first reintroduced tiger population and sustains 12 tigers. Two state highways dissect the reserve. However, road accidents leading to striped hyena mortality (n=6) were frequent until the traffic regulation (traffic ban during night and diversion during day through the protected area) was started on the two state highways in 2011.

Most carnivore populations are now confined to protected areas surrounded by human settlements and are exposed to ever-increasing pressure on their periphery. Such isolated populations are vulnerable to extinction due to demographic stochasticity. Therefore, demographic data is extremely crucial to manage large carnivore populations and to slow down their population decline since extinction is a demographic process. Striped hyena population dynamics was studied within the framework of conventional mark-recapture (CMR) and spatially explicit capture-recapture (SECR) using nine-year-long (2007 – 15) camera trap data. I tested three hypothesis to understand the influence of traffic regulation, tiger reintroduction, and village relocation on striped hyena population dynamics in STR. Although the population remained largely stable over nine years, my findings support the hypothesis that traffic regulation had a significant positive effect on striped hyena survivorship (Pre $\hat{S}$=0.66, Post $\hat{S}$=0.98) as well as on mean rate of population growth (Pre $\lambda$= - 2.3%, Post $\lambda$= 0.8%). Future population dynamics projection using count based population model shows that striped hyena population would have been severely affected if the traffic was not regulated. The current study provides empirical evidence and highlights the importance of the influence of road related mortality on large carnivore population dynamics which has global conservation implications for similar carnivorous species with comparable life history traits elsewhere.

Striped hyena site utilization was influenced by terrain ruggedness, distance to village and water and their site utilization and detection probability was higher in presence of tiger and leopard (0.53±0.09 and 0.83±0.09 respectively) which may be due to their scavenging habits. They were very specific about breeding den site selection and choose areas near waterholes with higher shrub density. This may be attributed to their limited ability to thermoregulation and for protection from other predators and human disturbance. Breeding den site availability was found to be patchy in the study area. Striped hyenas foraging activity peak was around midnight [00:11 (23:4 – 00.36)]. Their nocturnal activity might have facilitated their persistence in this human dominated landscape. The present study also indicated that although they are scavengers and primarily dependent on large mammals (wild ungulates and livestock, 56%), however they also actively predate on smaller prey species. Diet of striped hyenas in the semi-arid areas predominantly consists of large mammals as compared to smaller and rarer prey in African systems. Diet and dispersion of food are widely recognised as a key determinant of group formation. Given the difference in diet, greater resource availability and heterogeneity in the Indian semi-arid with African systems, the social organisation of striped hyena may likely be influenced by the former. Thus, findings of this study set the stage for further investigation of their sociality in this habitat concomitant to extant resources.

Social Network Analysis (SNA) and ethogram were used to understand striped hyena sociality at the dens in a human-dominated semi-arid landscape of India. Unlike their African counterparts, SNA revealed that Indian hyenas form den-centric clans which consist of a breeding female, multiple adult females and pups. Furthermore, individual centrality ($R^2 = 0.41$) in this pup-centric system decrease with increase in age class due to their solitary foraging nature. As hypothesized, the association among different age class decrease with increase in age ($P<0.05$) due to their solitary foraging nature. Ethogram demonstrated that they were highly interactive, engaging in social play (15.88%), grooming (12.35%), greeting (6.92%), proximity resting (14.93%), feeding (4.48%), food provisioning (1.76%) behaviour, and vigilance (8.55%) over pups while interacting at the dens. Interactions mostly occured during the twilight hours with a peak at dawn [4:29 AM (4:11 AM – 4:48 AM, 95% CI)] upon the return of adults from foraging. Adults, other than the breeding female, play a crucial role in rearing and survival of pups. Clan members have significant home range overlap (65%) among themselves as compared to significantly low overlaps among spatial units (only 8% in Laikipia, and 26% in Shompole) in the African systems.

Striped hyenas persist in comparatively higher densities across diverse habitats and different resource gradient in India as compared to Africa and Middle-East. Food resource abundance was found to be comparatively higher in India. Increases in overall resource abundance leads to increases in habitat quality per unit area, thus resulting in higher animal densities, and typically smaller ranging areas. However, reported home ranges from India (73.5±12.9 $km^2$) were comparable to Shompole system (66.89±13.31 $km^2$), Kenya wherein they survive in vast stretches of inviolate space and prey was scarce. This similarity in home ranges was probably due to clumped resource availability (food and den site) in Indian systems due to presence of human habitation. Higher population density also increases the chances of individual encounters in competitive circumstances, favouring formation of alliances. Since it is a risky landscape, the constraints of reproduction are so high for individuals, they benefit from such affiliative relations (den centric breeding clans) as observed in the present study. Clumped resources in the Indian semi-arid region reduce competition, thereby enhancing affiliative bonding to a great extant. This corroborates the Resource Dispersion Hypothesis whereby secondary benefits such as alloparenting has shaped the extant sociality in my study species. My findings, in a comparative context, suggest that cooperative behaviour of hyena in rearing pups in the Indian population is a secondary benefit, possibly increasing their survival in this risky human-dominated landscape.

## *Preface and Thesis Organization*

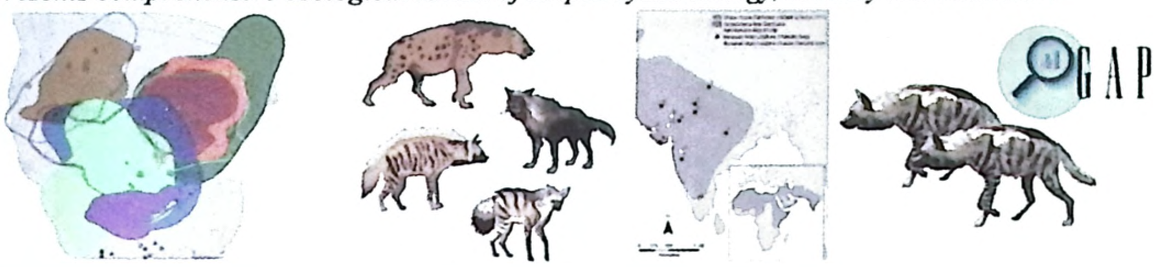
Striped hyena (*Hyaena hyaena*) has got relatively little research attention in spite of being a species with ecological and evolutionary significance, due to their wide distribution and diverse sociality. This study was conceived to fill gaps in our understanding of striped hyena population parameters, resource utilization pattern and their sociality.

The thesis consists of seven chapters, a chapter on introduction and study area each, four data chapters and a synthesis chapter **(Box 1)**. The first chapter discusses ecology of carnivore sociality, resource dispersion hypothesis, importance of family hyaenidae in studies on carnivore group formation and presents a comprehensive review of striped hyena ecology, sociality and behaviour **(Chapter 1)**. This chapter identifies lack of knowledge about vital population parameters, resource utilization pattern and sociality as research gap. Second chapter provides a detailed overview of Sariska Tiger Reserve where the study had been undertaken **(Chapter 2)**. Third chapter presents assessment of population parameters of striped hyena such as survival rate and growth rate **(Chapter 3)**. Resource utilization pattern (food, habitat and den) of striped hyena was examined in the fourth chapter **(Chapter 4)**. Striped hyena social organization and sociality were discussed in the fifth chapter **(Chapter 5)**. Sixth chapter discusses human-hyena interactions and threats to their population **(Chapter 6)**. Finally, the overall findings of the study was synthesized under the framework of Resource Dispersion Hypothesis to understand the underlying reasons of group formation and sociality, identify research gaps, suggest long term conservation strategies and discuss limitations of the current study **(Chapter 7)**.

Box 1

## CHAPTER 1: INTRODUCTION

*Presents comprehensive ecological review of striped hyena ecology, sociality and behaviour.*




**Why some species live communally, but forage alone?** Resource Dispersion Hypothesis

Importance of family hyaenidae in studies on carnivore group formation

Review of striped hyena distribution, population status, habitat use, diet and foraging

**Diverse sociality & behaviour across five subspecies of striped hyena**

Present study aims to understand survival rate, resource utilization pattern & behaviour of SH.

## CHAPTER 2: STUDY AREA

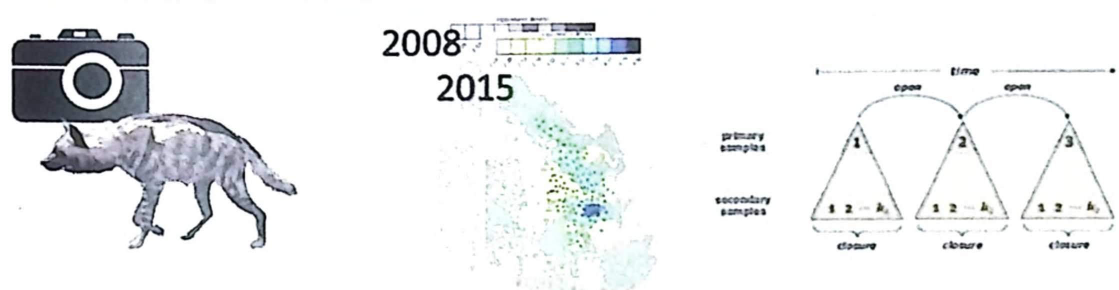
**Location, history & Climate**

**Habitat & Terrain**

**Co-predators & Prey**

**Villages & Livestock**

## CHAPTER 3: ABUNDANCE AND SURVIVORSHIP OF STRIPED HYENA

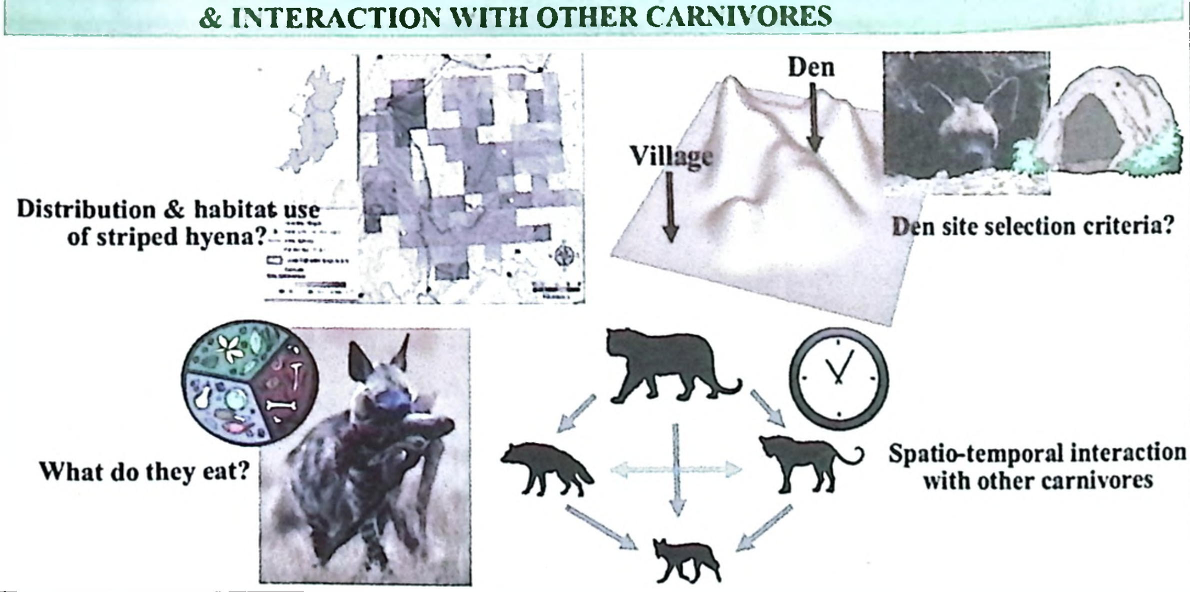



**Camera Trapping (CMR & SECR)**

**Density over years (2008 to 2015)**

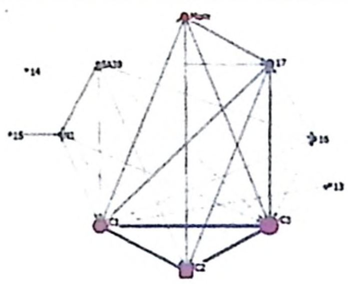
**Survivorship (Robust Design)**

## CHAPTER 4: STRIPED HYENA DISTRIBUTION, RESOURCE UTILIZATION PATTERN & INTERACTION WITH OTHER CARNIVORES

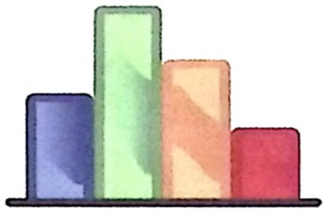


## Box 1 Continued

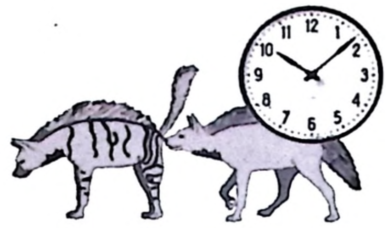
### CHAPTER 5: STRIPED HYENA SOCIALITY



How is their sociality at the den site? (Social Network Analysis)



Their behaviour at den site (Ethogram)



Temporal activity at the den

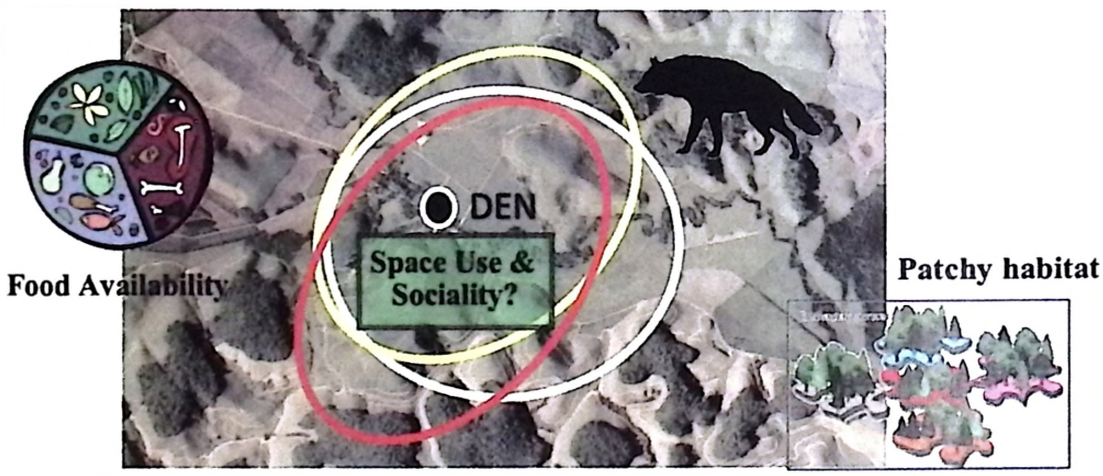
### CHAPTER 6: HUMAN-HYENA CONFLICT & THREATS

Human-Hyena Interactions

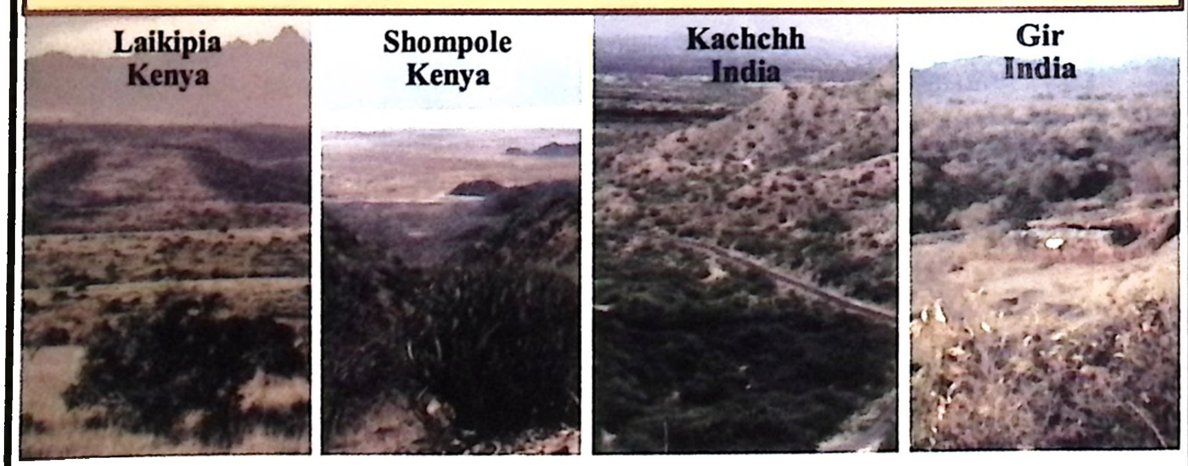
Road Accidents

Habitat Loss

### CHAPTER 7: CONCLUSION



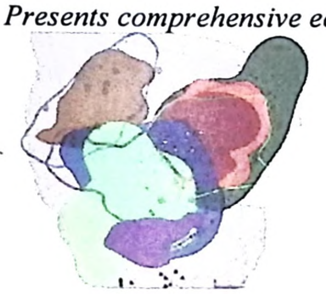

**Conclusion by comparing across sites within the framework of RDH**



# CHAPTER I INTRODUCTION

**CHAPTER 1: INTRODUCTION**

*Presents comprehensive ecological review of striped hyena ecology, sociality and behaviour.*



**Why some species live communally, but forage alone?**
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Review of striped hyena distribution, population status, habitat use, sociality, diet and foraging


**Diverse sociality & behaviour across five Subspecies of striped**

Present study aims to understand survival rate, resource utilization pattern & behaviour of striped hyena

# CHAPTER 1 INTRODUCTION

Although, group living has evolved in only 10 – 15% of carnivore species (Bekoff et al. 1984), disproportionately less research attention have been paid to them. Diet and dispersion for food has been considered key determinants in group formation. The Resource Dispersion Hypothesis (RDH) suggests that resource heterogeneity may allow animals to share space and form social groups at low costs (Macdonald 1983). Co-operation may arise secondarily in these circumstances. RDH thus nullifies the significance of interaction to explain sociality. Because, benefits in highly social species may be a consequence of grouping rather than the forces which initially fovoured it. Thus, comparing degrees of sociality within less or intermediately social species effectively enhances our understanding of carnivore social evolution (Wagner et al. 2008). Hyaenids exhibit remarkable diversity in their feeding habits and social diversity which makes them useful for studies on group formation (Mills 1989). Although three of the four extant members of the family (spotted hyena *Crocata crocata*, brown hyena *Hyaena brunea* and aardwolve *Proteles cristata*) have been studied in details, their striped cousins, the striped hyena (*Hyaena hyaena*) has got relatively little research attention in spite of being a species with ecological and evolutionary significance, due to their wide distribution and diverse sociality.

Striped hyenas were hitherto described as solitary. However, recent seminal studies suggest that they have diverse social organization. Striped hyenas (*H. h. dubbah*) of Laikipia, Kenya form stable polyandrous spatial groups of 2-4 individuals (Wagner et al. 2008). Califf (2013) reported spatial grouping among females from Shompole, Kenya population due to greater availability of resources than Laikipia where females are solitary. Striped hyenas of Israel (*H. h. syriaca*) are known to form feeding groups of 2-4 individuals to access large quantities of offal at the dump sites (Macdonald 1978). Offal at these dump sites contributes most (~ 90%) in their diet (Macdonald 1978). Indian striped hyenas although solitary foragers, are known to interact at the dens (Jhala 2013). Interestingly, all these studies indicate relation between resources and striped hyena sociality. Rieger (1979) believed comparative studies on five sub-species of striped hyenas will put light on the influence of different ecological settings on the social organization of striped hyenas. However, very few studies exists across the five subspecies of striped hyenas. Only striped hyenas among hyaenids are distributed outside Africa which makes them crucial for comparative studies. However, lack of long term studies on striped hyena ecology outside Africa makes it difficult. Although, India sustains significant proportion of striped hyena global population (20 – 25%) in diverse ecological settings (Mills and Hofer 1998), all the prior studies except for two doctoral theses, were either result of short term research work, or natural history observation, or have not been published for the global audience.

### *1.1. Distribution and Population Status*

Hyenas prefer arid to semi-arid environments in the tropics and occur widely in diverse habitats except for the moist forests of north-eastern region in the India sub-continent (AbiSaid and Dloniak 2015). Although, Mills and Hofer (1998) recognized the potential of individual identification based on pelage patterns for population estimation of striped hyenas, in Indian context, very few studies using photographic capture-recapture to estimate the population size of the species has been published to date

(Gupta et al. 2009, Harihar et al. 2010, Singh et al. 2010). Information on the abundance of the species from across representative habitats within India is necessary to make an objective assessment of their status in Indian sub-continent and for future conservation initiatives.

There are eight studies which reported striped hyena density estimates from six Protected Areas (PAs) and three outside Protected Areas **(Table 1.1.)**. The reported density estimates from inside PAs range from 3.91 to 15.1 individuals/ 100 $km^2$ **(Table 1.1.)**. Striped hyena density outside PAs ranges from 3.67 to 5.03 individuals/ 100 $km^2$ **(Table 1.1.)**. In these areas outside protected areas, 3 to 5 striped hyenas/ 100 $km^2$ share habitat with 50 to 300 human/ $km^2$ (Bopanna 2013, Athreya et al. 2013). Densities from inside and outside PAs did not vary much which indicates striped hyenas remarkable ability to survive in the human-dominated landscape. However, camera trap based study at two areas in the semi-arid region of India revealed the availability of potential hilly refugia offered by hilly terrain sustain higher densities of striped hyenas (Singh et al. 2010). The area with a higher proportion of hilly area (85%) sustained higher hyena densities (6.5 individuals/ 100 $km^2$) than the area with comparatively lower proportion of hilly area (35%, 3.67 individuals/ 100 $km^2$; Singh 2010). However, density estimates of striped hyena from India are higher as compared to the densities that are reported from Africa and the Middle East. Striped hyena occurs in very low densities in Africa (1.7 individuals/ 100 $km^2$ in Serengeti (Bouskilla 1984), 3 individuals/ 100 $km^2$ Laikipia and Shompole (Califf 2013) each) and the Middle East (0.3 individuals/ 100 $km^2$ in Negev Desert, Bouskilla 1984). The only exception is

Mpala Ranch in Kenya which has a hyena density of 6.39±1.65 individuals/ 100 km$^2$ (O'Brien and Kinnard 2011).

As part of the national tiger estimation program, striped hyena distribution was reported from 1, 19,180 km$^2$ in 2010 (Jhala et al. 2011) and 1, 09,842 km$^2$ in 2014 (Jhala et al. 2015) in India. However, this program focused mainly on the protected area network which are potential tiger habitats (PA network in India covers only 5% of the total land area), and leaves out most of the semi-arid and arid landscape and agro-pastoral habitats outside protected areas which are considered to be the strongholds of the species (Jhala et al. 2011, 2015). Since striped hyenas are also known to occur outside protected areas in the agro-pastoral landscape, this area is minimal occupancy of the species. Apart from the reported occupancy, arid and semi-arid region reported having a minimum striped hyena occupancy of approximately 4,500 km$^2$ (Kumar 2012). Given their vast occupancy throughout peninsular India, population size (1000 – 3000) estimated by Mills and Hofer (1998) appears to be a gross underestimate. However, their occupancy has declined approximately 8% throughout the Indian subcontinent during the two consecutive national tiger estimation surveys (Jhala et al. 2011, 2015).

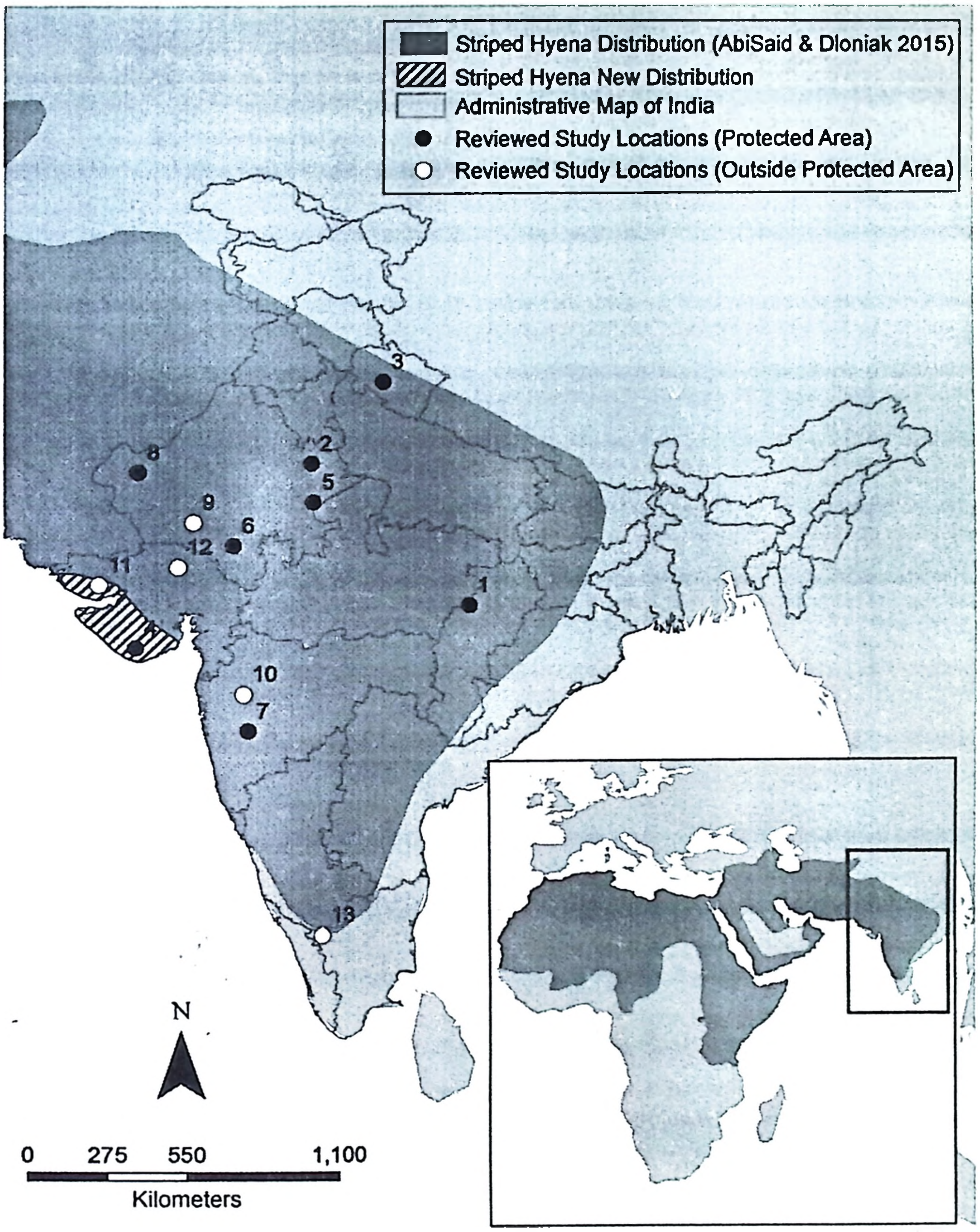



**Figure 1.1.** Reviewed study locations with IUCN distribution range (AbiSaid and Dloniak 2015) of striped hyena in India (Protected Area: 1. Achanakmar Tiger Reserve, 2. Sariska Tiger Reserve, 3. Rajaji Tiger Reserve, 4. Gir National Park, 5. Ranthambore Tiger Reserve, 6. Kumbhalgarh Wildlife Sanctuary, 7. Mayureshwar Wildlife Sanctuary and 8. Thar Desert. Outside Protected Area: 9. Esrana Forest Range, 10. Akole, Ahmednagar, 11. Kachchh, 12. North Gujrat and 13. Sigur Plateau.)

**Table 1.1. Details of reported striped hyena population status from inside and outside Protected Areas in India**

| Protection Status | Area | Effort | Mt+1 | N | Method for calculating ETA | Width (Km) | ETA (sq. Km) | D (/ 100 sq. Km) | Reference |
|---|---|---|---|---|---|---|---|---|---|
| Inside PA | Achankmar | 1702 | 11 | 12±2.3 (SE) | MMDM/2 | 1.802 | 312.631 | 3.84±0.94 (SE) | Mandal et al. 2017 |
| | | | | | ML Dens | | | 4.54±1.75 (SE) | |
| | Sariska | 1675 | 26 | 34±5.4 (SE) | MMDM/2 | 1.832 | 138.9 | 24.5±4.3 (SE) | Gupta et al. 2009 |
| | | | | | ML Dens | | | 12.7±2.8 (SE) | |
| | Rajaji | 600 | 6 | 6± 0.98 (SE) | MMDM/2 | 2.92 | 153.59 | 3.91±1.62 (SE) | Harihar et al. 2010 |
| | | | 6 | 6±0.82 (SE) | | 2.52 | 136.49 | 4.4±0.69 (SE) | |
| | | | 7 | 8±1.7 (SE) | | 2.64 | 141.19 | 5.67±3.15 (SE) | |
| | Ranthambore | 4450 | 21 | | SECR | 2.1±0.2 (σ) | 233 | 5.49±1.27 (SE) | Singh et al. 2014 |
| | Kumbhalgarh | 548 | 15 | 20±7.85 (SE) | MMDM/2 | 1.95±0.15 | 307 | 6.5±2.6 (SE) | Singh et al. 2010 |
| | GNPS | 600 | 24 | | | | | 6.5 | Alam 2011 |
| Outside PA | Esrana | 538 | 8 | 8±0.55 (SE) | MMDM/2 | 1.95±0.15 | 218 | 3.67±0.3 (SE) | Singh et al. 2010 |
| | Akole | 1110 | 12 | 18±6.48 (SE) | MMDM/3 | 1.85 | 193.44 | 9±3.35 (SE) | Athreya et al. 2013 |
| | | | | | SECR | 0.5756±0.2394 (σ) | | 5.03±1.3 (SD) | Athreya et al. 2013 |
| | Kachch | | | | Radio Telemetry | | | 5 to 10 | Jhala 2013 |

### *1.2. Ecology and Behaviour*

#### *1.2.1. Habitat use*

Radio-collared striped hyenas (n=08) from outside PA of Kachch area used scrub forest which is invaded by *Prosopis juliflora* and *Prosopis salvadora* thickets. Scrub forest reflects striped hyenas preference for thick vegetation and cover (Bopanna 2013, Jhala 2013) to avoid heat and human disturbance during the day. Bopanna (2013) also observed that hyenas avoid seasonal croplands. These croplands were guarded by guard dogs. However, they do use this land use during transits (57% of the collared animals died in snares in seasonal agricultural lands) (Bopanna 2013). However, he suggested that the duration of the usage by hyena was short. The relationship of hyenas with village distance is of significance, a decline in the probability of hyena presence was observed with increase in distance from villages. Village areas are important foraging sites for the species, facilitated by the maintenance of traditional pastoralist lifestyles. Most of their movement pattern were governed by the location of villages in the landscape (Bopanna 2013).

Singh (2014) reported striped hyena detection was influenced by terrain ruggedness, close canopy and shrub cover and distance to human settlements based on a camera trap based study from the north-west Indian PA of Ranthambore Tiger Reserve. Hyena capture was reportedly higher in rugged terrain (61%) as compared to flat areas including valleys (39%). He argued that rugged terrain provide better habitat free from disturbance (humans or guard dogs) for breeding, denning and raising cubs. Close canopy and shrub cover influenced detection of striped hyena which may provide concealed daytime resting sites. Interestingly, striped hyena captures were higher in areas which are less than three km from the human settlement (71.2%). Indian PA's are usually smaller and mostly has sharp boundaries with human habitations. For example, Ranthambore Tiger Reserve has 332 villages with approximately 1,50,000 livestock heads within 5 km of the reserve boundary. Singh (2014) reported that 20-30 livestock die every month due to starvation, poor veterinary care, and carnivore depredation. These live stocks are often dumped outside villages which may act as an easy and known food resources for hyenas. This finding is at par with findings in Kuchch. Radio-collared hyenas of Kachchh were recorded spending 10% of their daily time around villages probably for easy and known access to feeding sites (Bopanna 2013).

### *1.2.2. Diet and foraging*

Based on prior studies, striped hyena is found to demonstrate an opportunistic behaviour and scavenges on livestock and wild animals, and predates on small mammals, livestock, reptiles and ground-nesting or feeding birds (Prater 1965, Leakey et al. 1999, Kruuk 1972, Sankar and Jethwa 2001, Wagner 2006). Hyenas primarily depend on scavenging to obtain their food. Hyenas primarily rely on ungulate carrion predated by a tiger *Panthera tigris*, leopard *Panthera pardus*, and lions *Panthera leo* in the forested ecosystem, whereas they feed mostly on livestock carcass in human-dominated landscape (Jhala 2013). However, hyenas sometimes predate on small livestock like goats, sheep, cattle calf and dogs and hunt hare, gazelle, jackal, nilgai calves and wild pig (Jhala 2013). In Kachchh, cattle and dogs contributed over 70% of the hyena's diet (Jhala 2002). Chital remains were found in 35% of the hyena scats followed by domestic cattle in the protected area of Sariska (Sankar and Jethwa 2001).

Diet and distribution of food have known to play a significant role in striped hyena's social organization (Wagner et al. 2008, Califf 2013). Even though they live in colonies, striped hyenas are solitary foragers (Jhala 2013). Based on continuous monitoring (24 hrs) of 2496 hours of tracking seven radio-collared individuals, Bopanna (2013) reported average distance travelled by hyena in one night was 14 (±0.6 SE) km with an average speed of 1.2 (±0.05 SE) km/ hr outside PA in the human-dominated landscape of Kachchh. Most of the distance were reported to be covered between 11 pm and 5 am. Continuous monitoring of striped hyenas in Kachchh revealed that most of their daily time was (48%) spent in resting. Rest of the time (52%) was spent on movement (30%), around villages (10%), socializing in the centre of activity or den (10%) and foraging (2%). Movement patterns were governed by the location of food sources and den sites (Bopanna 2013, Jhala 2013). Califf (2013) reported similar observations on Shompole (Kenya) population based on her 536.15 hours of focal animal sampling on 15 collared hyena individuals. Shompole hyenas spent most of their time travelling (69.7%) and resting (29.4%) (Cliff 2013). Data on foraging from inside PA is not available from India. Minimum mean distance travelled per night in Africa was 19 km at an average speed of 2 to 4 km/hr (Kruuk 1976).

### *1.2.3. Sociability*

Striped hyenas are the least studied of the hyenas; their social behaviour is poorly understood and was usually reported to be solitary. Reiger (1979) expected variation in striped hyena's social organization across the five sub-species as ecological settings are different. He speculated that areas with higher density of striped hyenas are expected to live in family groups (Rieger 1979). Rieger (1979) reported that typical group size of striped hyenas is 1 to 2 in all sub-species. Although, groups up to seven individuals have been reported for *H. h. dubbah* in Libya (Hufnagi 1972). Striped hyenas in the coastal plain of Dead Sea have been reported to gather at feeding sites in pairs on more than 50% of occasions. Striped hyenas (*H. h. syriaca*) of Negev desert form feeding groups of two to four individuals (Macdonald 1978).

A recent long-term study (Wagner 2006) in Laikipia, Kenya reported that striped hyenas (*H. h. dubbah*) live in small groups composed of one adult female and one to three males sharing a common home range. Laikipia striped hyenas are behaviorally solitary, but have a polyandrous system of space use, and a polyandrous or promiscuous mating system (Wagner et al. 2008). Females appear to mate both with group males and males that reside elsewhere. It is not known whether sires contribute in any way to parental care, but lactating females are usually found alone at dens with their cubs, and females appear to be solely responsible for the care of young. Fundamentally, hyena spatial groups can be considered as breeding groups because all offspring can be assigned to the female of the natal group, and the majority of offspring are sired by males within the natal group (Wagner et al. 2007). All females in Laikipia population disperse from their kins and their ranges did not overlap with other females (Wagner et al. 2008). Although, each female range did overlap with multiple males providing evidence of an unusual mammalian system (Wagner et al. 2008). In a comparative study among two populations (Laikipia and Shompole, Kenya), Califf (2013) found out Shompole hyenas to follow typical mammalian system with overlapping female ranges and evidence of den sharing and provisioning in Shompole population. However, she never recorded more than two individuals at one den.

However, Califf (2013) reported despite having home range overlap, Shompole striped hyenas were alone during 95.6% of the time based on a total of 536.15 hours of Focal Animal Sampling on 15 radio-collared individuals. During 186.2 hours of opportunistic behavioural data collection at 16 dens, Califf (2013) observed den provisioning. However, she mostly observed one individual at one den during the study period. Califf (2013) proposed greater availability of resources have resulted in relaxed resource competition and consequently social tolerance among females in Shompole population (Kenya).

Striped hyenas especially females are known to interact at the breeding den sites in the Indian semi-arid system (Jhala 2013). However, anecdotal reports and natural history account from Southern India suggested that striped hyenas (*H. h. hyaena*) are solitary (Davidar 1985). Females raise young without the helper and male had no role in pup upbringing (Davidar 1985, Godbole et al. 2015). The social organization of striped hyena are not completely understood, described or classified, and the possibility of variations across regions cannot be ruled out. Descriptions of the species in one habitat cannot be and should not be generalized to the same species in another set of environmental conditions (Whitehead 2008, Califf 2013). It is highly likely that their social organization might vary within India across different ecological settings and disturbance regimes depending on the availability of resources like den site availability and food. Targeted scientific studies are crucial for understanding their social organization, behaviour and determining causes of their sociality for the conservation of this threatened species.

### *1.2.4. Litter Size*

Average litter size of hyena in the wild varies from one to four with a median of 3 (Mills & Hoffer 1998). Rieger (1979) reported an average litter size of hyenas as 2.4 (1 – 5) in captivity. Average litter size of hyena in India is 3 (n=17) as reported in four studies (**Table 1.2.**).

**Table 1.2. Litter size of striped hyena in India as reported in four published accounts**

| Area | Protection Status | Sample Size | Litter Size | Breeding Time | Reference |
|---|---|---|---|---|---|
| **Gir NP** | PA | 9 | 3±0.24 | Jan - Mar | Alam 2011 |
| **Sigur** | Outside PA | 1 | 3 | Feb - Mar | Davidar 1985 |
| **Mayureshwar WLS** | PA | 2 | 3 | Feb - Mar | Godbole et al. 2015 |
| **Kachchh** | Outside PA | 5 | 2.8±0.17 | Dec -Jan | Bopanna 2013 |

### *1.3. Conclusion*

Striped hyena persists in comparatively higher densities throughout India in both PAs as well as outside PAs in the agro-pastoral landscape (**Table 1.1.**). However, their persistence depends on the availability of hilly refugia or undulated terrain free from human disturbance for denning (Singh 2010). It might appear that the conservation status of striped hyena is secured due to their ability to survive in rapidly changing human-dominated landscape. However, striped hyena often comes in conflict with humans due to their habit of livestock depredation, targeted retaliatory killing directed at other carnivores and road accidents. Survival rates of striped hyena has not been studied in detailed yet. Striped hyenas are listed in Schedule II of the Indian Wild Life (Protection) Act 1972, and are considered near threatened due to their ongoing population decline.

Reiger (1979) suggested in areas with higher density of striped hyena are expected to live in family groups. Striped hyenas do persist in comparatively higher densities in India than their African counterparts. As population density increases, so will the rate of individual encounters with each other in competitive circumstances, favouring formation of alliances. However, studies investigating their sociality or underlying ecological reasons of the process are rare.

*Thus, the present study was focused to understand survival rate of striped hyena in a semi-arid protected area of western India. Also an attempt was made to understand resource utilization pattern of striped hyena in details which includes their habitat utilization, diet, breeding den site selection and spatio-temporal interaction with other carnivores in order to understand their sociality and threats to their population. Finally, synthesis of findings under the framework of Resource Dispersion Hypothesis to understand the underlying reasons of group formation and sociality was provided.*

### *1.4. Objectives*

i. To monitor abundance and survivorship of striped hyena population in Sariska Tiger Reserve.

ii. To study striped hyena distribution, resource utilization pattern and interaction with other carnivores, and

iii. To study the human-hyena conflicts and assess threats to their population.

# CHAPTER 2

## STUDY AREA

Sariska Tiger Reserve (STR) is an isolated reserve situated in Aravalli hills in Alwar district of north western Indian state of Rajasthan between Longitude: 79° 17' to 76°34'N and Latitude: 27° 5' to 27° 33'E (**Figure 2.1.**). The total area of Tiger reserve is 1200 km$^2$, with 400 km$^2$ as a notified National Park.

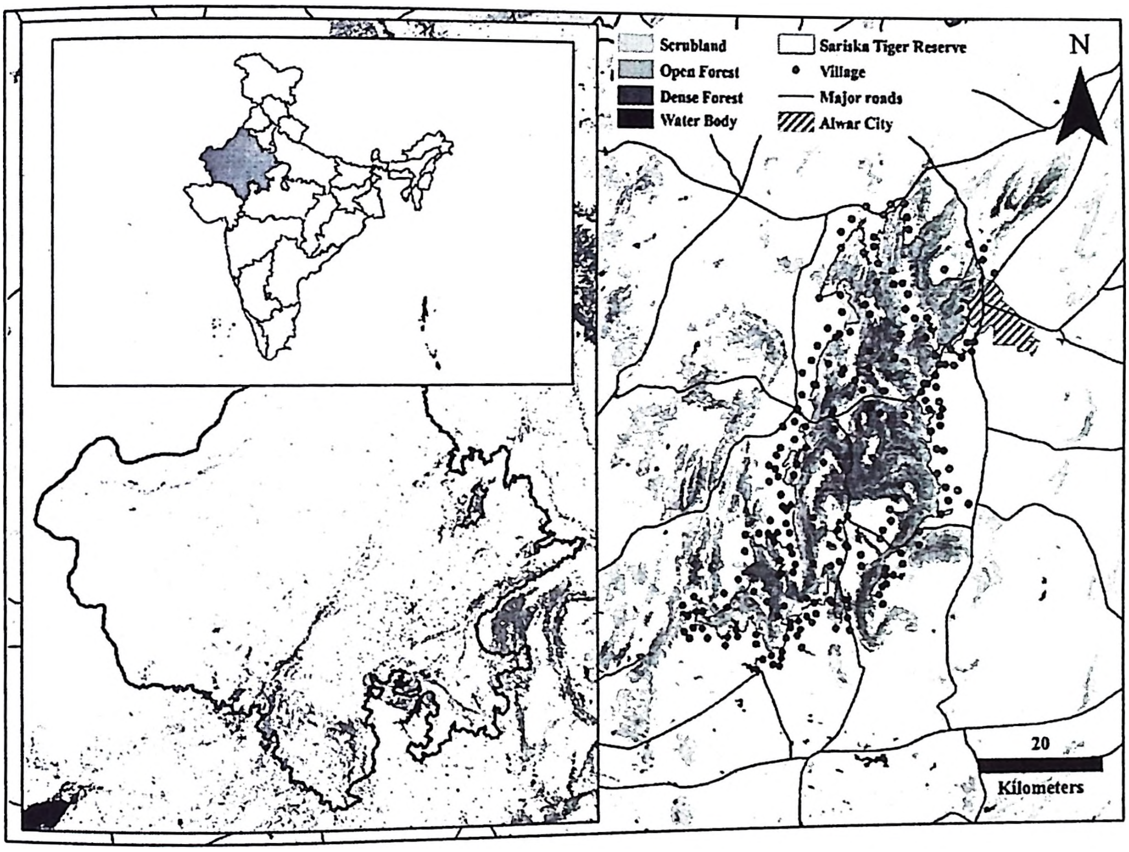



**Figure 2.1. Location of Sariska Tiger Reserve with villages inside and at the periphery (within 3 km)**

### *2.1. Climate*

The climate is subtropical, characterized by a distinct winter, summer and monsoon. Winter commences from November. In winter, the temperature has been observed to drop to 3° C. Summer commences from mid-March and continues till end of June. July and August are rainy season. Summer is followed by monsoon from south west in July and August. The study area also receives occasional winter and summer rains. Average annual rainfall recorded is 650 mm (Sankar 1994).

### *2.2. History and Archaeological Richness*

STR was created in 1978. In the pre-independence period, the forests within the Reserve were a part of the erstwhile Alwar State and maintained as a hunting preserve for the royalty. After independence, Sariska was declared as a Wild Life Reserve on 7$^{th}$ November, 1955, under the Rajasthan Wild animals and Birds Protection Act, 1951. The Reserve status was upgraded to that of a Sanctuary in 1958. STR was included in the list of Tiger Reserves by Government of India in 1978 as the 11th Tiger Reserve. In 1982, an area of 274 km$^2$ was declared as Sariska National Park vide Preliminary Notification *NO. F11 (22 ) Raj-8/78 Jaipur Dated 27 August 1982 under Wild Life Protection Act 1972 (Central Act No. 53) section 35 (1).*

### *2.3. Major Vegetation Types*

The vegetation of STR correspond to (1) Northern tropical dry deciduous forests (sub groups 5B; 5/E1 and 5/E2) and Northern Tropical Thorn forest (subgroup 6B) (Champion and Seth 1968). *Anogeissus pendula* is the dominant tree species covering over 40 per cent area of the forest (Sankar 1994). *Boswellia serreta* and *Lannea coromandelica* grow on rocky patches. *Acacia catechu* and bamboo are common in the valleys. Some valleys support *Butea monosperma* and *Zizyphus mauritiana. Dendrocalamus strictus* is extremely limited in distribution and is found along well drained reaches of the streams and moist and cooler parts of the hills. *Albizia lebbeck, Diospyros melanoxylon, Holoptepia integrifolia* and *Ficus spp.* are found in moist localities (Sankar 1994). Parmar (1985) and Rodgers (1991) have classified vegetation of Sariska as follows:

1. *Anogeissus pendula* forest

2. *Boswellia serrata* forest

3. *Acaccia catechu* forest and

4. *Miscellaneous forest,* which can be further sub-divided into three categories viz.

   a) *Butea monosperma* forest

   b) Forest along nallas and

   c) Scrub land

Nine different vegetation and land cover categories have been delineated in STR (Sankar et. al. 2008). They are *Anogeissus* dominated forest, *Boswellia* dominated forest, *Butea* dominated forest, *Acacia* mixed forest, *Zizyphus* mixed forest, Scrubland, Agricultural land, Water body and Barren land.

### *2.4. Terrain*

The major part of the area is occupied by rocks of the Delhi system and Aravalli system comprising of quartzite, conglomerates, grits, limestone, phyllite, granites and schist (Pascoe 1950, Sankar 1994). STR is characterized by rugged terrain, valleys and plateau with the altitudinal variation from 340 m to 777 m (**Figure 2.2.**). The two main plateaus are Kankawadi (524 m above mean sea level) and Kiraska (592 m above the mean sea level). The most remarkable characteristics of the hills are their homo-genetic regularity of height, level summits and uniform appearance, stretching out from northeast to south-west, in more or less parallel lines (Soni 2000). The depth of soil layer is more than 1 m in valleys, whereas it is only a few centimetres deep on the hill slopes. The soil is sandy loam and alkaline with pH varying from 7.25 to 8.00 (Yadav and Gupta 2006).

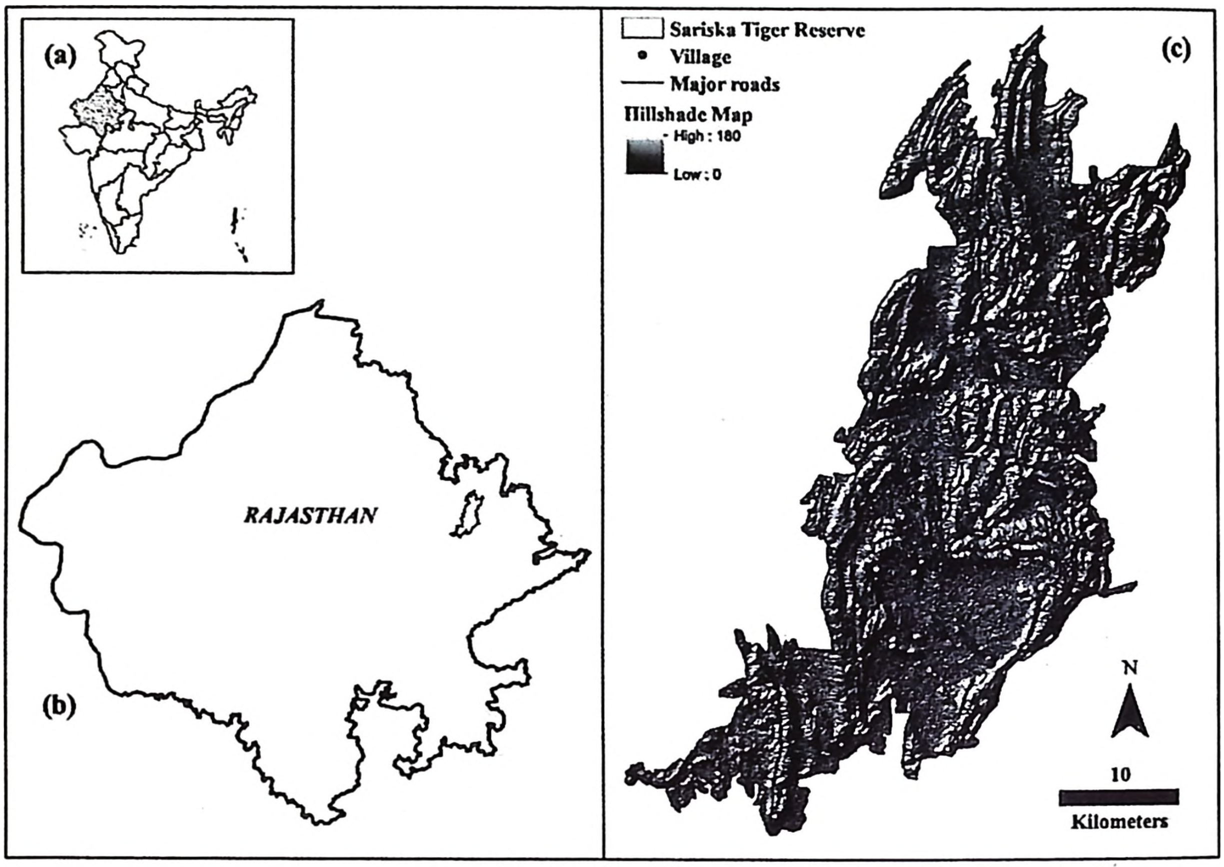



**Figure2.2. Hill shade map of Sariska Tiger Reserve showing terrain complexity**

### *2.5. Co-predators and Prey*

Large carnivores found are leopard (*Panthera pardus*), striped hyaena *(Hyaena hyaena),* and reintroduced tigers (*Panthera tigris*). STR sustains comparatively higher density of leopard (6.0±0.5 individuals/ 100 km$^2$, Mondal et al. 2012) and striped hyena (15.1±6.2 individuals/ 100 km$^2$, Gupta et al. 2009). Small carnivores are caracal (*Caracal caracal*), jungle cat (*Felis chaus*), common mongoose *(Herpestes edwardsi*), small Indian mongoose (*H. auropunctatus*), ruddy mongoose (*H. smithi*), palm civet

(*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*) and ratel (*Mellivora capensis*). Ratel density was 6.43 ± 2.79 animals/100 $km^2$ (Gupta et al. 2012).

Wild ungulates found in Sariska include chital (*Axis axis*), sambar (*Rusa unicolor*), and nilgai (*Boselaphus tragocamelus)*, and wild pig (*Sus scorfa).* STR sustains comparatively higher density of wild prey and livestock. Wild ungulate density of STR is 54.49 individuals/ $km^2$ and livestock density is 69.31 individuals/ $km^2$ **(Table 2.1.)**. Rhesus macaque (*Macaca mulatta*) and common langur (*Seminopithecus entellus*) are the two primates found here. Procupine (*Hystrix indica*), rufous tailed hare (*Lepus nigricollis ruficaudatus*) are also found in STR. STR sustains 11 species of rodents. The overall rodent density was 22.92 ±4.65 (SE) animals/ha in winter, and 7.81 ±2.25 (SE) animals/ha in summer. The overall rodent density was 16.15 ±2.76 animals/ha, and their estimated total biomass was 612.9 gm/ha (Gupta et al. 2013).

The most abundant galliform species was the Indian peafowl *Pavo cristatus* with an estimated density of 53.1 ± 5.6 individuals per $km^2$. Densities were also estimated for grey francolin *Francolinus pondicerianus* (21.6 ± 4.8 individuals per $km^2$), quail species (4.3 ± 1.40 individuals per $km^2$) and painted spurfowl *Galloperdix lunulata* (2.5 ± 0.9 individuals per $km^2$) in STR (Kidwai et al. 2011). Prey availability in the study area is given in **Table 2.1.**

**Table 2.1. Availability of wild and domestic prey (Density estimates) in Sariska Tiger Reserve**

| Prey Species | Density | Source |
|---|---|---|
| Wild Ungulates | 54.49 individuals/ $km^2$ | Bhattacharjee 2014 |
| Chital (*Axis axis*) | 16.25±3.00 individuals/ $km^2$ | Bhattacharjee 2014 |
| Sambar (*Rusa unicolor)* | 6.94±1.27 individuals/ $km^2$ | Bhattacharjee 2014 |
| Nilgai (*Boselaphus tragocamelus*) | 19.66±1.85 individuals/ $km^2$ | Bhattacharjee 2014 |
| Wild Pig (*Sus scrofa*) | 11.64±2.11 individuals/ $km^2$ | Bhattacharjee 2014 |
| Medium and small sized mammal prey | | |
| Common Langur (*Seminopithecus entellus)* | 15.30±2.90 individuals/ $km^2$ | Bhattacharjee 2014 |
| Rufous tailed hare (*Lepus nigricollis ruficaudatus*) | 1.92±0.4 individuals/ $km^2$ | Bhattacharjee 2014 |
| Rodent | 16.15 ±2.76 individuals/ ha | Gupta et al. 2013 |
| Birds | 74.7 individuals/ $km^2$ | Kidwai et al. 2011 |
| Indian peafowl *Pavo cristatus* | 53.1 ± 5.6 individuals/ $km^2$ | Kidwai et al. 2011 |
| grey francolin *Francolinus pondicerianus* | 21.6 ± 4.8 individuals/ $km^2$ | Kidwai et al. 2011 |
| Livestock | 69.31 individuals/ $km^2$ | Bhattacharjee 2014 |
| Buffalo (*Bubalus bubalis*) | 28.3±4.68 individuals/ $km^2$ | Bhattacharjee 2014 |
| Cattle (*Bos taurus*) | 41.01±6.58 individuals/ $km^2$ | Bhattacharjee 2014 |

### *2.6. Villages and Livestock*

There were 29 villages within the Tiger Reserve boundary and out of them twelve were situated in the notified National Park, which are due for relocation since 1984. Of these, village Bhagani was relocated during November 2007, Umri village was relocated during March 2012 and Rotkala village was relocated in March 2013. In the revenue villages the occupation of the people is based on agriculture but in the grazing camps it is animal husbandry. A large number of buffaloes and goats, cattle, sheep and a few camels are kept in the villages (Livestock density: 69.31 individuals/ $km^2$, Bhattacharjee 2014). The human population is over 8500 in the villages of Sariska TR. Additionally, there are approximately 170 villages in the periphery (within 3 km) of the reserve. These villagers depend totally on forests for their livelihood. The people inhabiting these villages are traditionally pastoralist and their main source of income is selling milk and its products like condensed milk and clarified butter.

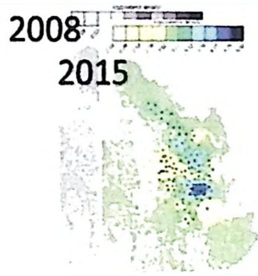
The Alwar Thanagazi-Jaipur State Highway passes through the reserve, and 2000 vehicles ply on it every day (Johnsingh et. al. 1997). Another main road passes through the reserve is Sariska- Kalighati- Pandupole road which is 20 km and along the wildlife rich valley of the reserve.

**Figure 2.3. Typical striped hyena habitat with villages visible at distance**

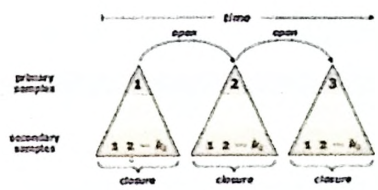
# CHAPTER III ABUNDANCE AND SURVIVORSHIP

**CHAPTER 3: ABUNDANCE AND SURVIVORSHIP OF STRIPED HYENA**

Camera Trapping (CMR & SECR)




Density over years (2008 to 2015)



Survivorship (Robust Design)

# CHAPTER 3 ABUNDANCE & SURVIVAL RATE

## 3.1. Introduction

Large carnivores are vulnerable to extinction due to their huge energetic requirement, slow life histories, low population densities and requirement of large home ranges to access prey (Carbone et al. 1999, Cardillo et al. 2004, 2005). Globally, carnivores have experienced a massive population decline, geographic range reduction and habitat fragmentation during the past two centuries (Caballos and Ehrlich 2002). Most carnivore populations are now confined to Protected Areas (PAs) surrounded by human settlements and are exposed to ever-increasing pressure on their periphery (Wittemyer et al. 2008). Rapid human growth on the periphery can limit carnivore populations within PAs (edge effects; Pulliam 1988; Woodroffe and Ginsberg 1998) and can draw individuals from PAs (attractive sinks; Loveridge et al. 2010). Such isolated populations are vulnerable to extinction due to demographic and environmental stochasticity (Shaffer 1981). Therefore, demographic data is crucial to manage large carnivore populations and to slow down their population decline since extinction is a demographic process. Lack of reliable demographic data makes population forecasting unreliable and impedes conservation initiatives (Coulson et al. 2001). However, long-term demographic data are difficult to obtain for carnivores due to their elusive nature and rarity (Karanth and Chellam 2009). There are approximately 52 studies on 'large carnivore demography' from around the world (www.scholar.google.com). Unfortunately, the existing studies were primarily confined to Africa (~43%) and North America (~33%) and mostly on felids (~44%) or canids (34%). Few studies on large carnivore demography from

Asia (only 10%), the global epicentre of growth, exists primarily for charismatic felids such as lions *Panthera leo* (Banerjee et al. 2011), tigers *Panthera tigris* (Karanth et al. 2006) and leopards *Panthera pardus* (Mondal et al. 2011). Interestingly, large carnivore species which thrive in human-dominated landscape and are vulnerable to demographic stochasticity such as striped hyena lacks demographic data.

Striped hyenas are behaviourally solitary scavengers (Wagner 2006), who are human tolerant and often found within proximity of urban centres and can survive on human organic waste generated at these sites (Mendelssohn and Yom Tov 1999). Arid regions of North-western India are important habitats for hyena persistence (Jhala 2013, Singh 2010), which is among the most densely populated arid regions of the world both for humans as well as livestock (Rahmani and Soni 1997). Majority of the human population traditionally avoids beef in these areas and dumps dead livestock near villages. Striped hyenas cover large areas every night (14 km/ night) and cross roads to access these food resources which is asynchronous over space and time. It increases the probability of striped hyenas getting killed by the vehicular collision. Road kills also attracts carnivorous scavengers which increases chances of the species to be a victim of a vehicular collision. Although, roads have been recognised as a significant threat to striped hyena population globally (Mills and Hoffer 1998), focused studies to understand their effect on a population level has not been undertaken yet. Mousavi (2010) suggested road-related mortality as the primary cause of carnivore mortality in Iran. He recorded 12 road-related striped hyena mortality during 2006 – 09. Bopanna (2013) reported 70% of collared striped hyenas in Kachchh, India died due to human-induced causes. Such demographic stochasticity may lead small isolated populations to extinction.

One such isolated population is Sariska Tiger Reserve (STR), situated in the semi-arid region of western India. STR has a sharp boundary with human habitations. Sariska has 29 villages inside the reserve and is surrounded by approximately 170 villages and a major city within the three kilometres of its boundary. Two state highways dissect the reserve. Tigers got locally exterminated in 2004 in STR as the reserve could not sustain the poaching pressure due to isolation. Sariska sustains a comparatively higher density of striped hyenas (Gupta et al. 2010). However, road accidents were frequent till the traffic regulation on the two state highways in 2011 that came into effect. STR was also beneficiary to India's first tiger reintroduction program in 2008. Following the tiger reintroduction in STR, population dynamics of leopard changed dramatically (Mondal et al. 2012). Village relocation has also been undertaken to create more inviolate areas for tiger breeding. All these factors mentioned above might have influenced striped hyena population dynamics in Sariska. The present study evaluated striped hyena population parameters within the framework of conventional mark-recapture and spatially explicit capture-recapture models using nine yearlong (2007 – 15) camera trap data and tested three hypothesis to understand the influence of traffic regulation, tiger reintroduction, and village relocation that may affect the demography of striped hyenas.

*Hypothesis I: Traffic regulation on two state highways might have a positive influence on striped hyena survival rate ($\hat{S}$).*

Roads have been widely recognised to have an adverse effect on animal abundance (Farig and Rytwinki 2009). Approximately 2000 vehicles used to ply to and fro every day on State Highway 13 causing disturbance in STR. The death of wild animals due to road accidents was also not uncommon in STR (Johnsingh et al. 1997, Johnsingh and Madhusudan 2009). Three leopard and six striped hyena mortality cases had been reported during 2008 – 10 in STR (Sankar unpublished). As per the Supreme Court of India decision, the traffic had been diverted during daytime and was stopped during the night on the State highways in 2011. The survival rate of striped hyena should have been affected due to high rates of mortality before traffic regulation. I expect survival rate *($\hat{S}$)* as well as growth rate ($\lambda$) of hyena population to be higher post-traffic regulation.

*Hypothesis II: Tiger reintroduction and following change in leopard demography may influence striped hyena survival rate ($\hat{S}$) as well as emigration ($\hat{\gamma}'$).*

There is growing evidence that interspecific competition affects population dynamics of large carnivores such as spotted hyena *Crocuta crocuta* (Watts and Holekamp 2009), lions *Panthera leo* (Cooper 1991), wild dog *Lycaon pictus* (Creel and Creel 2002) and cheetah *Acinonyx jubatus* (Duranr et al. 2004, Laurenson 1995). Long-term research on leopard demography in STR suggests that leopards changed their spatio-tempral behaviour and occupied peripheral habitat to avoid the tigers following the tiger reintroduction in STR in 2008 (Mondal et al. 2010). Consequently, leopard density decreased in the best available habitat (Mondal et al.

2012). Since, leopard and striped hyena are of similar body weight (Prater 1965) and known to compete with each other for food and habitat (Heptner and Sludkij 1988, Arivaghazan 2009), change in leopard demography may affect striped hyena population dynamics. Tigers also killed two striped hyenas during 2008 – 10 (Sankar unpublished). Tiger reintroduction and the consequent shift in leopard demography may influence survival rate ($\hat{S}$) as well as emigration ($\gamma''$) of striped hyenas negatively.

*Hypothesis III: Village relocation may increase den site availability which might influence immigration ($\gamma''$) of striped hyena.*

Although striped hyenas are human tolerant, they require inviolate areas for denning free from human disturbance and guard dogs. Denning serves important life history strategies (Jhala 2013, Bopanna 2013). Following the suggestion of tiger task force (MoEF 2005), three villages have been resettled from inside the core area of tiger reserve to create more inviolate space for tiger breeding from 2008 onwards. Village resettlement may have gradually increased suitable den sites for striped hyenas in the study area. Hence it is hypothesised that gradual increase in den site availability following village resettlement might influence striped hyena immigration rates *($\gamma''$)* during the study.

### 3.2. Methods

#### *3.2.1. Field data collection methods*

A grid-based sampling approach was used to photograph striped hyenas within the study area and Spatially explicit capture-recapture models (SECR, Efford 2004, Borchers and Efford 2008) and Pollock's robust design (Pollock 1982, Kendall et al. 1995) were used to estimate density and survival rate. Sampling units consisting of grids of the square cell (1 km x 1 km) was superimposed on the map of intensive study area of Sariska National Park (400 $km^2$). A pair of camera traps were deployed in each grid during winter of 2007 – 08 to 2014 – 15. Camera trapping was carried out in four blocks during each session. Approximately 20 pairs of camera traps were deployed in a block at a time. A total of 67 - 70 locations were selected for the placement of camera traps in the study area. One day was considered as a single occasion, resulting in 25 occasions and effort of 1675 trap nights in 2007 - 08, 1725 trap nights in 2011 - 12, 2012 -13 and 2013 – 14, and 1750 in 2014 - 15.

### *3.2.2. Analysis*

All photographs of striped hyena obtained from camera traps were identified using pelage markings on hind limbs, forelimbs and stripes on flanks (Singh, 2010; Gupta et al. 2010; Harihar, 2010). Following the identification, unique identification numbers were given to individual striped hyenas. I created three matrices that summaries detection/ non-detection history (X matrix) for program MARK v 8.1 (White and Burnham 1999) and spatio-temporal detection history of individuals and spatio-temporal layout of traps for SECR (Efford 2015).

***Abundance of striped hyena***

Spatially explicit capture-recapture models (Efford 2004; Borchers and Efford 2008) estimate density directly from the spatial capture histories thereby avoiding the use of ad hoc estimation of ETA done in traditional capture-recapture studies. SECR uses spatial histories of individual animals to construct centre of activity from where its detection declines as we move away. This process is modelled by two parameters - (1)g0, the detection probability at the activity centre and (2)sigma, the spatial movement parameter. We implemented SECR analysis in the maximum likelihood framework using the secr package (Efford 2015) in program R v 3.1.3 (R Core Team 2017). I used proximity detectors specifying a buffer of 5 km. I used a habitat mask wherein; we removed areas outside the temporary hard boundaries. Similar to the abundance estimation, I estimated striped hyena density of the five years separately, while g0 and sigma were kept constant over the years. I modelled both g0 and sigma as constant (null) or with two group heterogeneity (h2, differing in their movement patterns as two groups). The decline in detection as we move away from the activity centre was modelled using a half-normal distribution function. I then selected the model with minimal Akaike Information Criterion (Akaike 1974) as the best model and densities were estimated following the selected model.

***Estimation of survival rates of striped hyena***

Survival rates of striped hyena in the study area were estimated using the same X matrix (Otis et al. 1978) following 'Robust Design' (Pollock 1982, Kendall et al. 1995, 1997, Williams et al. 2002) model in program MARK v 8.1 (White and Burnham 1999). The robust design model includes several parameters such as detection and redetection probabilities (p and c respectively), and rates of temporary emigration ($\gamma''$, the probability of an individual temporarily moving off of the study area and becoming unavailable for capture and $\gamma'$, the probability of an individual remaining outside of the study area and thus remaining unavailable for capture) that must be estimated to provide unbiased estimates of survival rates. The study consisted of five "primary periods" covering nine years. The striped hyena population was expected to be open to gains and losses between these primary periods. There were multiple "secondary sampling periods" within each primary period. Five occasions were considered as one secondary sampling period, and the population was assumed to be closed to gains and losses among these secondary occasions.

I created 12 models to test three hypothesis. While modelling all the three hypothesis, I modelled detection probability (p) to be constant and to vary over time since different make of camera traps with changing proficiency has been used during the sampling period.

*Hypothesis I: Traffic regulation on two state highways will have a positive influence on striped hyena survival rate ($\hat{S}$).*

I modelled survival rate ($\hat{S}$) and emigration ($\gamma''$) to vary over pre and post traffic regulation (**Figure 3.1.**) in program Mark v 8.1. In total, I created four models to understand the effect of traffic regulation (Tra_Reg) on striped hyena demography (**Table 3.2.**).

*Hypothesis II: Tiger reintroduction and following change in leopard demography might influence striped hyena survival rate ($\hat{S}$) as well as emigration ($\gamma'$).*

Eight tigers were reintroduced from 2008 to 2013. Given the fact that tiger reintroduction (Tig_Intro) and consequent supplementation was undertaken over five years (Sankar et al. 2015), I modelled survival rate ($\hat{S}$) and emigration ($\gamma'$) to vary over time to understand their cumulative effect on striped hyena demography.

*Hypothesis III: Village relocation may increase den site availability which might influence immigration (γ") of striped hyena.*

Three villages have been resettled outside the protected area during 2008 – 13 (Sankar et al. 2013). I hypothesised that resettlement of three villages (Vil_Reloc) from inside the reserve may likely increase suitable denning areas for the species and, thereby will influence immigration during the study. I modelled immigration *(γ")* to vary over the years to understand the effect of village relocation on the population.

Finally, I selected the model with minimum AICc value as the best model to test the hypotheses. Model selection statistics for the full robust - design likelihoods **(Table 3.2.)** provided inferences about relevant sources of variation in the parameters. The model with the lowest AICc was judged to be substantially better than the others in the set of 12 models. Thus, inferences were based on this model, and it was decided not to use model averaging for parameter estimates.

### *3.2.3. Mean Rate of Population Change ($\lambda_t$)*

I also estimated the finite rate of population change (λ) using the robust-design Huggins full heterogeneity Pradel model (Pradel 1996) using Program MARK. Similar to the Huggins robust design model, I used five secondary trapping occasions (during which the population was assumed to be closed) to estimate p, c, and N. During the longer, primary intervals between the secondary periods, apparent survival (w), recruitment rate (f), seniority (c), and growth rate (λ) can be estimated by the Pradel model. All of the parameters cannot be estimated simultaneously (i.e., it is not possible to estimate w, c, f, and λ simultaneously) because they are effectively linear functions of each other; estimating any 2 of them can provide estimates of the remaining parameters. I chose a model structure that modelled w and $\lambda$ directly because these were the parameters that were crucial to evaluate the population dynamics.

### *3.2.4. Count based population viability Analysis*

I used the change in mean population growth rate ($\lambda_t$) for the chosen hypothesis to understand the effect on population dynamics in next 100 years using count based population viability analysis using package Primar (Stevens 2009) in R v 3.1.3 (R Core Team 2017).

## 3.3. Results

A total of 826 photographs of 65 individual striped hyenas were captured over nine years study, from 8600 successful trap nights (**Figure 3.1.**). 26 individuals were photo-captured during the first sampling occasion. Only four of them were recaptured during the second sampling occasion three years later. However, 13 individuals stayed in the population for over last four sampling occasions.

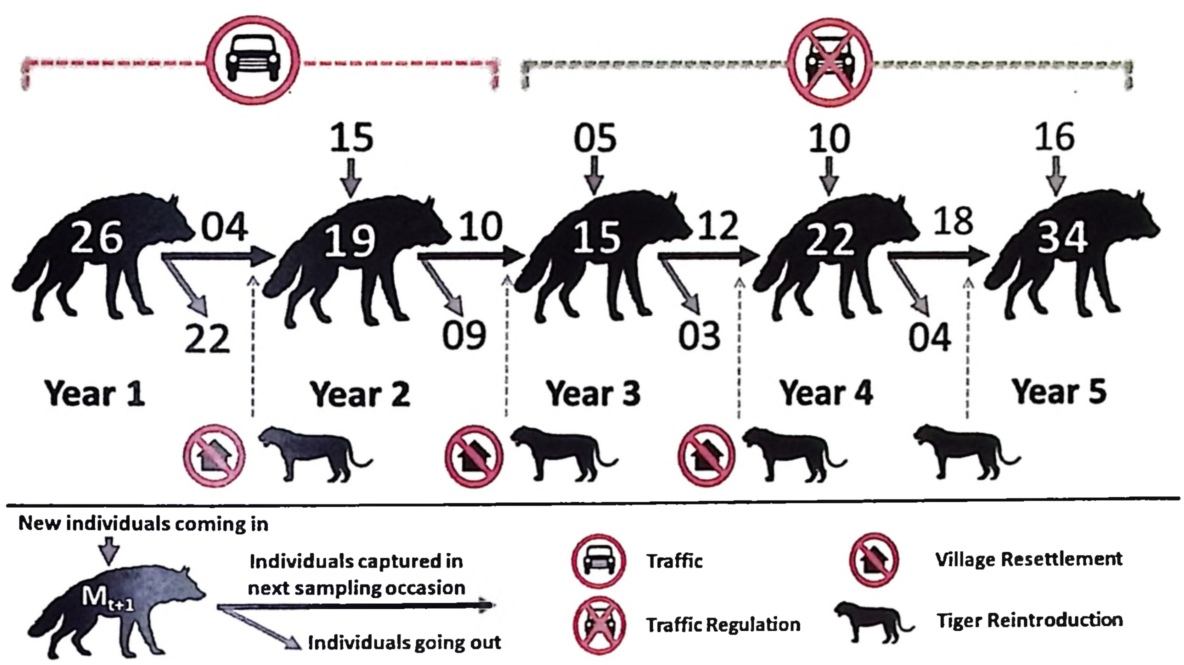



**Figure 3.1. Schematic representation of individual captures ($M_{t+1}$), emigration, immigration from the population with reference to traffic regulation, tiger reintroduction and village relocation**

### *3.3.1. Estimation of population size and density of striped hyena*

Since the population estimation was done separately over the years, it was found to be geographically and demographically closed for each year. The population remained roughly comparable over nine years. Density estimates of striped hyena slightly increased from 12.52±2.17 (SE) individuals/ 100 km$^2$ to 15.44±2.48 (SE) individuals/ 100 km$^2$ over the years (**Table 3.1.**).

**Table 3.1. Population density (D) estimates of striped hyena (/ 100 km$^2$), spatial movement parameter (σ), and detection probability at the activity centre (g0)**

| Year | Best Model | Sigma (σ) in meters (SE) and group 1 probability ($p_1$) (SE) | g0 (SE) | Density [striped hyenas / 100 km$^2$ (SE)] |
|---|---|---|---|---|
| 2007 - 08 | D (Year), g0 (h2), σ (h2) | $\sigma_1$ = 885.11 (35.10) | 0.101 (0.01)<br>0.016 (0.001) | 12.52 (2.17) |
| 2011 - 12 | | $\sigma_2$ = 2319.40 (194.45) | | 13.19 (1.67) |
| 2012 - 13 | | $p_1$ = 0.54 (0.07) | | 13.90 (1.43) |
| 2013 - 14 | | | | 14.65 (1.72) |
| 2014 - 15 | | | | 15.44 (2.48) |

### *3.2.2. Estimation of survival rates of striped hyena*

The findings suggest that traffic regulation had a significant effect on striped hyena demography. Model { Ŝ (Traffic Regulation), γ" (.), γ' (.), p (t)} (Emigration and immigration were constant over the years, whereas survival rate was modelled to vary pre and post traffic regulation and probability of capture was variable over the years) was the selected model with lowest AICc value (AICc = 1061.88, δ AICc = 0) which was used for striped hyena survival rate estimation in the study area (**Table 3.2.**). Three other models had similar AICc value (δAICc < 4). However, the closest models (Model 2 and 4) examining the effect of tiger reintroduction were not taken into consideration. Although these two models had similar AICc value, the survival rate (Ŝ) increased over the years, and emigration rate (γ") decreased contrary to my hypothesis. Model 3 had similar immigration rates with no significant difference and thus it was not considered.

**Table 3.2. Model selection statistics for 'Robust Design' analysis of striped hyena capture data**

| Model | AICc | Delta AICc | AICc Weights | Model Likelihood | Num. Par | Deviance |
|---|---|---|---|---|---|---|
| 1. Ŝ (Tra_Reg), γ" (.), γ' (.), p (Year) | 1061.88 | 0 | 0.43 | 1 | 9 | 1208.82 |
| 2. Ŝ (Tig_Intro), γ" (Tig_Intro), γ' (.), p (Year) | 1062.44 | 0.56 | 0.33 | 0.76 | 11 | 1205.10 |
| 3. Ŝ (Tra_Reg), γ" (Tra_Reg), γ' (.), p (Year) | 1063.94 | 2.06 | 0.15 | 0.36 | 10 | 1208.75 |
| 4. Ŝ (Tig_Intro), γ" (.), γ' (.), p (Year) | 1064.95 | 3.07 | 0.09 | 0.22 | 11 | 1207.62 |
| 5. Ŝ (Tra_Reg), γ" (.), γ' (.), p (.) | 1087.57 | 25.69 | 0 | 0 | 5 | 1242.89 |
| 6. Ŝ (Tig_Intro), γ" (.), γ' (.), p (.) | 1092.46 | 30.58 | 0 | 0 | 6 | 1245.70 |
| 7. Ŝ (Tig_Intro), γ" (Tig_Intro), γ' (.), p (.) | 1093.66 | 31.78 | 0 | 0 | 9 | 1240.60 |
| 8. Ŝ (.), γ" (.), γ' (.), p (Year) | 1098.06 | 36.18 | 0 | 0 | 7 | 1249.21 |
| 9. Ŝ (.), γ" (.), γ' (Vil_Reloc), p (Year) | 1104.56 | 42.68 | 0 | 0 | 7 | 1255.71 |
| 10. Ŝ (Tra_Reg), γ" (Tra_Reg), γ' (.), p (.) | 1109.50 | 47.62 | 0 | 0 | 6 | 1262.75 |
| 11. Ŝ (.), γ" (.), γ' (.), p (.) | 1126.75 | 64.88 | 0 | 0 | 2 | 1288.22 |
| 12. Ŝ (.), γ" (.), γ' (Vil_Reloc), p (.) | 1134.93 | 73.05 | 0 | 0 | 3 | 1294.36 |

The estimated survival rate ($\hat{S}$) of striped hyena pre-traffic regulation was 0.67 ± 0.06 (SE), while it was 0.99±0.01 (SE) after the imposition of traffic regulation (**Table 3.3.**). The probability of temporary emigration (γ") of one individual from the sample between sampling occasions was estimated to be 0.11±0.06 (SE), and the probability of remaining in the sample (1-γ") between sampling occasions was 0.89. The probability of remaining outside the sample (γ') (not emigration) was estimated to be 0.28±0.41 (SE), and the probability of an individual which was out of the sample (1−γ') in one sampling period but enters the sample in the next sampling period (i.e., return rate of temporary emigrants) was 0.62. The probability of captures was lowest during the first sampling year which increased over the sampling period from 0.28 in 2007 – 08 to 0.63 in 2014 – 15.

**Table 3.3. Survival rate, emigration, immigration and capture probability estimates of striped hyena in the study area**

| Parameter | Estimate | SE | 95% CI LCL | 95% CI UCL |
|---|---|---|---|---|
| $\hat{S}$ (Pre Traffic Regulation) | 0.67 | 0.06 | 0.54 | 0.77 |
| $\hat{S}$ (Post Traffic Regulation) | 0.99 | 0.01 | 0.94 | 1.00 |
| γ" | 0.11 | 0.06 | 0.04 | 0.27 |
| γ' | 0.28 | 0.41 | 0.01 | 0.95 |
| p-hat (2007 - 08) | 0.28 | 0.04 | 0.22 | 0.36 |
| p-hat (2011 - 12) | 0.42 | 0.05 | 0.32 | 0.53 |
| p-hat (2012 - 13) | 0.49 | 0.06 | 0.38 | 0.60 |
| p-hat (2013 - 14) | 0.49 | 0.04 | 0.41 | 0.57 |
| p-hat (2014 - 15) | 0.63 | 0.05 | 0.54 | 0.72 |

### *3.3.3. Mean Rate of Population Change ($\lambda_t$)*

Overall, the mean rate of population change before and after the traffic regulation was estimated as $\lambda_t$ (Before) = 0.977±0.015 (SE), and $\lambda_t$ (After) = 1.008±0.003 (SE) respectively, representing an approximate change of -2.3% and 0.8% in the population during the study period.

### *3.3.4. Population projection model*

Although the estimated extinction probability was low (only 9%) for the next 100 years, the projection showed a steady decline in striped hyena population given traffic regulation was not implemented (**Figure 3.3.**).

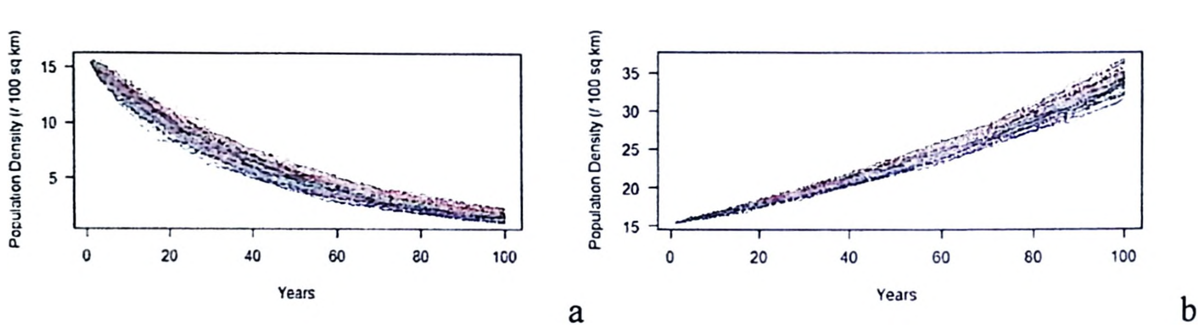



**Figure 3.3. Count based population viability analysis for striped hyena population in Sariska Tiger Reserve(a) if traffic regulation was not implement using $\lambda_t$ (Before) = 0.977±0.015 (SE) and, (b) traffic regulation implementation using $\lambda_t$ (After) = 1.008±0.003 (SE)**

### 3.4. Discussion

The findings of the current study highlight the influence of linear infrastructure on carnivore demography and suggest that traffic regulation had a positive effect on striped hyena survival rate in the study area. Striped hyena survival rate and population growth rate increased post-traffic regulation in STR. The population of striped hyena would have been severely affected if the traffic regulation was not implemented. Although the effect of roads has been studied in many taxa, the literature on population-level effect is still limited (Fahrig and Rytwinski 2009).

### *3.4.1. Inter-specific Interaction*

Although interspecific competition is widely recognised to affect large carnivore demography (Watts and Holekamp 2008), there was no evidence found with the reference to tiger reintroduction and subsequent change in leopard population to influence striped hyena population parameters. Contrary to the proposed hypothesis, the striped hyena survival rate increased, and emigration decreased over the years. Although leopard density declined from 7.6±0.6 (SE) to 3.1±0.4 (SE) over three years following the tiger reintroduction (Mondal et al. 2012), striped hyena density remained comparable throughout the study period (**Figure 3.4.**). A similar decline in leopard density (9·76±3·5 SE in 2004–2005 to 2·07±1·63 SE in 2007–2008) following tiger population recovery (3·31±1·51 SE in 2004–2005 to 5·81±2·26 SE in 2007–2008) was observed in Rajaji National Park. Diet of leopard in Rajaji also shifted towards higher intake of livestock and small prey. However, the area experiences considerable inter-annual variation in ungulate densities, thereby increasing competition towards leopards (Harihar et al. 2011). Low availability of prey and a consequent decrease in foraging efficiency of tigers, leading to intense competition towards leopards have also been observed in Bardia National Park, Nepal (Odden, Wegge and Fredriksen 2010). Similar observations were reported from Thailand where tigers displaced leopards and dholes to marginal habitats where prey was scarcer (Steinmetz et al. 2013). However, our long-term data suggests that

STR sustains an excellent density of wild ungulate (103.39±21.64 SE in 2008, Mondal et al. 2012; 55.2±13.7 SE in 2015) and livestock (90.61±27.7 SE in 2008, Mondal et al. 2012; 66.84±11.15 SE in 2015) without inter-annual variation in densities. During the present study only three hyena mortalities by co-predators such as tiger (n=2) and leopard (n=1) were recorded over nine years. Camera trap photographs revealed that the striped hyenas scavenged 50% of the tiger kills (n=14), and no subsequent killing has been observed during the study. In two events, leopard and striped hyena were photographed feeding together on a carcass (Mandal et al. 2018), indicating a likely relaxed competition among the carnivore guild. Thirteen individual hyena remained in the population from second sampling period onwards, indicating that they were no spatial exclusion of striped hyenas by other predators. Although leopard population initially declined and their diet shifted towards smaller prey, the population bounced back during 2012 – 13 probably due to compensatory immigration from peripheral areas (Sankar unpublished). It is arguable that decline in leopard population may have favoured immigration of striped hyenas in the study area from the periphery. However, emigration rate did not increase when leopard population bounced back during 2012 – 13 in the study area and density remained comparable (**Figure 3.4.**).

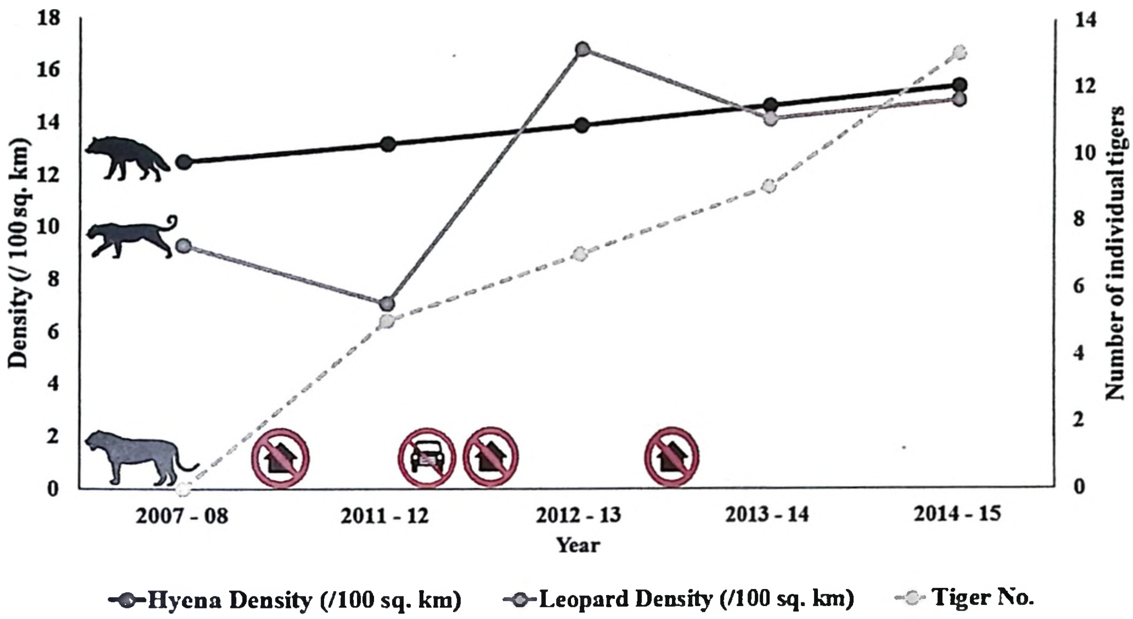



**Figure 3.4. Population trend of striped hyena (density estimates/ 100 km$^2$), leopard (density estimates/ 100 km$^2$) and tiger (total number of individuals in the reserve) in Sariska Tiger Reserve with reference to traffic regulation and village relocation**

### *3.4.2. Closed Population Hypothesis*

Human-induced deaths in high-quality habitats may create an attractive sink, leading to masking of population decline in the sink and surrounding source areas (Robinson et al. 2008). High rates of emigration can depress population growth, and high rates of immigration can increase population growth regardless of birth and death rates in the open population. Low hunting mortality of cougars (0.11) did not result in increased densities (Cooley et al. 2009), and high hunting mortality did not result in decreased densities (Robinson et al. 2008) due to compensatory emigration and immigration responses in smaller game units of USA. While I did not observe a decline in densities of striped hyenas, I did record significant change in the growth rate of the population in the study area which may be due to the isolation of the reserve. Compensatory immigration from surrounding areas failed to mask population growth rate before traffic regulation. My findings is substantiated by the fact that tiger (Sankar et al. 2010), caracal and wild dog (Sankar 1994) have gone locally extinct from Sariska due to its isolation.

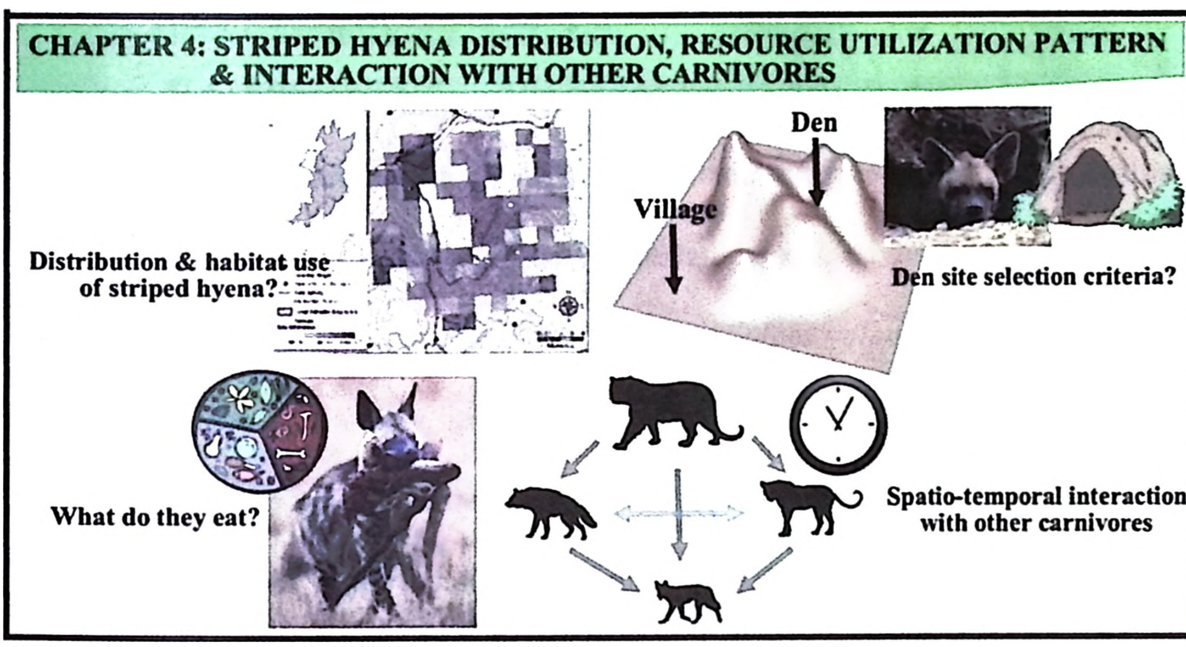
### *3.4.3. Adverse impact of roads*

The adverse impact of roads has been reported from a wide variety of large terrestrial mammals (Noss et al. 1996). Seventeen percent of the analysed global terrestrial mammal species were at risk from roads. Approximately one-third of the species most affected by road have not been identified by IUCN as threatened (Ceia-Hasse et al. 2017). Twenty one percent of the 117 endangered terrestrial mammals in South East Asia were threatened by planned roads (Clements et al. 2014). Carnivores are rare and elusive and occur at low densities with low reproductive success. Small changes in the reproductive success and survivorship can have severe implications for isolated carnivore populations (Knight and Ederhardt 1985). As hypothesised, findings of the present study suggest traffic regulation had a significant positive effect on the striped hyena survival rate (Pre $\hat{S}$=0.66, and Post $\hat{S}$=0.98) as well as population growth rate [$\lambda_t$ (Before) = 0.977±0.015 (SE), and $\lambda_t$ (After) = 1.008±0.003 (SE)]. Six striped hyena road mortalities were recorded during in STR 2008 to 2011. Since striped hyenas form den centric breeding clans in the Indian semi-arid system, death of helpers can have serious implications for the survival of pups (Jhala 2013, Alam 2011). I showed using a robust population projection model that striped hyena population would have been affected during the next 100 years if the traffic regulation was not implemented. Similar population recovery following conservation action was reported from Australia. The populations of eastern quolls became extinct and Tasmanian devil population halved in Saint Clair National Park, Australia following road upgradation in 1991. Measures were implemented to mitigate road related accidents. Both the population recovered within two years (Jones 2000).

### *3.4.4. Implications for Management and Conservation*

While there has been a lack of studies on the effect of roads on a population level, especially form South Asia, the findings of the present study employing robust methods using long-term data suggest that road-related mortality can have severe impact on carnivore populations in isolated habitats. Most of the protected areas in densely populated South Asia are smaller, fragmented and human-modified (Clark et al. 2013) and are often dissected by roads or linear infrastructure. Wild animal deaths due to vehicular collision are common. For example, In India where the road density is 1.43 km/ $km^2$ (GOI), and the average size of protected areas are approximately 300 $km^2$ (Rodgers et al. 2003), 23 leopards were killed within 60 months in the southern state of Karnataka alone (Gubbi et al. 2014). Ten tigers were also killed in accidents in last five years in India. The intensity of road kills has prompted Non-Governmental Organizations in India to launch citizen science-based apps that records road kills. However, most of the studies aiming to understand the impact of roads are either confined to recording species that are impacted by roads or mapping hotspots of wildlife vehicular collision areas to provide mitigation measures (Sultan 2017). Although these studies provide a first-hand snapshot of road-related mortalities, however, it lacks a comprehensive analysis of a more substantial population-level impact that it may have. The present study bridges this gap and provides globally appropriate conservation solutions for carnivorous species with similar life history traits such as longevity, birth rates and growth rates affected by roads in India and elsewhere.

# CHAPTER IV RESOURCE UTILIZATION PATTERN



# CHAPTER 4 RESOURCE UTILIZATION PATTERN

## 4.1. Introduction

Ecologists have long debated whether top-down or bottom-up control is the more important determinant of a species distribution and abundance (Hunter and Price 1992). Top-down control refers to the effect of top predators in regulating prey population and it generally operates through species interactions, whereas bottom-up control occurs when individuals and populations are limited by their own available resources rather than predation (Hunter and Price 1992). Bottom-up and top-down effects usually operate simultaneously. Earlier studies have shown sharp decline in apex predator (wolf *Canis lupus* and Eurasian lynx *Lynx lynx*) did not result in increase of smaller predators such as red foxes (*Vulpes vulpes*, a mesopredator) due to low resource availability, indicating that foxes are strongly driven by bottom-up control (e.g., abundance of hare *Lupus timidus*) (Elmhagen and Rushton 2007). Tiger *Panthera tigris* displaced leopard *Panthera pardus* and dhole *Cuon alpinus* spatially from areas where ungulate prey was most common to marginal habitats where prey was scarcer (Steinmetz et al. 2013). These processes have been studied in herbivores and a few large carnivores primarily charismatic felids (St-Pierre et al. 2006, Thompson and Gese 2007, Harihar et al. 2011, Steinmetz et al. 2013) but less so in the hyenids that inhabit tropical forests, and are sympatric with tiger and leopard.

In this study, I tried to understand resource utilization pattern (diet, den site selection, and habitat use) of striped hyena (bottom-up effects) and predation risk from large predators such as tiger and leopard (top-down effects) on the spatial distribution and activity patterns of striped hyena.

## 4.2. Methods

### *4.2.1. Food Habits*

Diet of striped hyena was studied using scat analysis (Wagner 2006, Chourasia et al. 2012). Hyena scats (n=303) were collected on animal trails and roads (n=44) by systematic search resulting in an effort of 227.25 km during winter and summer season from 2013 to 2015 in the entire study area. Hyena scats were identified by the patterns of shape, size and colour, mostly oval to cylindrical-shaped with white or off-white colouration (Bopanna 2013). Each collected scat sample was labelled with date and location (Area, Beat, Range and GPS coordinates). Collected scats were sun-dried and later broken down and washed under running water through a sieve of 1 mm. The scat contents were then teased apart and remain of different food items such as hair, feather, and scales of reptiles, hoof, and vegetative matters (grass and fruit seeds) were separated (Mukherjee et al. 1994). Scat contents were then studied under a microscope, identified and recorded following standard methods (Mukherjee et al. 1994). Percent frequency of occurrence (%FO) and relative frequency of occurrence (RFO) was calculated for each food item to understand how often striped hyena feeds on a certain food item and relative importance of the food item in their diet (Loveridge and Macdonald 2003). %FO is defined as the number of times a particular prey item occurred in the scat in terms of percentage of prey remains. RFO is defined as the number of times a prey item was encountered in a sample of scats expressed as a percentage of total occurrence of all food items. Niche breadth of the species was estimated using Shannon-Winner Index (H) (Krebs 1999). Following the scat analysis, I randomised the original order of scat samples, and the adequacy of scat samples to assess species richness was assessed using rarefaction and extrapolation curve (Chao et al. 2014).

I also visited hyena den sites (n=27) regularly to record the predated prey items weekly every season. Striped hyenas are known to bring back food to their den sites (Kruuk 1976, Ilani 1975). I considered predation in case we found fresh and intact prey species with canine bite marks of striped hyena.

### *4.2.2. Breeding Den site selection*

A systematic walking search was conducted in the study area with two/ three observers to locate striped hyena breeding dens (resting dens were excluded). Approximately 90 man days covering 260 km were spent searching for striped hyena breeding dens over 2 months in 2014 in an area of approximately 700 $km^2$. I also opportunistically enquired shepherds about locations of dens. Dens were identified using a combination of signs such as bone depositions, pup tracks, scats and direct sightings. Breeding dens which were active or have been used during the last one year was considered for analysis.

A used (den locations) and available (random locations within 500 m of the den site) design was used to construct resource selection function (Manly et al. 2007). In total, 27 breeding dens were identified in the study area. A circular buffer of 500 m radius was generated around the identified den site and random locations were generated using ArcGIS v 9.3. Breeding den site and a random point within 500 m radius was then surveyed and data on eco-geographic variables were collected on a circular plot of 15 m. At the den site and random location, data on den substrate, major vegetation type, terrain, aspect, canopy cover, tree density, shrub density and human disturbance (cutting and lopping) was collected. Data on ruggedness, distance to village and water was collected using ArcGIS v 9.2.

In total, 27 natal dens and 27 random points has been identified and surveyed across the study area. Binomial Generalized Linear Model (GLM) was used to understand den site selection by striped hyenas in the study area. I also used the above mentioned linear equation to map den site suitability of striped hyena in the study area using ArcGIS v 9.3. Jenks natural breaks was used to categories suitable areas for denning (i.e. High, Medium and Low).

Visibility of the den at each den site was also measured at two, five and ten meter distances at six cardinal directions to understand how striped hyenas use cover and terrain to guard themselves from guard dogs, humans and predators using package reshape2 (Wickham 2007) and gg plot2 (Wickham 2009) in R v 3.1.3. I used linear regression to understand the effect of distance on visibility and sin curve to understand effect of directions on visibility. Finally I mapped average visibility around the den at six cardinal directions.

***4.2.3. Striped hyena distribution and spatio-temporal interaction with co-predators***

*Field methods and study design*

Striped hyena site utilization pattern ($\psi$) and spatio-temporal interaction of the species with other carnivores were studied through photographic evidences obtained from camera trapping. A total of 114 camera traps were deployed in two blocks during February to April 2014 in 2 $km^2$ grid cells covering an area of 217.21 $km^2$ resulting in 2896 trap nights. Binary matrices of camera trap locations against photocaptures were prepared for striped hyena and other carnivores from camera trap data using package camtrap R (Niedballa 2016) in R v 3.1.

***Distribution of striped hyena in the study area***

Level-I resource utilization pattern of striped hyena was studied using occupancy based analysis with covariates (Mackenzie *et al.* 2005) using the program PRESENCE 6.4 (Hines 2006). Based on prior knowledge, ruggedness, distance to water resources and villages were considered as co-variates likely to influence striped hyena occupancy in the study area (Singh et al. 2010, Bopanna 2013, Singh et al. 2014).

***Spatial interaction of striped hyena with other carnivores***

This matrix was then analyzed for presence/absence site utilization in program PRESENCE 6.4 (Hines 2006) following single session two species conditional occupancy ($\psi$) model (Richmond et al. 2012). This parametrization is stable when covariates are included. Also, this parameterization assumes that Species A is the dominant species, and Species B the subordinate species. The detection probabilities (*p*) of striped hyena and other carnivores in the study area in the presence or absence of either species were analyzed using the program PRESENCE 6.4 (Hines 2006).

The parametrization for this 2-species conditional occupancy model (Richmond et al. 2010) follows.

$\psi^{A}$ = Probability of occupancy for species A

$\psi^{BA}$ = Probability of occupancy for species B, given species A is present

$\psi^{Ba}$ = Probability of occupancy for species B, given species A is absent

$p^A$ = Probability of detection for species A, given species B is absent

$p^B$ = Probability of detection for species B, given species A is absent

$r^A$ = Probability of detection for species A, given both species are present

$r^{BA}$ = Probability of detection for species B, given both species are present and species A is detected

$r^{Ba}$ = Probability of detection for species B, given both species are present and species A is not detected

*Species Interaction Factor (SIF)*

For the conditional occupancy model, SIF = $(\psi^A\ \psi^{BA})\ /\ (\psi^A\ (\psi^{A}*\psi^{BA} + (1 - \psi^A)\ \psi^{Ba})$.

If the two species occur independently, then the SIF is equal to one. An SIF less than one indicates that species B is less likely to co-occur with species A than expected under a hypothesis of independence (i.e., avoidance), whereas values greater than one indicate that species B is more likely to co-occur with species A than expected under a hypothesis of independence (i.e., aggregation).

***Temporal interaction of striped hyena with other carnivores***

Temporal activity pattern of striped hyena and other carnivores was studied through photographic time evidences obtained from camera traps. Time evidences obtained from camera traps of striped hyena, other carnivores, human, livestock and dog was then recorded systematically and was analysed using circular statistics (Andersen et al. 2000) in program Oriana and package camtrapR (Niedballa et al. 2016).

## 4.3. Results

### 4.3.1. Food Habits

Altogether, 303 scat samples of striped hyena were collected and analysed. The proportion of different prey species in scats got stabilised once a sample of 150 scats was analysed. In total 25 food items have been identified in the striped hyena scat samples, wherein remains of large mammals dominated the most. Wild ungulates (Sambar, Chital, Nilgai and Wild Pig) and domestic livestock (Buffalo, Cattle and Goat) together contributed the most (~56%) in striped hyenas diet. Rodents, birds, reptiles, hare and small carnivores contributed 21.45% of striped hyena diet that is unlikely to be scavenged. Vegetative matter consisting primarily of grass and *Zizyphus* sp seeds contributed 17.95% to the diet of striped hyena. Relative frequency of occurrence and percent frequency of occurrence of each food item found in striped hyena scats are given in **Table 4.1.** The overall diversity of food items in striped hyena diet was 2.22 (H).


**Figure 4.1. Camera trap photograph showing (a) active predation of spotted deer fawn by striped hyena, and (b) striped hyena scavenging on a livestock kill of a tiger**

**Table 4.1. Percent frequency of occurrence and Relative Frequency of Occurrence (RFO) of food items in striped hyena diet from scat analysis (n=303)**

| Broad Prey Category | Prey Item | RFO | % Occurrence |
|---|---|---|---|
| **Domestic Livestock** | | **10.72** | **15.18** |
| | Buffalo (*Bubalus bubalis*) | 1.17 | 1.65 |
| | Cattle (*Bos tourus*) | 6.29 | 8.91 |
| | Goat (*Capra aegagrus hircus*) | 3.26 | 4.62 |
| **Ungulate** | | **45.22** | **64.03** |
| | Chital (*Axis axis*) | 17.25 | 24.42 |
| | Nilgai (*Boselaphus tragocamelus*) | 1.17 | 1.65 |
| | Sambar (*Rusa unicolor)* | 26.34 | 37.29 |
| | Wild Pig (*Sus scrofa*) | 0.47 | 0.66 |
| **Rodent** | | **11.89** | **16.83** |
| | Indian Bushrat (*Golunda ellioti*) | 0.23 | 0.33 |
| | House Rat (*Rattus rattus*) | 0.47 | 0.66 |
| | Indian Gerbil (*Tatera indica*) | 0.23 | 0.33 |
| | Rat (Unidentified) | 10.96 | 15.51 |
| **Primates** | | **3.96** | **5.61** |
| | Common Langur (*Seminopithecus entellus)* | 3.73 | 5.28 |
| | Rhesus macaque (*Macaca mulatta*) | 0.23 | 0.33 |
| **Birds** | | **7.69** | **10.89** |
| | Cattle Eagret (*Bubulcus ibis*) | 0.23 | 0.33 |
| | Peafowl (*Pavo cristatus*) | 6.76 | 9.57 |
| | Parakeet (*Psittacula sp.*) | 0.23 | 0.33 |
| | Grey Frankolin (*Francolinus pondicerianus*) | 0.23 | 0.33 |
| | Rufous Treepie (*Dendrocitta vagabunda*) | 0.23 | 0.33 |
| **Rufous tailed hare (*Lepus nigricollis ruficaudatus*)** | | **1.40** | **1.98** |
| **Domestic Cat (*Felis catus*)** | | **0.23** | **0.33** |
| **Reptiles** | | **0.23** | **0.33** |
| **Insects** | | **0.70** | **0.99** |
| **Vegetative Matter** | | **17.95** | **25.41** |

Striped hyenas were observed to predate on wild ungulate fawns/calves (48.72%), reptiles (5.13%), ground-dwelling birds such as peafowl and grey francolin (28.21%), small carnivores (7.69), primates (Rhesus macaques juvenile, 5.13%), rufous-tailed hare (2.56%) and livestock (Goat, 2.56%). We recorded fawn/calf (sambar, chital and nilgai, n=18) predation during the onset of winter during November and December when fawns/calves are less than six months old (**Figure 4.1. (a) & 4.2.**).

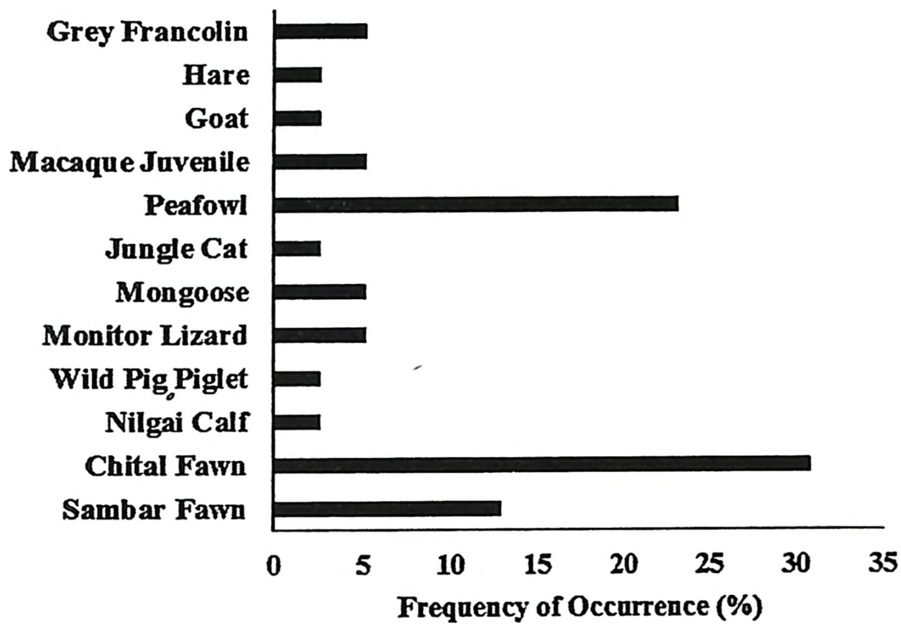



**Figure 4.2. Percentage of different food items in the kills (n=39) of striped hyena**

### 4.3.2. Breeding Den site selection

Among the 27 identified hyena dens, 10 dens are active dens, and 17 dens are recently abandoned (within last six months) dens. Most of the dens were either south (25%) or South-East (20.83%) or South-West (16.67%) facing (**Figure 4.4.**). Striped hyenas selected *Anogeissus* dominant forest or *Boswellia* dominant forest, probably because *Anogeissus* occurs on the slopes and *Boswellia* occurs on the hill top (**Figure 4.3.**). They choose ravine followed by undulating or hilly terrain as den sites, and mines or rocky outcrop as substrate (**Figure 4.4.**). No breeding den was found in flat terrain.

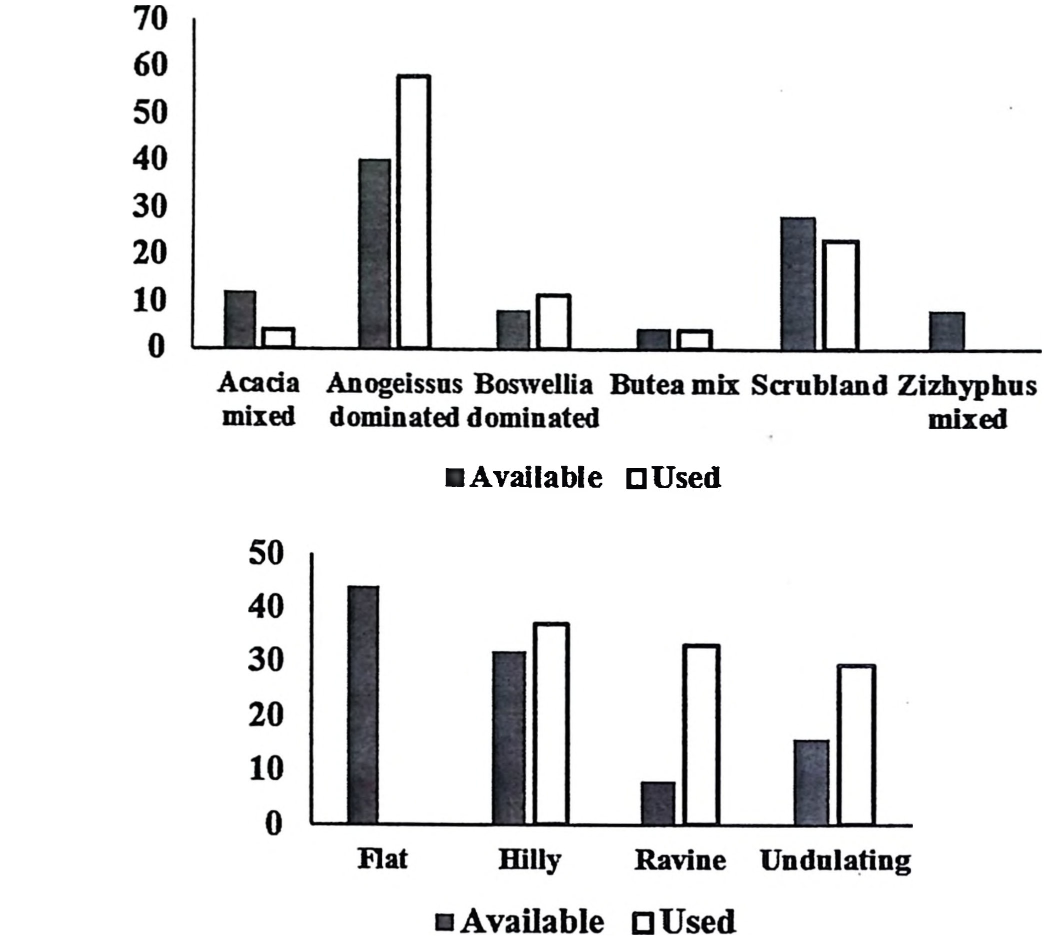



**Figure 4.3. Proportion of breeding dens found in different (a) vegetation, and (b) terrain type, as compared to proportion of the same available at random points**

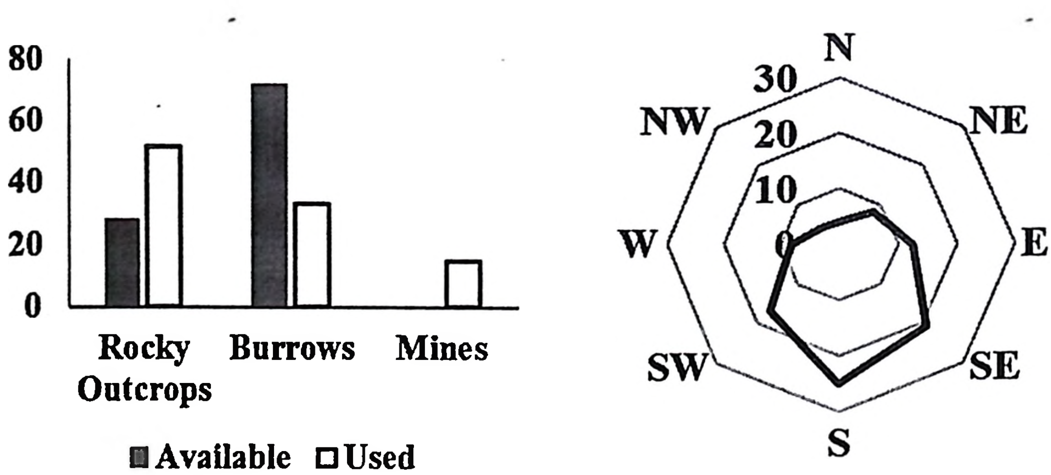



**Figure 4.4. (a) Proportion of breeding dens found on different substrate as compared to proportion of the same available at random points, and (b) aspects of breeding dens**

Average number of breeding den openings were 1.42±0.12 (SE) m. Average length and width of the dens were 0.48±0.06 (SE) m and 0.41±0.05 (SE) m respectively.

Striped hyena breeding den site selection was significantly influenced by shrub density, and distance to waterholes ($P < 0.05$) at the den site scale. Average distance of striped hyena natal dens from nearest villages and waterholes were 2144.83±236.89 (SE) and 535.87±105.09 (SE) respectively.

**Table 4.2. Results of binomial generalised linear model indicating den site selection criteria of striped hyenas**

| | Estimate | Std. Error | Z value | Pr(>\|z\|) | |
|---|---|---|---|---|---|
| (Intercept) | -1.56E+01 | 7.56E+00 | -2.058 | 0.0396 | * |
| Canopy Cover | 2.96E-02 | 3.27E-02 | 0.903 | 0.3664 | |
| Shrub Density | 3.37E-02 | 1.69E-02 | 1.999 | 0.0456 | * |
| Distance to Village | 8.11E-04 | 5.61E-04 | 1.446 | 0.1483 | |
| Distance to Water | 8.68E-03 | 4.98E-03 | 1.741 | 0.0816 | . |
| Human Disturbance | -1.79E+00 | 2.09E+01 | -0.086 | 0.9317 | |
| Ruggedness | -3.56E-02 | 6.99E-02 | -0.51 | 0.6101 | |

Striped hyena den site suitability was mapped using the above mentioned linear equation (Binomial GLM) which was showing patchy availability of suitable sites (**Figure 4.5.**).

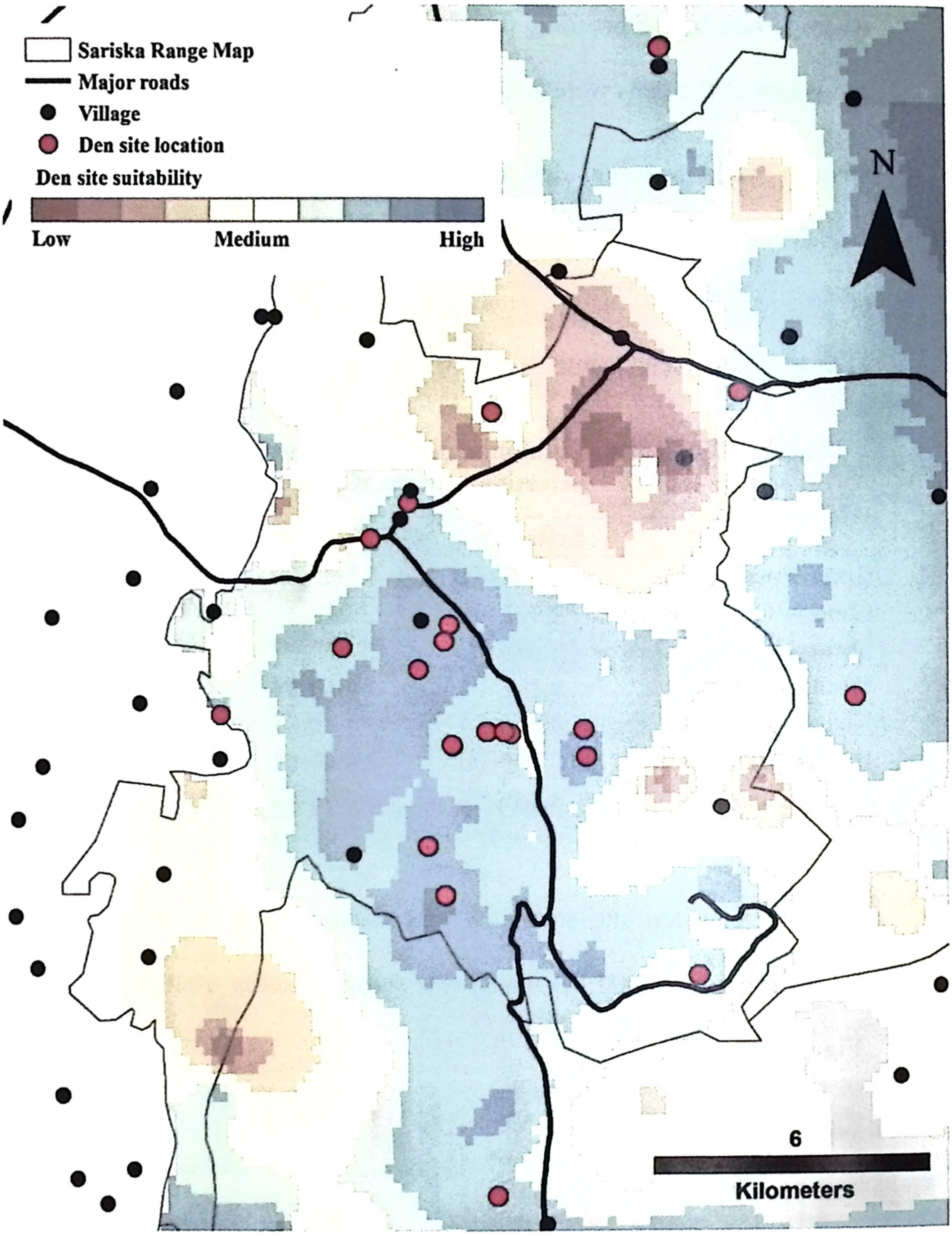



**Figure 4.5. Breeding den site suitability map of striped hyena**

The present study revealed that visibility of the den decreases with increase in distance from the den (Adjusted $R^2$=0.35). Visibility was observed to be higher at the front of the dens (**Figure 4.6.**), thereby probably providing cover from other predators and humans at the back.

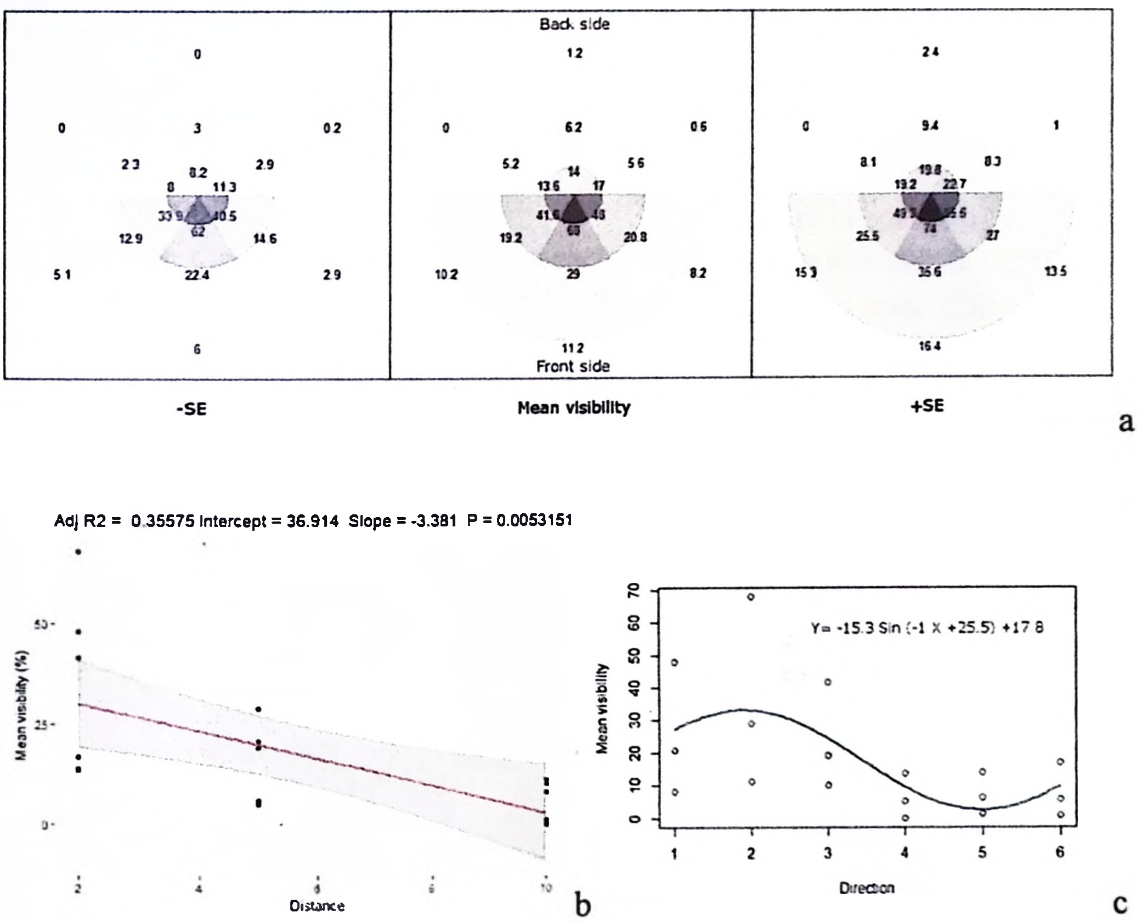



**Figure 4.6. (a) Visibility around the breeding den sites, (b) relation of visibility with distance, and (c) relation of visibility with direction**

*4.3.3. Distribution of striped hyena in the study area*

Striped hyena occupancy was influenced by terrain ruggedness in the study area. Distance to village and waterholes also influenced striped hyena occupancy positively in the study area. Striped hyena occupancy in the study area was 0.58 (0.42 – 0.72, 95% CI).

**Table 4.3. Model details of striped hyena site utilization pattern**

| Model | ΔAICc | $\omega_i$ | Model Likelihood | nPars |
|---|---|---|---|---|
| ψ (ruggedness), ρ(.) | 0 | 0.32 | 1 | 3 |
| ψ (distance to village), ρ(.) | 0.43 | 0.26 | 0.8 | 3 |
| ψ (distance to water), ρ(.) | 0.47 | 0.26 | 0.79 | 3 |
| ψ (distance to village + water), ρ(.) | 2.42 | 0.09 | 0.29 | 4 |
| ψ (distance to village + water + ruggedness), ρ(.) | 3.86 | 0.04 | 0.14 | 5 |

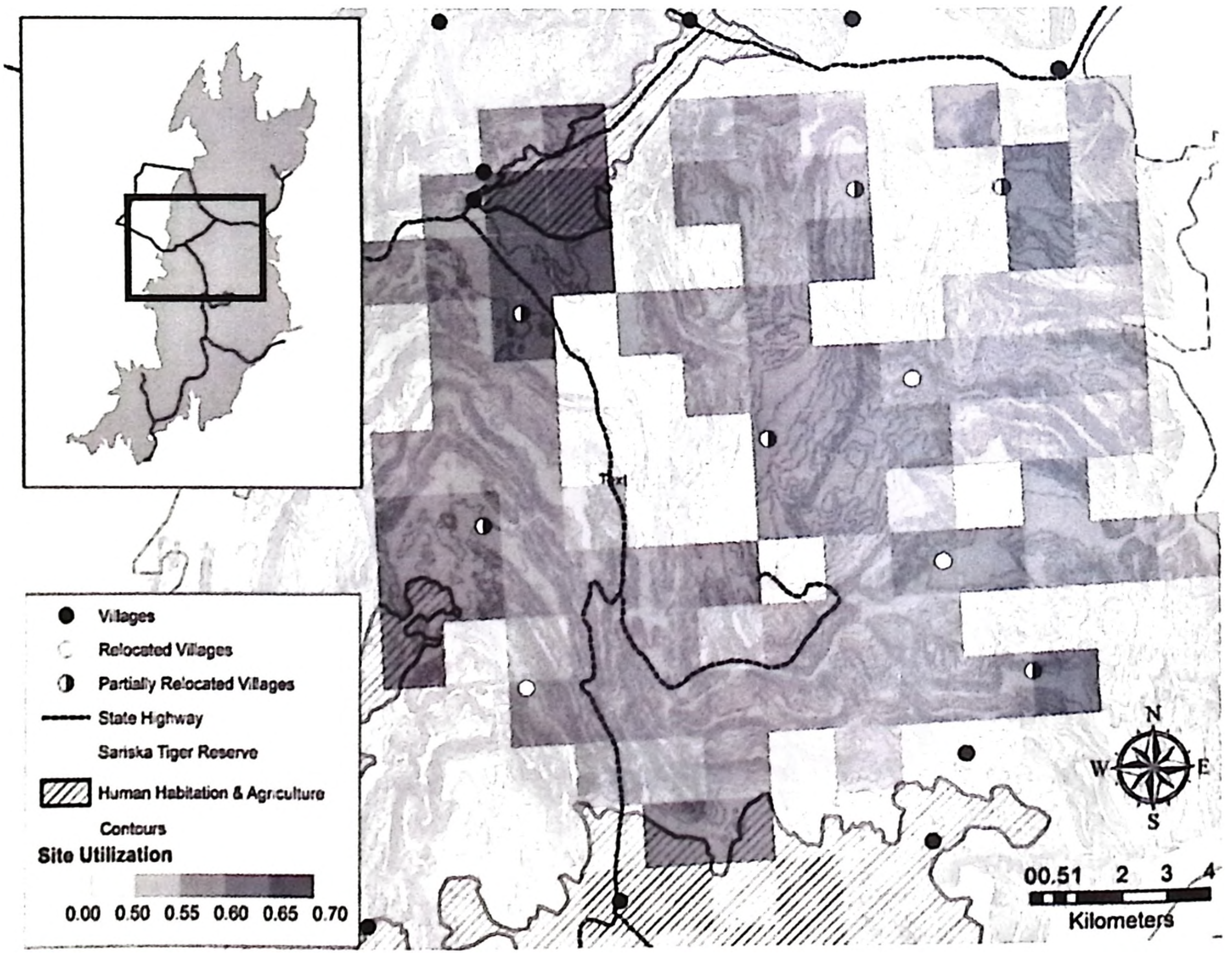



**Figure 4.7. Striped hyena site utilization map**

*Spatial interaction of striped hyena with other carnivores*

The probability of site utilization by striped hyena in presence of tiger and leopard were 0.53±0.09 and 0.83±0.09 respectively in the study area. Whereas, the probability of site utilization by striped hyena in absence of tiger and leopard were 0.37±0.79 and 1.00±0.00 respectively. Detection probability of striped hyena in the presence of tiger and leopard were higher than in the absence of the co-predators **(Table 4.4.)**.

The present study indicates than tiger and striped hyena occur independently (SIF=1.02).

**Table 4.4. Conditional occupancy estimates between tiger and leopard with striped hyena**

| Conditional Occupancy Parameters | Tiger (A) & Striped Hyena (B) | Leopard (A) & Striped Hyena (B) |
|---|---|---|
| $\psi^{A}$ | 0.93±0.11 | 0.55±0.08 |
| $\psi^{BA}$ | 0.53±0.09 | 0.83±0.09 |
| $\psi^{Ba}$ | 0.37±0.79 | - * |
| $p^{A}$ | 0.04±0.01 | 0.09±0.06 |
| $p^{B}$ | 0.08±0.08 | 0.05±0.01 |
| $r^{A}$ | 0.31±0.02 | 0.12±0.02 |
| $r^{BA}$ | 0.13±0.03 | 0.58±0.07 |
| $r^{Ba}$ | 0.08±0.01 | 0.28±0.03 |
| **Species Interaction Factor (SIF)** | **1.02** | - |

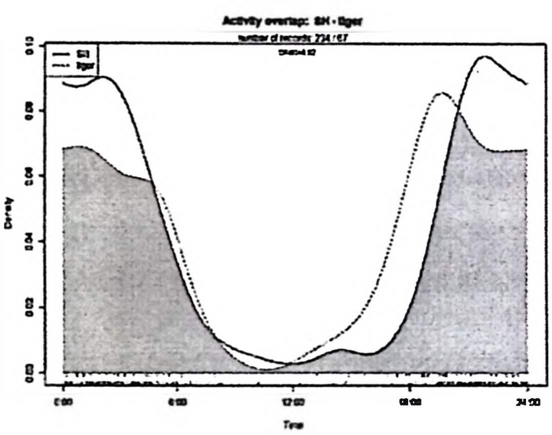
* Could not assess as striped hyena captures were very less in areas where leopards were not captured.

*Temporal interaction of striped hyena with other carnivores*

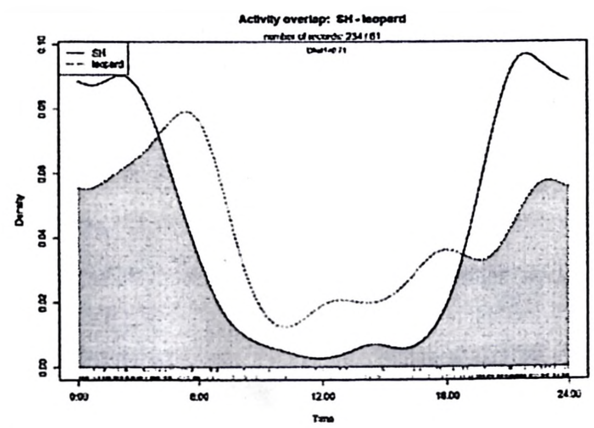
The major peak of striped hyena foraging activity was observed during midnight 23:45 to 12:36 h. Whereas, tiger's major activity peak was observed just before striped hyena's activity peak during 21.32 to 12:02 h. Leopard showed a broader span in major activity peak from midnight to early morning during 23:22 to 03:38 h. Jackal also showed broader temporal activity period during 20:20 to 01:17 h.

**Table 4.5. Circular statistics of temporal activity pattern of striped hyena, other carnivores, livestock, and humans**

| Variable | Number of Observations | Mean Peak Activity | Peak Activity Period (95% CI) | Watson's U² Value |
|---|---|---|---|---|
| **Striped Hyena** | 241 | 00:11 | (23:45 - 00:36) | 5.752 (< 0.005) |
| **Tiger** | 64 | 22:47 | (21:32 - 12:02) | 0.837 (< 0.005) |
| **Leopard** | 63 | 01:30 | (23:22 - 03:38) | 0.331 (< 0.005) |
| **Jackal** | 10 | 22:49 | (20:20 - 01:17) | 0.233 (< 0.025) |
| **Jungle Cat** | 14 | 22:10 | (20:14 - 00:07) | 0.419 (< 0.005) |
| **Human** | 1952 | 13:07 | (12:58 - 13:17) | 44.518 (< 0.005) |
| **Livestock** | 4060 | 12:48 | (12:40 - 12:56) | 66.049 (< 0.005) |
| **Dog** | 22 | 12:31 | (11:18 - 13:45) | 0.657 (< 0.005) |




a

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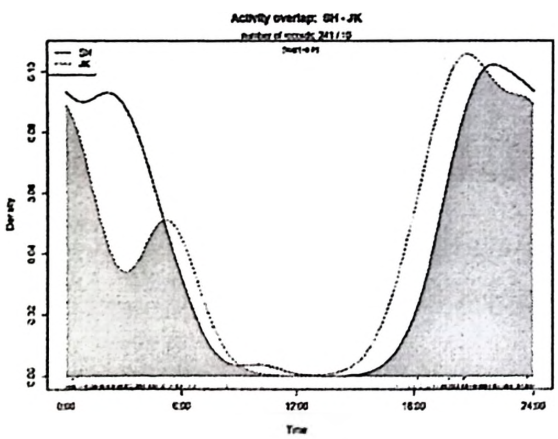


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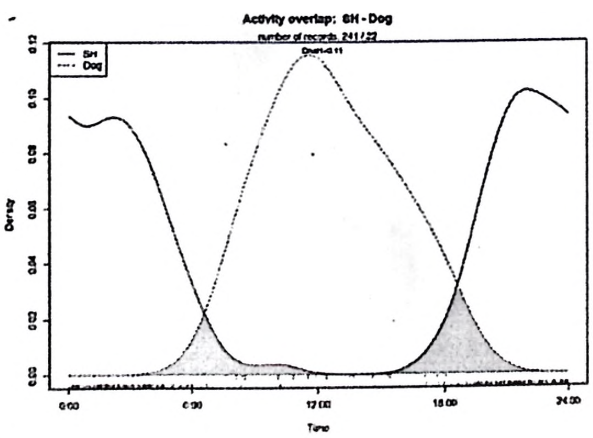


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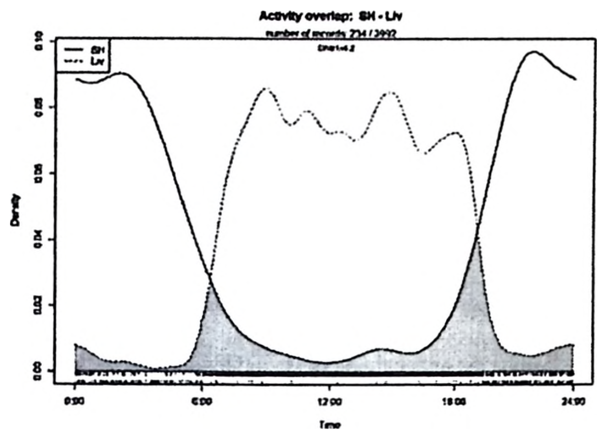


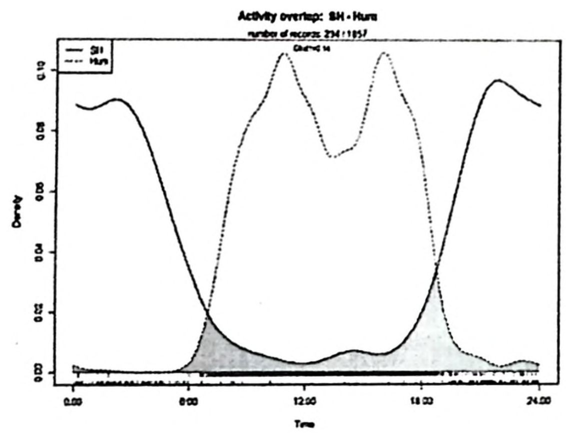


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**Figure 4.8. Kernel density graphs of temporal overlap between striped hyena and (a) tiger, (b) leopard, (c) jackal, (d) dog, (e) livestock, and (f) human**

Human, livestock and dog activity was observed to be confined during the day time. Striped hyena had significant overlap in temporal activity with all the three co-predators i.e. tiger, leopard and jackal **(Table 4.6.)**. Whereas, all the carnivores segregated themselves temporally with anthropogenic activities **(Table 4.6.)**.

**Table 4.6. Temporal use of striped hyena, other carnivores with respect to anthropogenic pressure**

| Results in matrix format | Striped Hyena | Tiger | Leopard | Dog | Jackal | Human | Livestock |
|---|---|---|---|---|---|---|---|
| Striped Hyena | ----- | < 0.002 | < 0.001 | < 0.001 | 0.5 > p > 0.2 | < 0.001 | < 0.001 |
| Tiger | 0.346 | ----- | < 0.05 | < 0.001 | > 0.5 | < 0.001 | < 0.001 |
| Leopard | 0.54 | 0.201 | ----- | < 0.001 | 0.5 > p > 0.2 | < 0.001 | < 0.001 |
| Dog | 1.63 | 1.147 | 0.872 | ----- | < 0.001 | 0.5 > p > 0.2 | 0.2 > p > 0.1 |
| Jackal | 0.076 | 0.059 | 0.114 | 0.578 | ----- | < 0.001 | < 0.001 |
| Jungle Cat | 0.224 | 0.187 | 0.245 | 0.594 | 0.112 | < 0.001 | < 0.001 |
| Human | 17.066 | 4.013 | 2.96 | 0.076 | 0.788 | ----- | < 0.001 |
| Livestock | 16.746 | 3.603 | 2.535 | 0.128 | 0.713 | 2.083 | ----- |

$U^2$ scores (lower half) and probabilities (upper half)

## 4.4. Discussions

The present study indicates that striped hyena, being scavengers primarily rely on large mammals (56%). They scavenge as well as actively hunt on small ground nesting birds and mammals. Although, they occur close to human habitation, they are very specific about breeding den site selection. They choose areas near waterholes with higher shrub density. Their site utilization as well as detection probability increases in areas frequented by other carnivores such as leopard and tiger. There was significant overlap among the large carnivore guild of STR. However, all the carnivores including striped hyenas temporally segregate themselves from humans and anthropogenic activities which may have allowed them to survive in the human dominated landscape.

***Diet***

The present study showed that striped hyenas maintain a catholic diet which is dominated by large mammals (~56%) in the semi-arid region of North-Western India. Inside PA's they rely more on wild ungulates (45.22%) as shown in the present study. However, their reliance on livestock was comparatively less (10.72%), although STR supports a high density of livestock (222 animals/ $Km^2$, Sankar et al. 2009). This might be attributed to the fact that other carnivores (tiger and leopard) rely less on livestock (~7% and 19% respectively) and more on wild ungulates (approximately 60 – 70%) in the study area (Mondal et al. 2012). STR sustains comparatively high wild ungulates density (56.2 animals/ $Km^2$; Jhala et al. 2015). Striped hyena being a scavenger, may likely access these carcass killed by tiger and leopard. Earlier dietary studies on spotted hyena suggest that the striped hyena requires approximately 946g of dry meat/ Day (Nagy et al. 1999). Striped hyena likely requires access to a similar quantity of dietary resources which can be easily met through available food resources (active predation) and tiger and leopard kills (scavenging) in STR.

When comparing the frequency of occurrence of prey species in striped hyena diet with previous studies conducted in STR, it was evident that the utilization rate of both ungulate (49% during 1990, Sankar and Jethwa 2002; 70.9% during 2010 – 11, Chaurasia et al. 2012) and livestock (31% during 1990, Sankar and Jethwa 2002; 33.7% during 2010 – 11, Chaurasia et al. 2012) have decreased, while rodents (1.2% during 2010 – 11, Chaurasia et al. 2012) and birds (2.3% during 2010 – 11, Chaurasia et al. 2012) have increased over the years **(Table 4.1.)**. Owing to the opportunistic nature of striped hyena, total number of prey species recorded depends very much on the sample size. Both the studies have recorded only nine food items in hyena diet and had a low sample size (n=26 and n=86) as compared to the present study (n=303). The present study reveals that the proportion of different prey species in scats got stabilised once a sample 150 scats of striped hyena were analysed. Hence, it is suggested that a minimum of 150 scats should be analysed to understand the food habits of striped hyena in the study area.

The diet diversity of striped hyena in STR (2.22) and Gir National Park (2.64; Alam et al. 2015) was comparable. Sariska and Gir PAs support high availability of wild prey. However, striped hyena diet diversity outside PA in Kachchh [3.08 (H) with 32 food items] was higher (Bopanna 2013) as compared to both STR and Gir indicating their reliance on a broader spectrum of food resources which may be attributed to the species adaptability and versatility. Traditionally, dead livestock is dumped near villages in India which also serves as food source for scavengers (Chhangani 2009).

***Den site selection***

Although they are human tolerant and are known to occur near human habitations, they are very particular about den site selection. Denning is extremely crucial for striped hyenas since it serves important life history strategies of the species (Jhala 2013). Den sites serve as their centre of activity, breeding and raising cubs free from disturbance, other predators, and daytime heat (Alam 2011, Bopanna 2013, Jhala 2013). The present study reveals that they prefer areas with higher shrub density as breeding den site probably as cover from other predators, dogs and humans. Selection of areas near waterholes was probably because they have limited thermoregulatory capabilities. Similar findings were reported by earlier studies. Alam (2011) found that striped hyenas in western Indian PA of Gir preferred hilly forests and grass cover for denning and were extremely selective about northern aspect. Striped hyenas were selective about drainage network, the presence of water, village distance and scrub forest outside PA in Kachchh (Bopanna 2013). Selection of drainage may be explained by their preference for areas that tend be undulating, eroded, rocky which can provide better habitat for denning, shade, cover and free from human disturbance. Their presence declined with increased distance from the water body. However, hyena dens were found at an optimal distance from villages was not an artefact of den selection; rather the availability of space. The area is dotted with villages which are between 1 and 3 km from each other.

*Spatio-temporal interactions*

Striped hyena had high spatio-temporal overlap with other carnivores in the study area (**Table 4.6.**). This is probably because of high anthropogenic pressure and greater availability of food resources that exists in the study area. Striped hyena has high overlap in diet with tiger, and leopard indicating their reliance on kills of other carnivores. Striped hyena was observed to avoid anthropogenic pressure on temporal scale. This has probably permitted them to survive in the human dominated landscape in high density by segregating themselves on temporal scale.

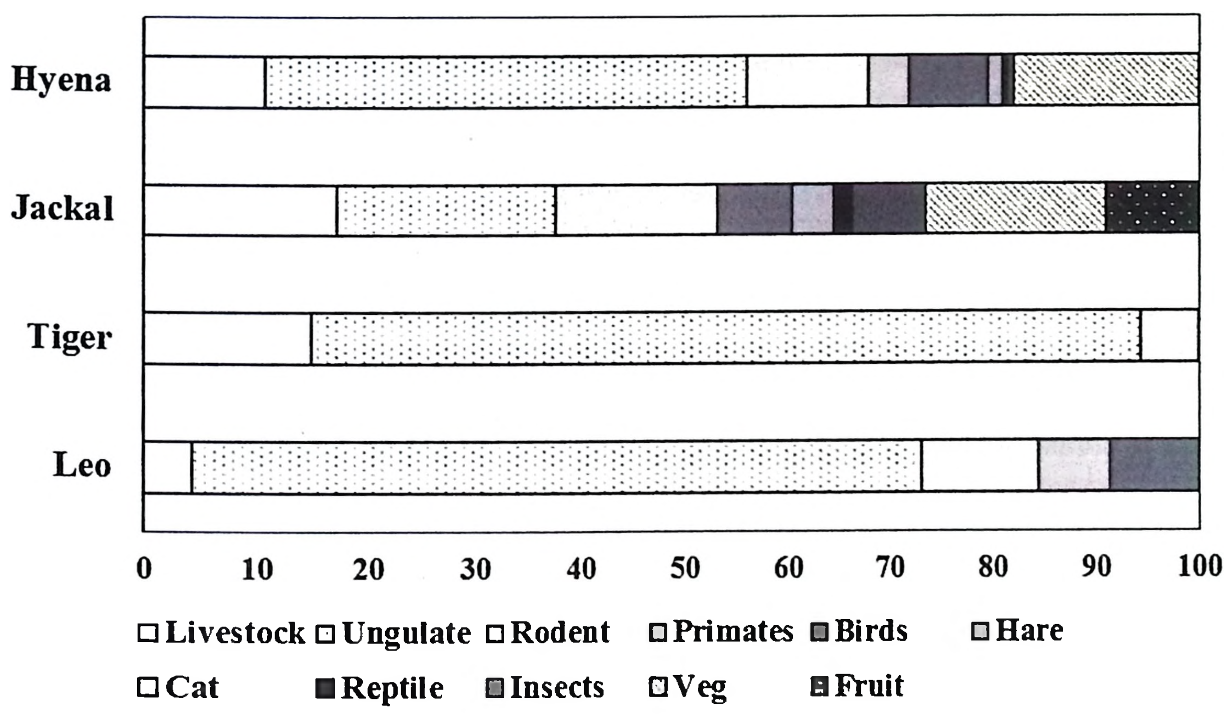



**Figure 4.9. Frequency of occurrence of food items in hyena (Present study), jackal (Chaurasia et al. 2012), tiger and leopard (Mondal et al. 2012) diet**

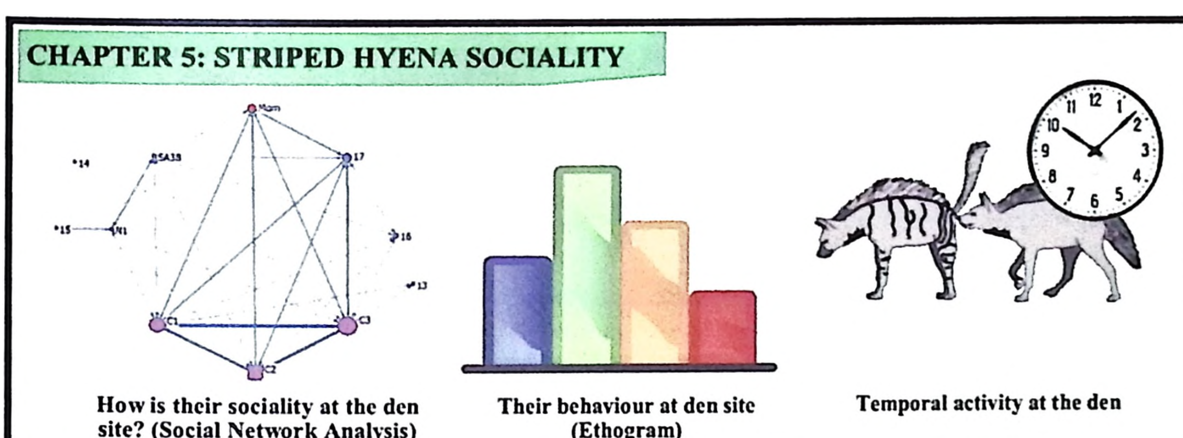
Mills and Hofer (1998) also suggested that striped hyena population is declining as a result of global population decline of other sympatric carnivores due to decrease in natural sources of carrion as hyena primarily depend on ungulate carcasses predated by tiger, leopard and wild dog in forested ecosystem. An earlier study suggested that striped hyena competes with leopards for shelter (Heptner and Sludskij 1992). Many instances of striped hyena chasing away leopards from their quarry have been reported (Pocock 1941, Prater 1965). Striped hyena and leopard's diet niche also overlap considerably in less disturbed areas (Arivazhagan 2005). However, knowledge on interaction of striped hyena with other carnivores is limited.

The present study indicates relaxed competition among the large carnivore guild of STR probably due to greater availability of food resources.

**Conclusion**

Diet of striped hyenas in the semi-arid areas predominantly consists of large mammals (Alam 2015, Bopanna 2013, and Present Study) as compared to smaller and rarer prey in African systems (Wagner 2006). Diet and dispersion of food are widely recognised as a key determinant of group formation (Crook 1965, Gittleman 1989, Mills 1989). Given the difference in diet, greater resource availability and heterogeneity in the Indian semi-arid with African systems, the social organisation of striped hyena may likely be influenced by the former. Thus, findings of the presnt study set the stage for further investigation of their sociality in this habitat concomitant to extant resources.

# CHAPTER V STRIPED HYENA SOCIALITY



# CHAPTER 5 STRIPED HYENA SOCIALITY

## 5.1. Introduction

Although, group living has evolved in only 10 – 15% of carnivore species (Bekoff et al. 1984), disproportionately less research attention has been paid to them. Carnivore sociality has traditionally been explained in terms of cooperative hunting, vigilance or defence of kill (Kruuk 1975, Gittleman 1989). However, these explanations cannot be applied to species who are solitary foragers, but display flexible social behaviour such as European Badger *Mele mele*, red foxes *Vulpes vulpes*, brown hyena *Hyaena brunea*, dwarf mongooses *Helogale parvula* or striped hyena *Hyaena hyaena* (Macdonald 1983). For eg. Badgers exhibit remarkable plasticity in sociality from being solitary or pair-living or groups up to 25 individuals occupying the same den across their distribution (Woodroffe and Macdonald 1983). This behavioural plasticity in intermittently social species is of profound importance (Macdonald 1983, Macdonald and Johnson 2015) and seem to have questioned cooperation as an explanation of carnivore sociality. Thus, comparing degrees of sociality in such species which show behavioural plasticity may enhance our knowledge about carnivore social evolution (Wagner 2008), because benefits in highly social species may be a consequence of grouping rather than the forces which initially fovoured it.

Behavioural plasticity aid individuals in coping with varying environmental conditions (Krebs and Davis 1987) such as resource appropriation in a heterogeneous landscape. Resource heterogeneity may lead to formation and maintenance of social/ spatial groups at low costs even in the absence of direct benefits (Waser 1981, Macdonald 1983, Johnson et al. 2001, Johnson et al. 2002, Wagner et al. 2008). Formation and maintenance of such spatial groups enhance chances of individual encounters. Direct interactions between individuals may establish or enhance sociality in spatial groups of individuals. Cooperation such as alloparenting, increased vigilance and occasional group defence may arise secondarily in these circumstances (Macdonald 1983). Resource dispersion hypothesis (RDH) thus nullifies the significance of interaction to explain sociality (Johnson and Macdonald 2015). If, being social is the climax, diverse sociality in such intermittently social species are the intermediate stages that might be evolutionary stable strategies depending upon the selection pressures prevailing on the species. Intra-specific comparison of flexible social systems across different resource gradient thus becomes very crucial in identifying these underlying selection pressures favouring social evolution.

Here, I focused on striped hyena which exhibits diverse sociality across their wide range. Although they are solitary forager, they form spatial groups (both polyandrous and polygynous) with rare direct interaction between individuals in the African systems (Wagner 2008, Califf 2013). However, striped hyenas from polygynous social groups in the Indian semi-arid system are known to interact with each other at the breeding den sites (Jhala 2013). Anecdotal reports and natural history account from southern India suggested females raise young without the helper and male had no role in pup upbringing (Davidar 1985, Godbole et al. 2015). All these above mentioned areas differing in ecological settings might lead to such trends in sociality which sets the stage for further investigation. I studied sociality of striped hyena in the Indian semi-arid system and tried to understand influence of resource heterogeneity on striped hyena sociality. Striped hyenas are long lived carnivores and pups depend on breeding dens for a very long time. I postulate grouping in such a social system might be to avail benefits by ensuring pup survival. Thus the system will be pup centric and interactions will decrease with increase in age since striped hyenas are behaviourally solitary. However, I expect greater home range overlap among individuals of the same social group than African system.

## 5.2. Methods

Striped hyenas of semi-arid region of western India are known to interact at dens (Jhala 2013). Based on a priori knowledge about striped hyena behaviour, I identified two active breeding dens in the semi-arid protected area of north-western India and deployed camera traps in both dens to understand their social structure. The camera traps were run for a total of 179 days during the year 2014 and 2015. Social Network Analysis (SNA) and ethogram were used to understand striped hyena sociality and the differences with reported populations were explained within the framework of Resource Dispersion Hypothesis. Hyena's temporal activity at the den site was also studied.

### *Behavioural Ethogram*

I went through each and every photograph and recorded type of interaction between the photographed individuals and created a behavioural catalogue (**Table 5.1.**). Later these interactions were used to estimate frequency of occurrence (%) of each behaviour.

**Table 5.1. Social behaviour catalogue used in the study (Only behaviours observed during the study have been catalogued and defined)**

| Broad Category | Sub Category | Definition |
|---|---|---|
| Greeting | Muzzle Sniffing | The individual sniffs the muzzle of a conspecific - both stand still and smell each other |
| | Muzzle - Anal Sniffing | Sniffs the anal region |
| | Anal Sniffing - Standing/ Laying/ Tail Lift | Non greeting function- performed at random - when arrived on den site-then it is 'greeting' function. Here the individual is standing and sniff conspecific's anal region. |
| Social Play | Muzzle Biting | Playfully biting the muzzle of conspecific, can involve licking of muzzle and face |
| | Body Biting | Biting and grabbing conspecific's body |
| | Object Play | Two or more individual simultaneously carry, chew, toss an object |
| | Tug of War | Unwilling to share/part with food item-Circumstances crops when 'opponent' has 'griped' the food item- a rough 'pull and push' accompanied with raised tail |
| | Parallel Walk/ Circles | Playing as conspecifics are walking/brisk walking/trotting/ circling next to each other |
| Social Grooming | Allo - Nibble Groom | The individual uses its incisors to nibble the fur/skin of the conspecifics |
| | Allo - Lick Groom | The individual licks the fur, face, genitals of the conspecifics |
| | Nuzzling | The individual pushes its nose against the receiver's fur and then rubs it back and forth or in circles, ruffling the receiver's fur |
| | Suckling | A function performed by breeding female to provide the cubs with nourishment |
| Resting | Proximity Resting | Resting (sitting/laying) at close proximity to each other |
| | Resting | Resting alone |
| Feeding | | Feeding on meat/ provisioned meat |
| Wallowing | | Dust Wallowing |
| Food Provisioning | | Bringing back scavenged meat to den by adults/ sub-adults |
| Vigilance | | Watching over pups by sub-adults/adults |
| Movement | | Moving away from the frame (not detected before 10 mins) |
| Ground Sniffing | | Sniffing ground typically on arriving the den by adults/ sub-adults |
| Pasting | | Defecating at the latrine site |

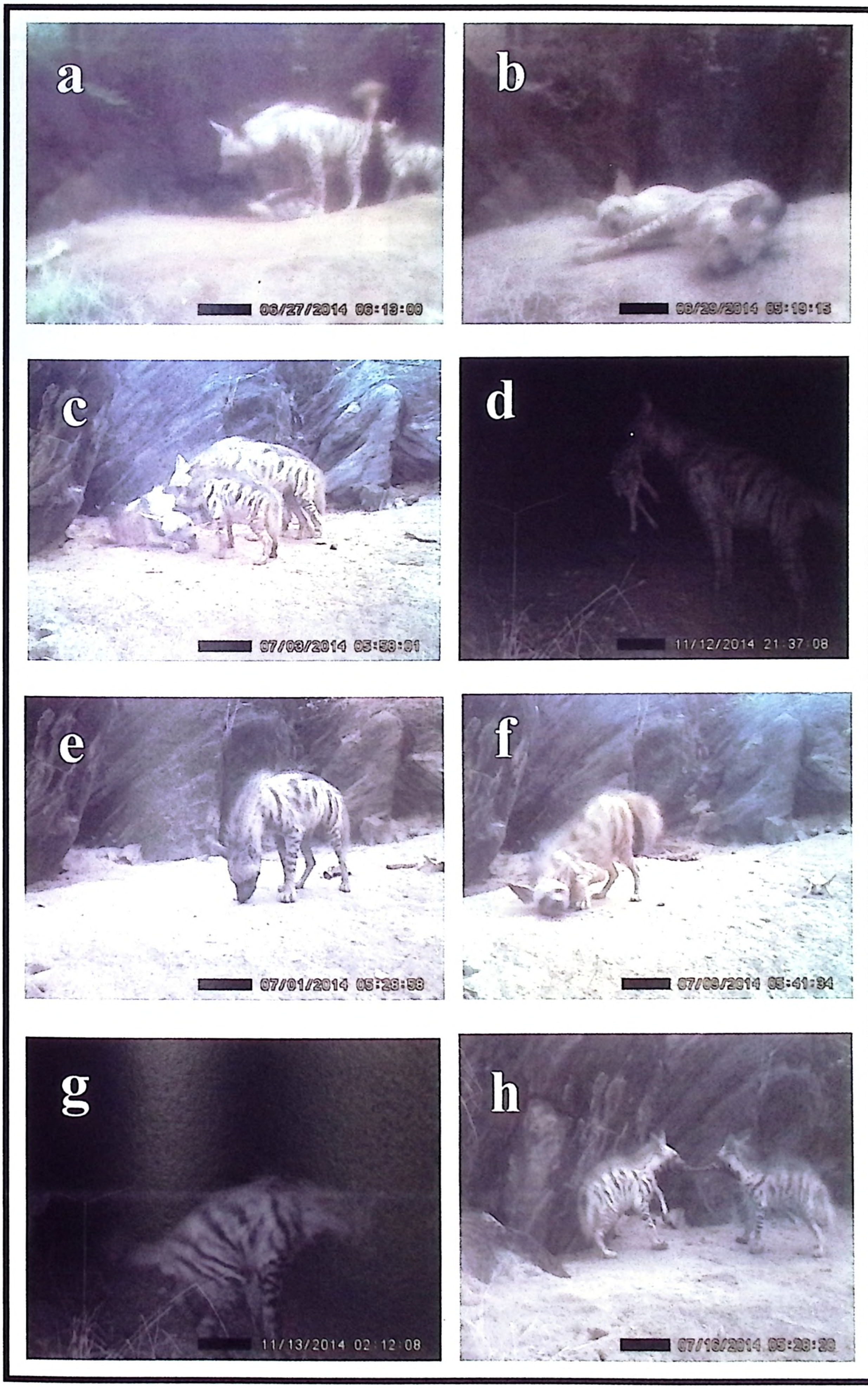

a
b
c
d
11/12/2014 21:37:08
e
07/01/2014 05:28:58
f
g
11/13/2014 02:12:08
h


**Figure 5.1. Photographs showing different recorded behaviours of striped hyena at the den site [a. Greeting, b. Proximity resting, c. Social grooming, d. Food provisioning, e. Ground sniffing, f. Wallowing, g. Pasting, h. Social play (Tug of war), i. Social Grooming (Suckling), and j. Feeding]**

*Social Network Analysis*

I constructed social networks based on observations for each clan in each breeding cycle. In this study, 'nodes' represent individuals and 'tie' represents association between two individuals. To understand association pattern between two individuals, simple ratio index was calculated. Here, the edge weight is calculated using the following formula:

$E_{AB} = x/\ (x+y_A+y_B+y_{AB})$

Where x = the number of camera trap nights individual A and B were photographed interacting together

$y_A$= the number of camera trap nights individual A was photographed without B

$y_B$ = the number of camera trap nights individual B was photographed without A

yAB = the number of camera trap nights both A and B were photographed but not together

I constructed two matrices, 1) n*n matrix, where n represents nodes, and 2) attribute matrix which includes information on age and sex. Social networks were constructed using UCINET 6.0 (Borgatti et al. 2006).

***Who are important at the breeding dens?***

I calculated eigenvalue centrality of each individual to understand importance of individuals and age class using UCINET 6.0. Eigenvalue centrality is the sum of the centralities of an individual's neighbours. High centrality can be achieved by having either a large degree or being connected to associates with a high degree (or both). This is a useful property as it captures the potential 'importance' of individuals in the network, as social hubs, or for the propagation of information or diseases through animal populations. Then, eigenvalue centrality was regressed with age of individuals to understand the relation between the two. We postulated that pups will have highest eigenvalues and it will decrease with increase in age.

***Prediction 2: Since they are behaviourally solitary, association between individuals are going to decrease with increase in age.***

I also tested if age class was a significant predictor of network structure using quadratic assignment procedure (QAP) regression using UCINET. QAP is a special case of Mantel test and allows a dependent relationship matrix (DM) to be regressed simultaneously against multiple independent matrices (IM) representing dyadic attribute relationships. After performing a standard multiple regression across the corresponding cells of the DM and IM, the procedure then randomly permutes the rows and columns of the DM and recomputed the regression, thereby generating a matrix-specific distribution against which the coefficients of the observed matrix can be compared to determine P values. In this case, the DMs were the networks of interactions. IMs were weighted matrices based on our prediction about decreasing association with increase in age class. It was achieved by defining three age classes, i.e. pups (P), sub-adult (SA), and adult (A), amongst which six possible interactions can happen. I created weighted matrices wherein pup-pup interaction had highest value (1), followed by Pup-subadult (0.84), Pup-adult (0.84), Subadult-subadult (0.68) and so on.

I ran the procedure with 2000 permutations per DM. We regressed networks simultaneously against one attribute matrices (age class). In UCINET, this was achieved using the 'Tools>Testing Hypotheses>Dyadic (QAP)>QAP Regression> Double Dekker Semi-Partialling MRQAP' function. In this case, the unit of analysis was the network (the breeding year). QAP regression results would support the prediction if the characteristics had a significant ($P < 0.05$) positive coefficient in association networks.

***Home Range Overlap among clan members***

Long term camera trapping data to estimate striped hyena abundance and survivorship (see Chapter 3) was used to construct home range polygons (Minimum Convex Polygon) of clan members (adults and sub-adults) using ArcGIS 9.3. Intersection tool in ArcGIS v 9.3 was then used to assess home range overlap between individuals. However, one den falls away from my study area. So, home ranges of only five individuals from the Tarunda den was calculated resulting home range overlap assessment of ten dyads.

*Temporal Activity Pattern at the den site*

Information about time was recorded from each and every photograph to understand temporal activity pattern of each age group (breeding female, adults and pups), and various behaviours at the den site using circular statistics in Oriana and camtrapR.

## 5.3. Results

179 days of camera trapping revealed a total of 2264 photographs of 12 different adult individuals and nine pups. Den site 1 (Tarunda Clan) was used by eight adults during two consecutive littering by two different breeding females during 2014 and 2015. Den site 2 (Indokh Clan) was used by four adult individuals and three pups during 2014. However, they abandoned the den following killing of one of the adult individual by a leopard.

***Behaviour at the den site***

My findings suggest that striped hyenas are extremely interactive at the breeding den sites. In total, 737 interactions belonging to 19 behavioural sub-categories were recorded across ten behavioural broad categories. Social play (15.88%), social grooming (12.35%), resting (14.93) and ground sniff (10.18%) behaviour was observed the most.

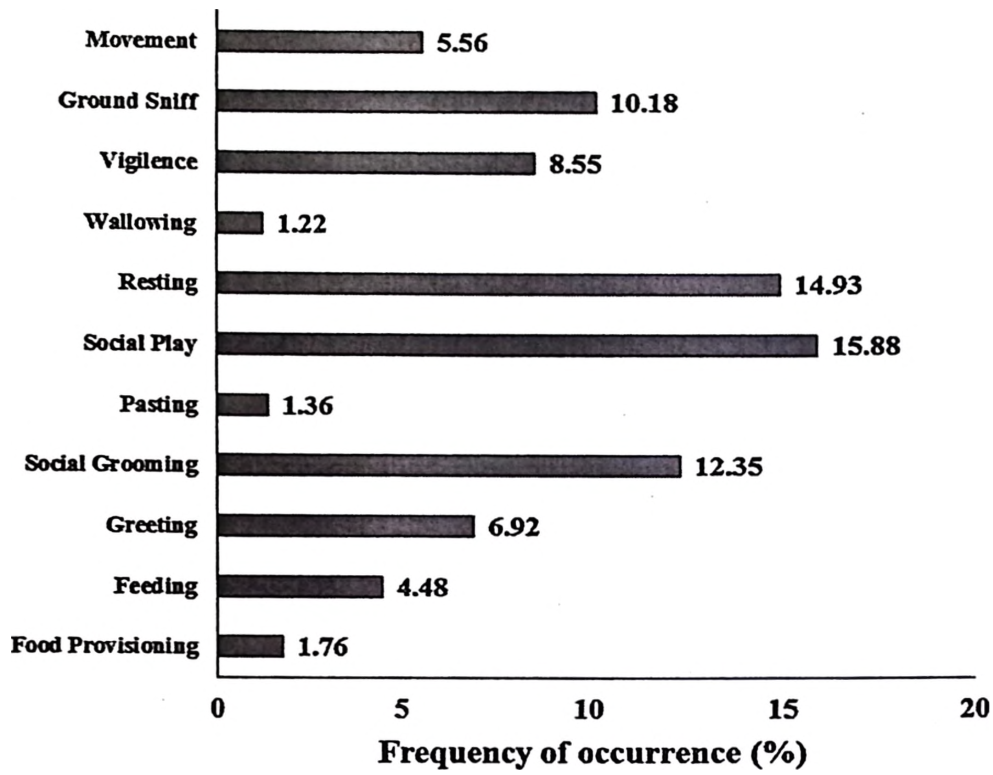



**Figure 5.2. Frequency of occurrence of each behavioural category observed during the study**

*Social Networks*

During the study period, average±SE clan size was 8.66±0.98 (range: 7 – 11) including pups. **Figure 5.3.** illustrates the social networks of three striped hyena clans. These clans consisted of a breeding female, multiple adult/ sub-adult helpers especially females and pups. There were seven adults helpers in the Tarunda clan during 2014 breeding cycle. One individual during this cycle was only captured during food provisioning (n=05). During the next breeding cycle, one adult from the 2014 cycle littered and breeding female of the earlier cycle acted as helper, whereas two pups, now sub-adults (one male and one female) acted as helpers during this cycle.

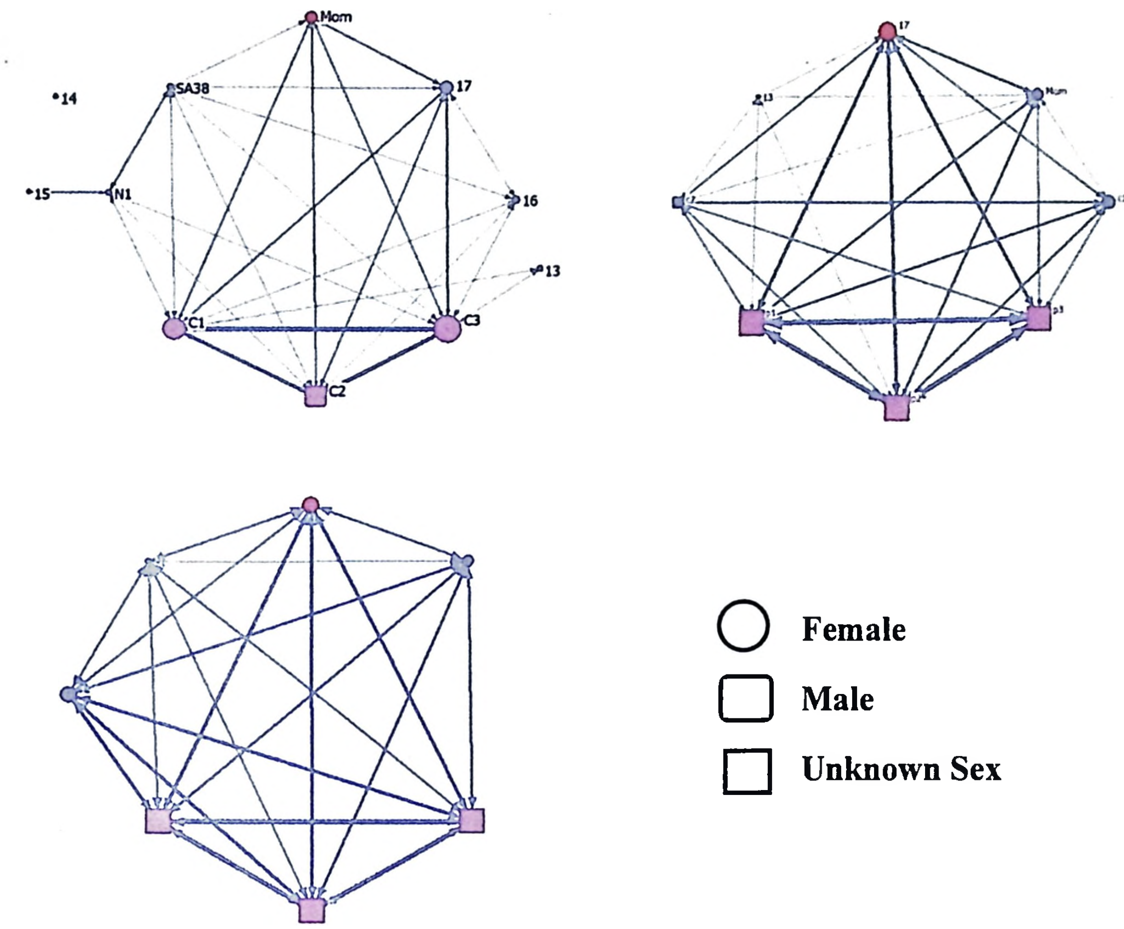



**Figure 5.3. Social Network of association during two consecutive litters of Tarunda clan and Indokh clan (Red indicates Breeding Female, Blue indicates adults other than breeding female, and pink indicates pups). Size of nodes indicate importance of the individual in the network.**

### *Pups were Central to the System*

Average eigenvalue centrality was observed to be highest for pups (0.48±0.02 SE), followed by breeding female (0.30±0.04 SE) and adults/ sub-adult helpers (0.15±0.03 SE). Pups were the most important in this system. As postulated, the present study reveals that centrality ($R^2$ = 0.40) in this pup-centric system has a significant negative relationship with age. Eigenvalue centrality or the importance of the individual decreased with increase in age.

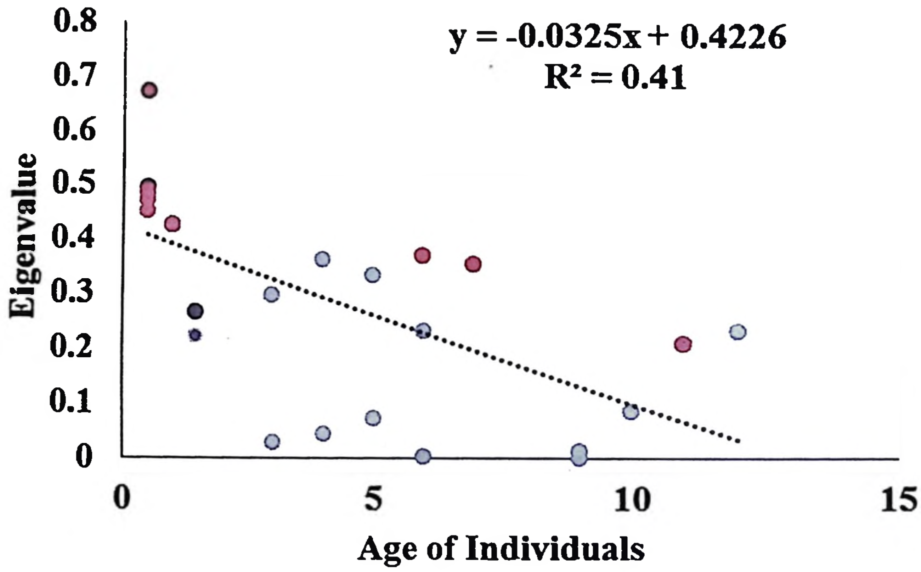



**Figure 5.4. Negative relation of eigenvalue centrality with age of the individual in the pup centric system of striped hyenas**

As hypothesized, association networks showed decreased interaction with increase in age class ($P<0.05$). Pup-pup association was highest followed by pup-subadult, subadult-subadult association and so on.

**Table 5.2. QAP regression result for colony years in association matrix**

| Clan | Coefficient | P Value |
|---|---|---|
| Tarunda Clan (2014) | 0.44 | 0.001 |
| Tarunda Clan (2015) | 0.57 | 0.009 |
| Indokh Clan (2014) | 0.71 | 0.029 |

***Home Range Overlap***

In total, 75 captures of five individuals from the Tarunda den during winter 2014 - 15 (Trap Night: 1650) were used for home range overlap calculation resulting in 10 dieds and 20 overlaps. There was a significant overlap (65%) among group members of the same clan.

*Temporal Activity*

Interactions mostly occur during the twilight hours with a peak at dawn [4:29 AM (4:11 AM – 4:48 AM, 95% CI)] at the den site. Activity peak of different age class is given in **Table 5.3.** Temporal overlap between pups and adults was found to be higher (**Table 5.4.**) than with the breeding female.

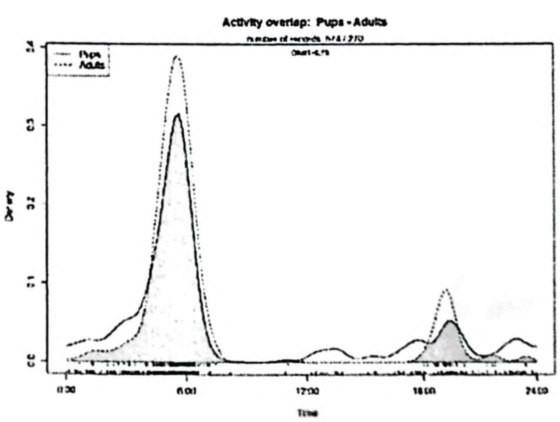
**Table 5.3. Activity peak of adults, breeding female and pups at the den site**

| Variable | Sub-adults/ Adults | Breeding Female | Pups |
|---|---|---|---|
| Number of Observations | 270 | 139 | 574 |
| Mean Vector (95% CI) | 04:56 (04:33 - 05:19) | 05:09 (04:44 - 05:34) | 04:22 (04:01 - 04:43) |

**Table 5.4. Activity overlap between different age class (Adults, breeding female and pups)**

| | Adults | Breeding Female | Pups |
|---|---|---|---|
| **Adults** | ----- | < 0.05 | < 0.001 |
| **Breeding Female** | 0.222 | ----- | < 0.001 |
| **Pups** | 0.407 | -0.726 | ----- |

$U^2$ scores (lower half) and probabilities (upper half)



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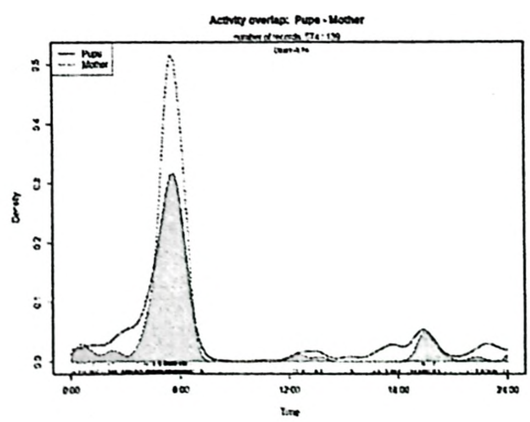

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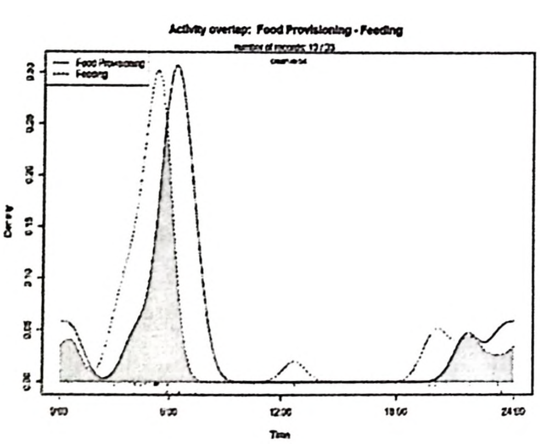
**Figure 5.5. Temporal activity overlap between (a) pups – helpers (78%), and (b) pups – breeding female (74%)**

**Temporal patterns of different behaviours**

Most of the activities showed a peak during the early morning or dawn (**Table 5.5.**) after the adults/ sub-adults return from foraging except suckling. However, vigilance had a broader peak probably ensuring cub safety during all these interactions at the breeding den site.

**Table 5.5. Temporal activity peak of different behaviour at the den**

| Variable | Number of Observations | Mean Vector (95% CI) |
|---|---|---|
| Suckling | 8 | 22:19 (19:24 - 01:13) |
| Feeding | 33 | 03:48 (02:38 - 04:58) |
| FP | 13 | 05:01 (03:10 - 06:53) |
| Greeting | 47 | 04:26 (03:39 - 05:14) |
| Grooming | 90 | 04:25 (03:26 - 05:24) |
| Ground Sniff | 62 | 05:35 (04:45 - 06:25) |
| Miscelleneous | 104 | 04:18 (03:27 - 05:09) |
| Movement | 41 | 04:48 (02:19 - 07:17) |
| Pasting | 10 | 01:25 (16:41 - 10:09) |
| Play | 117 | 04:48 (04:15 - 05:21) |
| Resting | 108 | 04:33 (03:47 - 05:20) |
| Vigilance | 63 | 02:51 (01:23 - 04:19) |

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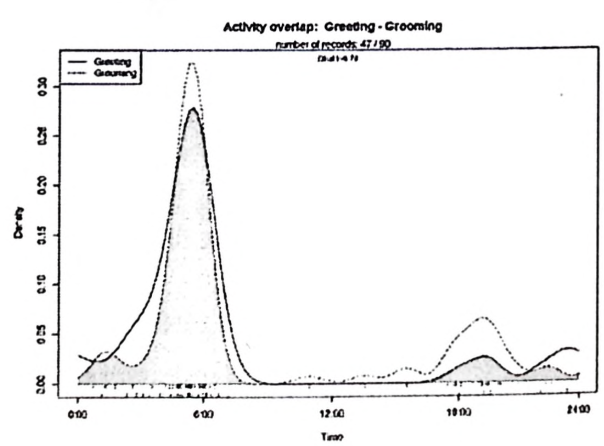


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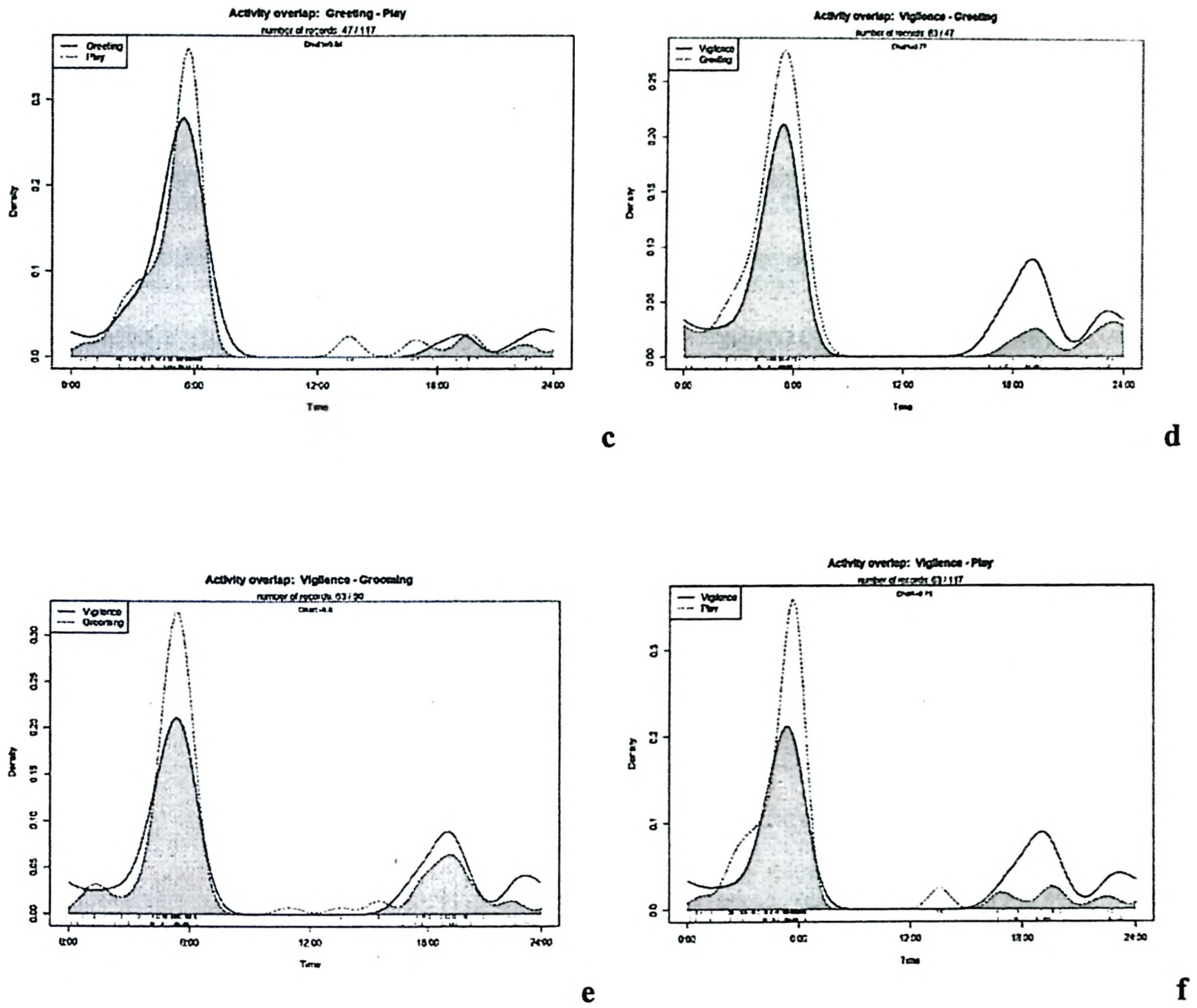



**Figure 5.6. Temporal activity overlap (a) Food Provisioning and Feeding, (b) Social Greeting and Grooming, (c) Social Greeting and Social Play, (d) Social Greeting and Vigilance, (e) Social Grooming and Vigilance, and (f) Social Play and Vigilance**

### 5.4. Discussion

In overwhelming majority of avian and mammalian species, individuals other than the parent assist in rearing young (Wilson 1975), and this caring behaviour is termed as allo-parental behaviour (Emlen 1997). These alloparents/ helpers are often related to the breeding individuals in bird and mammal societies (Clutton-Brock 2002). According to inclusive fitness theory (Hamilton 1964), alloparenting may alter both direct (experiences enhance later reproductive success) and indirect benefit (by increasing fitness of close relatives). Alloparental behaviour has been reported from smallest of gregarious mammals such as rodents (eg. prairie vole *Microtus ochrogaster*, Wang and Novak 1994; Mongolian Gerbil *Meriones unguiculatus*, Ostermeyer and Elwood 1984) to social carnivores (eg. Lion *Pathera leo*, Bertram 1979; Wolf *Canis lupus*, Mech 1970), primates (eg. Bonobo *Pan paniscus*, Enomoto 1990; Wild Chimpanzes *Pantroglodytes schweinfurthii*, Badescu et al. 2016) to that of largest terrestrial and marine mammals such as elephant *Loxodonta africana* (Lee 1987) and sperm whales *Physeter microcephalus* (Whitehead 1996). The present study provides empirical evidence that intermittently social species such as striped hyena form complex social systems in the Indian semi-arid region which is similar to their close cousins, brown hyena (Mills 1983). This den centric social system consists of a breeding female, multiple sub-adult/ adults especially females and pups. Pups are central to the system, however adults other than the breeding female plays a crucial role in rearing pups and engages in social grooming, play, food provisioning and vigilance. Although, they are solitary foragers, they regularly interact at the den during the twilight hours especially during dawn. Similar social systems has been reported from the Indian semi-arid system (Alam 2011, Bopanna 2013, Jhala 2013). Striped hyenas in the Indian semi-arid region exhibit higher degrees of spatial overlap (65%) between individuals of a social group compared to just over 8% and 26% in the African system. My findings suggest that there is a stark difference in sociality with the reported African systems (Laikipia and Shompole), wherein striped hyenas form spatial groups and exhibit both polyandrous and polygynous systems which is probably to access smaller and rarer prey (Wagner 2008, Califf 2013) as compared to larger prey in the Indian system (Present study).

Evolution of altrusim in animal groups have been explained by kin selection in conjunction with philopatry (Pusey 1987). Environmental and resource limitations may cause individuals to stay and help, and may create situations in which allopaternal care and cooperation are necessary and beneficial. Limitations may include territory quality, food supply, rainfall, and temperature (Koenig, Walters, and Haydock, 2011). Alloparental care in marmots has been associated with environmental harshness. Environmental harshness increase maturation time and is associated with dispersal delayed beyond sexual maturity (Blumstein and Armitage 1999). Indian striped hyenas thrive in the agro-pastoral landscape interspersed with human habitations (Jhala 2013) which highlights the fact that inviolate areas free from human disturbance and guard dogs for denning are scarce and patchy (Present study, Bopanna 2013) in contrary to vast stretches of inviolate areas in Africa and Middle East. Although, food resources are-abundant and large in this landscape, are asynchronous over space and time which might take substantial time to locate. Thus, experienced females may use their knowledge for resource appropriation in this risky landscape, while helpers help in rearing of pups. Matriarchal societies in elephants depend on the dominant female for resource appropriation in African savannah during harsh conditions. Thus by helping the breeding female, striped hyenas not only secure indirect fitness, but also food and later may avail mutualistic help during their litters (observed during the study) or may be go up in the dominance ladder. Since it is a risky landscape, the constraints of reproduction are so high for individuals, they benefit from such affiliative relations. Clumped resources in the semi-arid reduce competition, thereby enhancing affiliative bonding to a great extant. This corroborates the Resource Dispersion Hypothesis whereby secondary benefits such as alloparenting has shaped the extant sociality in my study species. The findings of the present study highlight the adaptive value of plasticity in social behaviour, further evidencing disparity in social trends of other group living species like lion, elephant and dolphin inhabiting ranges differing widely in resources and threats (Chakrabarti and Jhala 2017, de Silva et al. 2016, Connor et al. 2017).

# CHAPTER VI HYENA-HUMAN CONFLICT AND THREATS

## 6.1. Introduction

Direct persecution (especially poisoning), a decrease in natural sources of carrion, illegal trade of skins, use of body parts, habitat fragmentation are considered principal reasons for the apparent decline in the striped hyena population worldwide (AbiSaid & Dloniak 2015, Jhala 2013). However, mortality events are not reported or underreported from India. There was no comprehensive effort to understand the threats to striped hyena population in India or abroad.

## 6.2. Methods

Structured Questionnaire Survey (Kumar and Shahabuddin 2006) from all villages (n=28) was conducted to assess human-hyena conflict and livestock depredation. In total, 152 interviews were conducted across 28 villages. Also, the State Highways (roads) were regularly monitored to record for any hyena mortality due to the vehicular collision. I have also performed a comprehensive review of existing literature to collate information on reasons behind striped hyena mortality in India using Google Scholar. Furthermore, I have compiled the existing literature in two groups, i.e. from inside Protected Area (PA) and from outside Protected Area (outside PA) to understand threats to their population across varying protection levels.

## 6.3. Results

No records of livestock depredation by striped hyena was recorded during the survey. Only one human attack case by striped hyena was recorded during the study period in 2014.

Six cases of striped hyena mortality due to the vehicular collision were recorded during 2008 – 11. However, no striped hyena mortality due to vehicular collision has been recorded from 2012 onwards.

In total, 40 records of striped hyena mortality across India from three published accounts were compiled (**Figure 6.1.**) to understand the threat to striped hyena population across the subcontinent. Most of the reported mortality cases were from outside PA (n=36). Human-induced threats appear to be the major reasons behind hyena mortality in India (n=40).

### *6.4. Discussion*

Livestock depredation by striped hyena appeared to be rare probably due to the higher availability of food resources in the form of the carcass in the study area. In total, 31 livestock depredation cases mostly goat and two human attacks were recorded from the periphery of Sariska Tiger Reserve during 2008 to 2013. Six striped hyena mortality due to road accidents was recorded during 2008 – 12. However, road accidents of striped hyena were not recorded after 2012 in the study area probably due to the traffic regulation (daytime traffic diversion and nighttime traffic ban) on the state highways dissecting the reserve. The present study has shown that striped hyena population would have been severely affected if the traffic regulation was not imposed (**Chapter 3**).

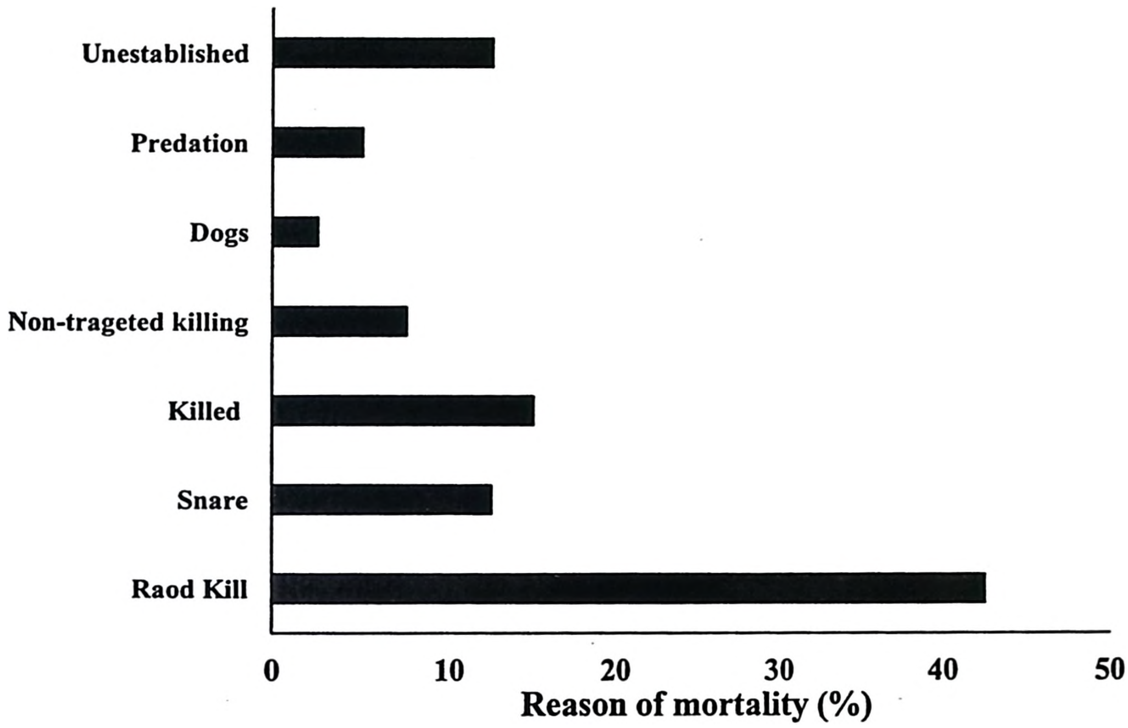
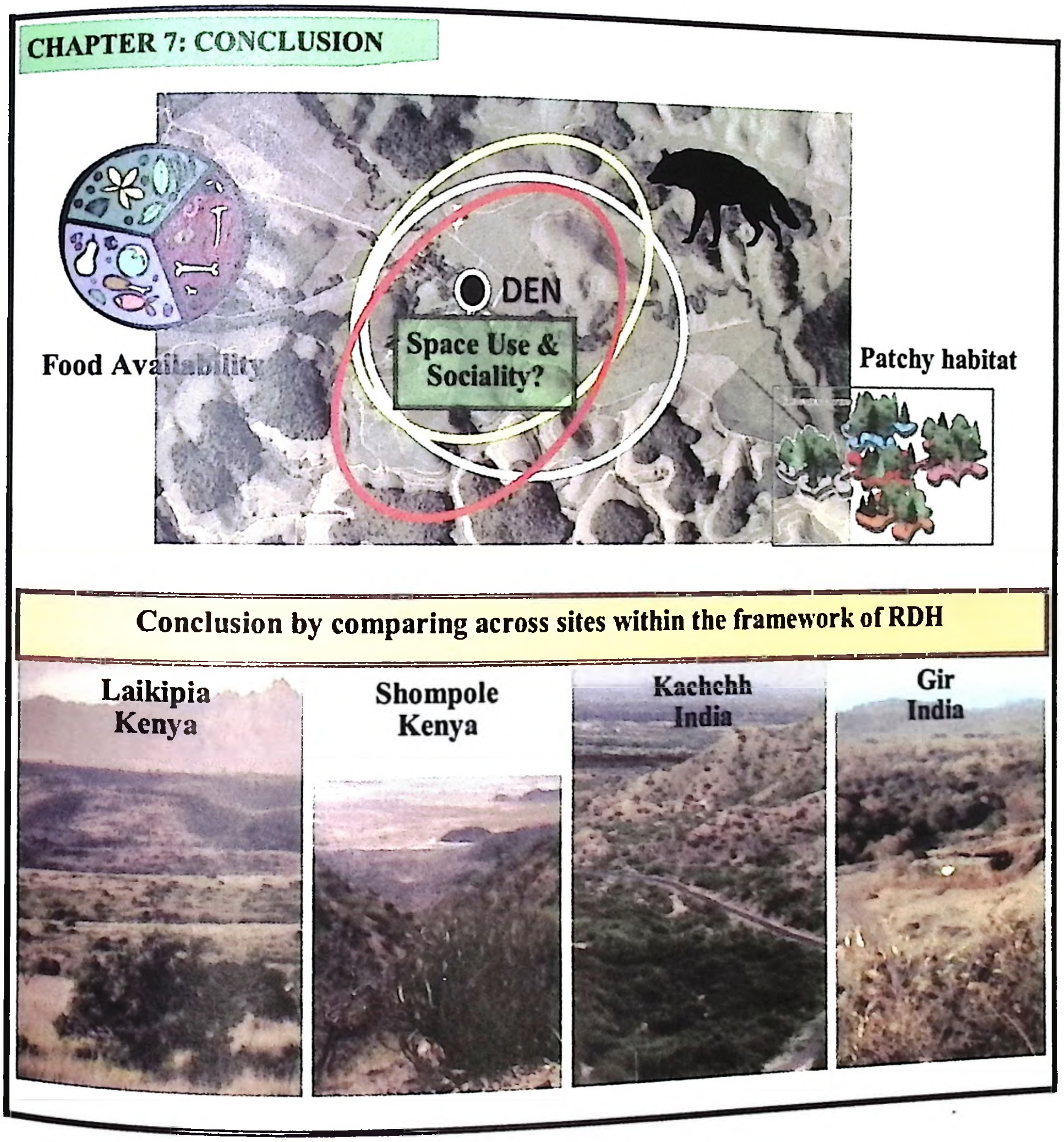



**Figure 6.1. Reasons behind striped hyena mortality in India reported in 3 published accounts (Arumugam 2012, Bopanna 2013, Rajpurohit et al. 2011) and the present study**

Bopanna (2013) recorded 16 cases of road kills through questionnaire survey in the human-dominated landscape of Kachch in western India. However, striped hyenas are also killed by larger predators like leopard and tiger (n=2) inside protected areas where they are sympatric with them. Striped hyena occupancy also declined approximately 8% during two consecutive national tiger population estimation (Jhala 2011, Jhala 2015). Given the fact that this program was focused mainly on forested areas with potential tiger distribution, reported loss of striped hyena distribution appears to be a gross underestimate. Overall, human-induced mortality and habitat loss seem to be the primary threats for striped hyena population in the study area and India.

# CHAPTER VII

# CONCLUSION



# CHAPTER 7

# CONCLUSION

The present study reveals that although striped hyenas persist in comparatively higher density in the study area, long term persistence of their population was under threat due to human induced mortality in this landscape. Their population outside Protected Area without protection status may face slow population decline if conservation actions are not implemented. Hyenas preferred areas which were rugged, near to human habitation and waterholes for foraging in the study area. Their site utilization increased in areas frequented by tiger and leopard. Village areas serve as known feeding sites for hyenas at livestock carcass dumping sites and also they scavenge on tiger and leopard kills. However, they are very specific about breeding den site selection since it serves important life history strategies of the species. They preferred areas near water resources with higher shrub density, which may be attributed to predator and human avoidance and also for thermoregulation. Their nocturnal behaviour allowed them, to survive in human dominated landscape despite having significant spatial overlap with humans.

Knowledge about striped hyena spatial ecology and complex sociality has been enriched primarily by studies on two populations (Laikipia and Shompole) in Kenya (Wagner 2006, 2008, Califf 2013, Spagnuolo 2016). The present research outcome provides comprehensive knowledge about striped hyena spatial ecology and sociality from an entirely different ecological setting that is crucial for formulating conservation strategies and to conduct future studies on hyenas underlying ecological reasons behind the formation of groups. Similar findings were reported from the Indian semi-arid system wherein they form polygynous social systems (Bopanna

2013, Jhala 2013). Clan members have significant home range overlap (65%) among themselves in Indian semi-arid region (Present study, Jhala 2013) as compared to significantly low overlaps found among spatial units (only 8% in Laikipia, and 26% in Shompole) in the African systems. Despite spatial grouping, striped hyenas in India remained behaviourally solitary. They forage and feed alone. Even at the socially active centre, the level of association is low, and group members remain isolated most of the time in Sariska (90%). Califf (2013) reported similar observations based on a total of 536.15 hours of Focal Animal Sampling on 15 radio-collared hyena individuals of Shompole, Kenya population. Shompole striped hyenas were found alone during 95.6% of the time.

**Table 7.1. Clan size of striped hyena in the Indian semi-arid region**

| Area | Sample Size | Clan Size | Lower Limit | Upper Limit | Reference |
|---|---|---|---|---|---|
| Gir | 10 clans across 1.7 years | 3.74±0.05 (SE) | 3 | 8 | Alam 2011 |
| Kachch | 6 clans across 7 year | 6±0.73 (SE) | 4 | 8 | Bopanna 2013 |

Diet of striped hyenas in the Indian semi-arid areas predominantly consists of large mammals as compared to smaller and rarer prey in African systems. In Sariska, the study areas was characterised by high prey and livestock density which supports striped hyena in high density than elsewhere **(Table 7.3.)**. In forested ecosystems, natural sources of carrion predated by tiger, leopard or wolves also serve as food sources for hyenas (Jhala 2013). Traditionally beef is avoided in India (Chhangani 2009, Karanth et al. 2009) and livestock is reared under semi-starved condition and without proper veterinary care (Robbins 1998, Sharma and Mehra 2009). Dead livestock is usually dumped outside villages which serve as food source for hyenas outside PAs (Bopanna 2013). These food resources although abundant and large, are asynchronous over space and time and may be adequate for more than one individuals. Increase in overall resource abundance leads to increase in habitat quality per unit area, thus resulting in higher animal densities, and typically smaller ranging areas (Powell et al. 1997, Reiss 1988). However, the reported hyena home ranges from Indian semi-arid region were comparable to Shompole system (Kenya) wherein they survive in vast stretches of inviolate space (**Table 7.2.**). This similarity in home ranges was probably due to clumped resource availability (food and den site) in Indian landscapes due to presence of human habitation. For example, Kachchh has a village density of 0.75 villages/ $km^2$ (Jhala 2012) which points out to the fact that inviolate areas free from human disturbance and guard dogs for denning are scarce and patchy (Bopanna 2013) in contrary to vast stretches of inviolate areas available in Africa and Middle East (**Table 7.3.**).

**Table 7.2. Home range sizes of striped hyena (HR±SE) in different Protected Areas**

| Population | Overall HR size (sq. km) | Male HR size (sq. km) | Female HR size (sq. km) |
|---|---|---|---|
| Kachchh, Western India (Bopanna 2013) | 73.5±12.9 (n=8) | 125.3 (n=1) | 66.1±11.3 (n=7) |
| Serengeti, East Africa (Kruuk 1976) | 58 (n=2) | 72 (n=1) | 44 (n=1) |
| Negev Desert, Israel (Van Aarde et al. 1988) | - | - | 60.9 (n=1) |
| Laikipia, Kenya (Wagner et al. 2008) | 68.9±7.8 (n=10) | 76.0±13.8 (n=4) | 64.2±9.8 (n=6) |
| Laikipia, Kenya (Califf 2013) | 122.24±21.34 (n=19) | 100.36±13.15 (n=11) | 152.32±45.97 (n=8) |
| Shompole, Kenya (Califf 2013) | 66.89±13.31 (n=8) | 119.37±32.03 (n=2) | 49.4±4.16 (n=6) |

**Table 7.3. Comparative information on general ecological settings of fivesites from where striped hyena social organization have been reported. Information of different sites are primarily obtained from Alam 2011 (Gir), Bopanna 2013 (Kachchh), Schuette et al. 2012 (Shompole), Wagner 2006 (Laikipia).**

| Category | Sariska TR, India (PA) | Gir NP, India (PA) | Kachchh, India (Outside PA) | Shompole, Kenya | Laikipia, Kenya |
|---|---|---|---|---|---|
| **Striped Hyena Social Organization** | Den centric breeding clans | Den centric breeding clans | Den centric breeding clans, Spatial Overlap | Spatial Grouping among females | Polyandrous spatial grouping |
| **Home Range Overlap (%)** | 65% | - | Similar area utilization by clan members | 26% | 8% |
| **Striped hyena density (/100 $km^2$)** | 15 | 6.5 | 5 – 10* | 3 | 3 |
| **Prey Density (/km2)** | 54.49 | 56.2 | 8.4** | 38.61 | 11.0 |
| **Livestock Density (/km2)** | 69.31 | 25 - 31† | 41†† | 74.90 | 4.3 - 5.9 |
| **Human Density (/$km^2$)** | 15 individuals/ $km^2$, 29 villages | 50 Maldhari settlements | 50 individual/ $km^2$, 0.75 villages/ $km^2$ | 10 individuals/ $km^2$ | - |

*Jhala 2013, **Dave 2010, †Banerjee 2013, ††Jhala et al. 2012

Higher population density also increases the chances of individual encounters in competitive circumstances, favouring formation of alliances (Whitehead and Connor 2005, Connor and Whitehead 2005). Since it is a risky landscape due to anthropogenic pressures, the constraints of reproduction in hyenas are so high for breeding individuals, they benefit from such affiliative relations as observed in the present study (Chapter 5). Clumped resources, which are rich in the semi-arid region reduce competition amongst hyena individuals, thereby enhancing affiliative bonding amongst them to a great extant. This corroborates the Resource Dispersion Hypothesis whereby the secondary benefits such as alloparenting that has shaped the extant of sociality of hyenas in the present study. My findings, in a comparative context, suggest that cooperative behaviour in rearing pups of hyenas in the Indian context is a secondary benefit that possibly increase their survival in this human-dominated landscape.

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# Diet of striped hyena (*Hyaena hyaena*) in a semi-arid protected area of Western India

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## Abstract

Striped hyena (*Hyaena hyaena*), having the largest distribution and most diverse in the social organisation among hyenids, remains the least studied. The availability of food is known widely as one of the key determining factors of social organization in animals. In the present study, the food habits of striped hyena were investigated by analysing the scat samples collected (n=303) during 2013-15 from the semi-arid region of Sariska Tiger Reserve, Western India. Totally, the prey remains belonged to23 species were identified from hyena scats. It was found that the striped hyena had a catholic choice of diet with great reliance on large mammals (sambar, *Rusa unicolor*; chital, *Axis axis*; nilgai, *Boselaphus tragocamelus*; wild pig, *Sus scrofa*; and livestock; 56%) in the Indian semi-arid region. Rodents, birds, reptiles, hare and small carnivores contributed 21.45% of the diet of striped hyena. Vegetative matter consisted primarily of grass and *Zizyphus sp.* seeds contributed 17.95% to the striped hyena diet.The scat analysis showed that the overall diversity of food items in striped hyena diet was 2.22 (Shannon-Winner Index, H). It was also found that 39 kills were belonged to 12 different prey species at the den sites (n=27). Striped hyenas were observed to predate on wild ungulate fawns/calves (48.72%) followed by ground-dwelling birds (28.21%), small carnivores (7.69), primates (5.13%), reptiles (5.13%), Rufous-tailed hare (2.56%) and livestock (goat, 2.56%). The present study also revealed that though the hyenas are scavengers and primarily dependent on large mammals, they also actively predate on smaller prey species.

**Key words:** Feeding ecology, striped hyena, scatology, carnivore kill, semi-arid region

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## INTRODUCTION

Studies on food habit are crucial to understand the carnivore ecology and for conservation and management of the species (Mills,1992; Levitus, 2000).Knowledge of diet is essential when carnivore sociality (Wagner et al., 2008) or predator-prey relationships are studied (Jedrzejewski et al., 2002), or when predators are perceived as a threat to livestock (Marker etal. 2003), or when rare prey species are required protection (Napolitano et al., 2008), or when srategies are evolved to mitigate human-animal conflict. Carnivores have witnessed a massive decline in their population globally and are now confined to fragmented populations in a human-dominated landscape. In human-dominated landscape, the most vulnerable species are the largest and most specialised species, often top predators (Cardillo, 2003) such as striped hyena.

Striped hyena (*Hyaena hyaena*) is a nocturnal scavenger with a patchy geographic range among the hyaenids (Mills and Hofer, 1998). Striped hyena exhibits little fear of humans and are human tolerant. It is often found within the proximity of urban centres and can survive on human organic waste generated at these sites (Mendelssohn and Yom Tov, 1999). Most of the populations of hyena in India live outside the protected areas in the agro-pastoral landscape. Arid regions of North-western India are important habitats for hyena persistence (Singh, 2010; Gupta et al. 2009), which is among the most densely populated arid regions of the world both for humans as well as livestock (Rahmani and Soni, 1997). Striped hyenas have been reported to consume a wide variety of vertebrates, invertebrates, vegetative matter, fruits and human originated organic wastes (Ilani, 1975), and the limited data have led to the interpretation that striped hyenas are essentially omnivorous scavengers. However, recent studies suggest that they feed on variety of food item from small sized to large-bodied prey depending on the availability (Wagner, 2006; Bopanna, 2013; Jhala, 2013). Based on prior studies, striped hyena is found to demonstrate an opportunistic behaviour and scavenges on livestock and wild animals, and predates on small mammals, livestock, reptiles and ground-nesting or feeding birds (Leakey et al., 1999; Kruuk, 1972; Sankar and Jethwa, 2002;

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Wagner, 2006). However, hyenas sometimes predate on small livestock like goats, sheep, cattle calf and dogs and hunt hare, gazelle, jackal, nilgai calves and wild pig. In Kachchh, cattle and dogs contributed over 70% of the hyena's diet(Jhala, 2013).

Striped hyena often comes into conflict with humans due to their habit of livestock depredation, targeted retaliatory killing directed at other carnivores and road accidents. The literature on striped hyena diet is limited and often restricted to studies confined to outside protected area (Bopanna, 2013; Gajera et al., 2009). The present article deals with the results of the investigation on food habit of striped hyena in a semi-arid protected area of North-Western India so as to understand their diet composition and reliance on livestock for long-term conservation of this near threatened (Abisaid and Dlonaik, 2015) species in this landscape.

## MATERIALS AND METHODS

### Study Area

The study was carried out in the Sariska Tiger Reserve (STR), (76.28° to 76.56° E and 27.08° to 27.55° N) which is situated in the Aravalli Hill Range and lies in the semi-arid part of north-western India. The total area of the Tiger Reserve is 1200 km². The terrain is undulating to hilly, has numerous narrow valleys and two large plateaus. The altitude of Sariska ranges from 540 to 777 m. The vegetation of Sariska corresponds to northern tropical dry deciduous forests (subgroups 5 B: 5/E1 and 5/E2) and Northern Tropical thorn forest (subgroup 6 B) (Champion and Seth, 1968). Wild herbivores found in Sariska include chital (*Axis axis*), sambar (*Rusa unicolor*), and nilgai (*Boselaphus tragocamelus*). Omnivores found includewild pig (*Sus scrofa*) and jackal (*Canis aureus*). Large carnivores found include reintroduced tigers (*Panthera tigris*), leopard (*Panthera pardus*), striped hyaena (*Hyaena hyaena*). STR sustains a comparatively higher density (15 individuals/ 100 km²) of striped hyenas (Gupta et al. 2009). Small carnivores include caracal (*Caracal caracal*), jungle cat (*Felis chaus*), common mongoose (*Herpestes edwardsi*), small Indian mongoose (*H. auropunctatus*), ruddy mongoose (*H. smithi*), common palm civet (*Paradoxurus hermaphroditus*), small Indian civet (*Viverricula indica*) and ratel (*Mellivora capensis*). Rhesus macaque (*Macaca mulatta*) and common langur (*Seminopithecus entellus*),Procupine (*Hystrix indica*), rufous tailed hare (*Lepus nigricollis ruficaudatus*),Indian gerbil (*Tatera indica*), Indian bush rat (*Golunda ellioti*), spiny tailed mouse (*Mus platythrix*), house mice (*Mus musculus*), little Indian field mice (*Mus booduga*) long tailed tree mouse (*Vandeleuria oleracea*), sand coloured Rat (*Millardia gleadowi*), soft fur field rat (*Millardia meltada*), brown rat (*Rattus norwegicus*), house rat (*Rattus rattus*) and pygmy gerbil (*Gerbillus nanus*) are also found in STR.

There are two State Highways, which are over 44 km in length and traverse through the heart of the reserve. There are 29 villages within the Tiger Reserve boundary and approximately 170 villages and a city situated along the periphery of the reserve (**Figure 1**). The human population is over 8500 in the villages inside STR along with a population of 30000 domestic livestock including buffalo, cattle, goat and sheep (Sankar et al.,2008). The people inhabiting these villages are traditionally pastoralist, and their primary source of income is selling milk and its products like condensed milk and clarified butter.

Usually, dead livestock are dumped outside the villages (n=29) which are located inside STR. We recorded 39 livestock carcass around 11 villages during the study.

### Diet

Diet of striped hyena was studied using scat analysis (Wagner, 2006; Chourasia et al., 2012). Hyena scats (n=303) were collected on animal trails and roads (n=44) by systematic search resulting in an effort of 227.25 km during winter and summer from 2013 to 2015 in the entire study area. Hyena scats were identified by the patterns of shape, size and colour, mostly oval to cylindrical-shaped with white or off-white in colour(Bopanna 2013). Each collected scat sample was labelled with date and location (Area, Beat, Range and GPS coordinates). Collected scats were sun-dried and later broken down and washed under running water through a sieve of 1 mm. The scat contents were then teased apart and the remains of different food items such as hair, feather, scales of reptiles, hoof and vegetative matters (grass and fruit seeds) were separated (Mukherjee et al., 1994). Scat contents were then studied under a microscope, identified and recorded following standard methods (Mukherjee et al.,1994). Percent frequency of occurrence (%FO) and relative frequency of occurrence (RFO) were calculated for each food item to understandas to how often striped hyena feeds on a certain food item and relative importance of the food item in their diet (Loveridge and Macdonald, 2003). The %FO is defined as the number of times a particular prey item occurred in the scat in terms of percentage of prey remains. The RFO is defined as the number of times a prey item was encountered in a sample of scats expressed as percentage of total occurrence of all food items. Niche breadth of the species was estimated using Shannon-Winner Index (H) (Krebs, 1999). Following the scat analysis, we randomised the original order of scat samples, and the adequacy of scat samples to assess species richness using rare faction and extrapolation curve (Chao et al., 2014).

We also visited hyena den sites (n=27) to record the predated prey items every week in all seasons. Striped hyenas are known to bring back food to their den sites (Kruuk, 1976; Ilani, 1975). We considered predation whenever we found fresh and intact prey species with canine bite marks of striped hyena.

**RESULTS**

Altogether, 303 scat samples of striped hyena were collected and analysed. The proportion of different prey species in scats got stabilised once a sample of 150 scats was analysed (Fig.2). In total 23 food items were identified in the striped hyena scat samples, wherein remains of large mammals were found frequently. Wild ungulates (sambar, chital, nilgai and wild pig) and domestic livestock (buffalo, cattle and goat) together contributed the most (~56%) in thestriped hyena diet.Rodents, birds, reptiles, hare and small carnivorescontributed 21.45% of striped hyena diet that is unlikely to be scavenged. Vegetative matter consisting primarily of grass and *Zizyphus sp.* seeds contributed 17.95% to the diet of striped hyena. Relative

**Table.1.** Percent frequency of occurrence and Relative Frequency of Occurrence (RFO) of food items in striped hyena diet from scat analysis (n=303)

| Broad Prey Category | Prey Item | RFO | % Occurrence |
|---|---|---|---|
| Domestic Livestock | | **10.72** | **15.18** |
| | Buffalo (*Bubalus bubalis*) | 1.17 | 1.65 |
| | Cattle (*Bos tourus*) | 6.29 | 8.91 |
| | Goat (*Capra aegagrus hircus*) | 3.26 | 4.62 |
| Ungulate | | **45.22** | **64.03** |
| | Chital (*Axis axis*) | 17.25 | 24.42 |
| | Nilgai (*Boselaphus tragocamelus*) | 1.17 | 1.65 |
| | Sambar (*Rusa unicolor*) | 26.34 | 37.29 |
| | Wild Pig (*Sus scrofa*) | 0.47 | 0.66 |
| Rodent | | **11.89** | **16.83** |
| | Indian Bushrat (*Golunda ellioti*) | 0.23 | 0.33 |
| | House Rat (*Rattus rattus*) | 0.47 | 0.66 |
| | Indian Gerbil (*Tatera indica*) | 0.23 | 0.33 |
| | Rat (Unidentified) | 10.96 | 15.51 |
| Primates | | **3.96** | **5.61** |
| | Common Langur (*Seminopithecus entellus*) | 3.73 | 5.28 |
| | Rhesus macaque (*Macaca mulatta*) | 0.23 | 0.33 |
| Birds | | **7.69** | **10.89** |
| | Cattle Eagret (*Bubulcus ibis*) | 0.23 | 0.33 |
| | Peafowl (*Pavo cristatus*) | 6.76 | 9.57 |
| | Parakeet (*Psittacula sp.*) | 0.23 | 0.33 |
| | Grey Frankolin (*Francolinus pondicerianus*) | 0.23 | 0.33 |
| | Rufous Treepie (*Dendrocitta vagabunda*) | 0.23 | 0.33 |
| Rufous tailed hare (*Lepus nigricollis ruficaudatus*) | | **1.4** | **1.98** |
| Domestic Cat (*Felis catus*) | | **0.23** | **0.33** |
| Reptiles | | **0.23** | **0.33** |
| Insects | | **0.7** | **0.99** |
| Vegetative Matter | | **17.95** | **25.41** |

frequency of occurrence and percent frequency of occurrence of each food item found in striped hyena scats are given in Table 1 and Fig.3. The overall diversity of food items in striped hyena diet was 2.22 (H).

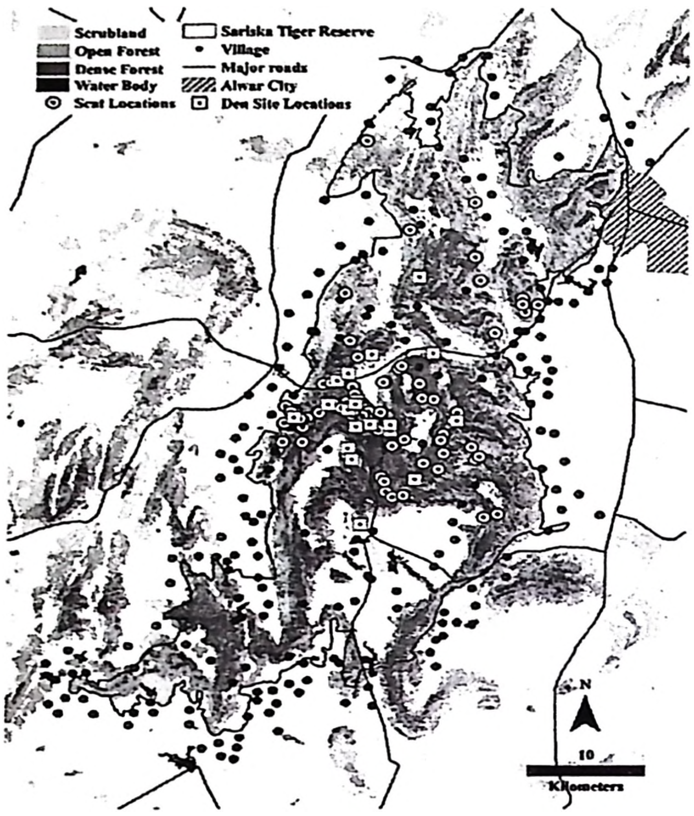


Fig. 1. Sariska Tiger Reserve with villages inside the park and in the periphery

In total, we recorded 39 cases of predation by striped hyena during the study period.Striped hyenas were observed to predate on wild ungulate fawns/calves (48.72%), reptiles (5.13%), ground-dwelling birds such as peafowl and grey partridge (28.21%), small carnivores (7.69), primates (Rhesus macaque juvenile, 5.13%), Rufous-tailed hare (2.56%) and livestock (goat, 2.56%). We recorded fawn/calf(sambar, chital and nilgai, n=18) predation during the onset of winter during November and December when fawns/calves were less than six months old (Fig. 4 & 5).

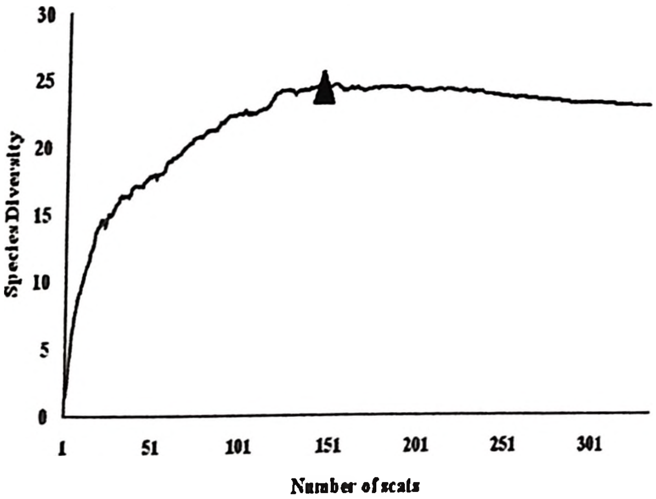


Fig.2. Diet stabilization curve of striped hyena in Sariska Tiger Reserve, Rajasthan

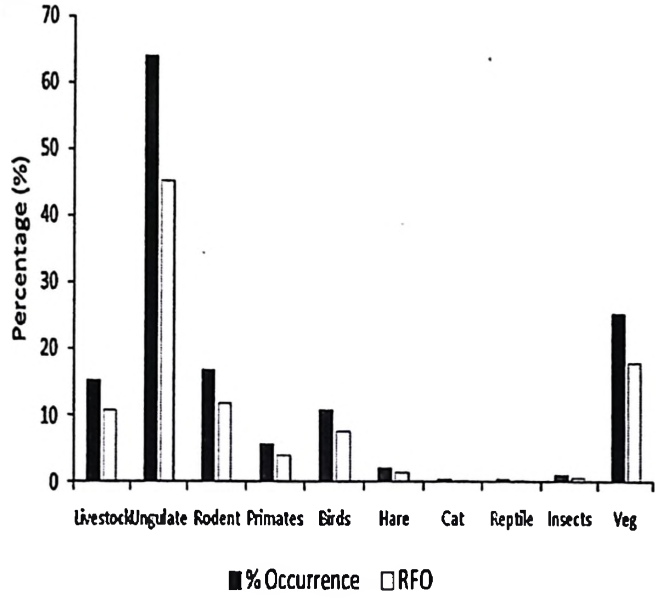


Fig. 3. Percent Frequency of Occurrence (% Occurrence) and Relative Frequency of occurrence (RFO) of different food items in the scat samples (n=303) of striped hyena in STR.

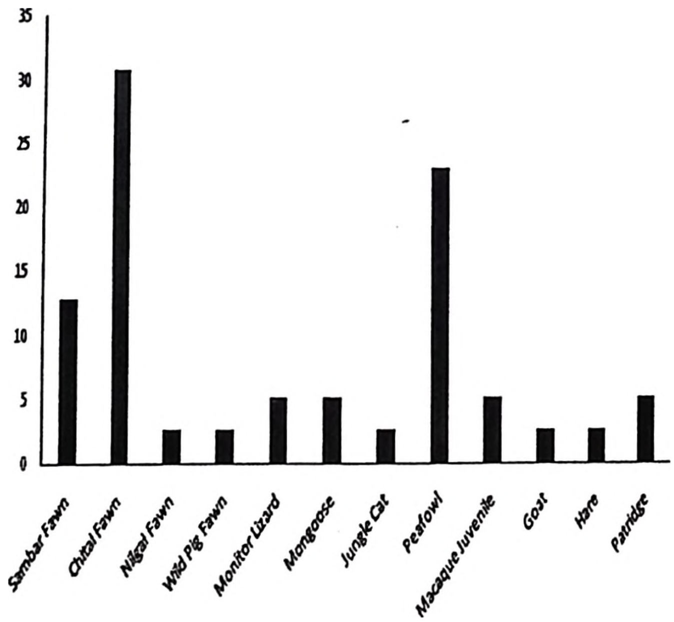


Fig. 4. Percentage of different food items in the kills (n=39) of striped hyena


**Fig. 5.** Camera trap photograph showing active predation of spotted deer fawn by striped hyena

## DISCUSSION

Knowledge about striped hyena ecology is largely known based on studies done in Africa (Kruuk, 1976; Leakey, 1999; Wagner, 2006; Califf, 2013). Our study showed that striped hyenas maintain a catholic diet which is dominated by large mammals (~56%) in the semi-arid region of North-Western India. Inside PA's they rely more on wild ungulates (45.22%) as shown in the present study. However, their reliance on livestock was comparatively less (10.72%), although STR supports a high density of livestock, which was 222 animals/ Km$^2$, (Sankar et al., 2008).This might be attributed to the fact that other carnivores (tiger and leopard) rely less on livestock (~7% and 19% respectively) and more on wild ungulates (approximately 60 – 70%) in the study area (Mondal et al., 2012). STR sustains comparatively high wild ungulates density, 56.2 animals/ Km$^2$ (Jhala et al., 2015). Striped hyena being a scavenger, may likely access these carcass killed by tiger and leopard. Earlier dietary studies on spotted hyena suggest that the striped hyena requires approximately 946g of dry meat/ Day (Nagy et al., 1999). Striped hyena likely requires access to a similar quantity of dietary resources which can be easily met through available food resources (active predation) and tiger and leopard kills (scavenging) in STR.

When comparing the frequency of occurrence of prey species in striped hyena diet with previous studies conducted in STR, it is evident that the utilization rate of both ungulate was 49% during 1990(Sankar and Jethwa, 2002), 70.9% during 2010 – 11 (Chaurasia et al., 2012), and livestock 31% during 1990 (Sankar and Jethwa, 2002) 33.7% during 2010 – 11, (Chaurasia et al., 2012) which was in decreasing trend, while rodents, 1.2% during 2010 – 11, (Chaurasia et al., 2012) and birds, 2.3% during 2010 – 11, (Chaurasia et al., 2012) showed increasing trend over the years (Table 1). Owing to the opportunistic nature of striped hyena, total number of prey species recorded depends very much on the sample size. Both the studies recorded only nine food items in hyena diet and had a low sample size (n=26 and n=86) as compared to the present study (n=303). Our study reveals that the proportion of different prey species in scats got stabilised when a sample containing 150 scats of striped hyena were analysed. Hence, it is suggested that the sample size of atleast 150 scats should be analysed so as to understand the food habits of striped hyena in the study area.

The diet diversity of striped hyena in STR (2.22) and Gir National Park (2.64) can be compared (Alam et al., 2015). STR and Gir PAs support high availability of wild prey. However, striped hyena diet diversity outside PA in Kachchh [3.08 (H) with 32 food items] was higher (Bopanna, 2013) as compared to both STR and Gir indicating their reliance on a broader spectrum of food resources which may be attributed to the species adaptability and versatility. Traditionally, dead livestock is dumped near villages in India which also serves as food source for scavengers (Chhangani, 2009).

## CONCLUSION

Diet of striped hyenas in the semi-arid areas predominantly consists of large mammals (Alam, 2015; Bopanna, 2013), smaller and rare prey species in African systems (Wagner, 2006). Diet and dispersion of food are widely recognised as a key determinant of group formation (Crook, 1965; Gittleman, 1989; Mills, 1989). Given the difference in diet, greater resource availability and heterogeneity in the Indian semi-arid with African systems, the social organisation of striped hyena may likely to be influenced by the former. Thus, our findings set the stage for further investigation of their sociality in this habitat concomitant to extant resources.

## ACKNOWLEDGEMENTS

We would like to thank Director, Dean and Research Coordinator, Wildlife Institute of India, Dehradun for their encouragement and support extended to the study and Rajasthan Forest Department for necessary support and permissions to carry out the fieldwork. We sincerely thank Dr. T. Ramesh, SACON for reviewing our manuscript. We would also like to thank Rajesh Meena and Ratanlal Gujjar for their assistance and support during the field work.

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DIBYENDU MANDAL[1], DIBYADEEP CHATTERJEE[1], QAMAR QURESHI[1] AND K SANKAR[2*]

# Behavioural observations on interaction of leopard and striped hyena, western India

**Interspecific interactions are crucial for community composition since they govern species distribution, abundance and broadly species coexistence. Interspecific interactions among carnivores have been well studied in India. However, these were limited to a few species only and direct observations are rare. Studies on interspecific interaction between two sympatric carnivores such as leopard and striped hyena with a wide distribution range throughout peninsular India are rare. We report two instances of interactions between leopard *Panthera pardus* and striped hyena *Hyaena hyaena.* In one instance, a leopard and a striped hyena were photographed feeding together on an adult nilgai *Boselaphus tragocamelus* kill of a tigress *Panthera tigris.* We have also recorded a breeding female leopard that killed a striped hyena (sub-adult female) at a densite. We report here photographic evidence on these interactions between leopard and striped hyena for the first time.**

Leopard and striped hyena largely coexist with tiger in most of its distribution range in the Indian sub-continent. Although leopard is a predator, it sometimes demonstrates opportunistic behaviour and scavenges on tiger kills (Prater 1965). Leopard interaction with tiger has been well documented. However, literature on leopard interaction with striped hyena is limited. Heptner & Sludjkij (1982) had suggested that leopard competes with striped hyena for food and shelter. As striped hyena and leopard are both generalists, their diet niches also overlap considerably (Arivazhagan 2005). Many instances of striped hyena chasing leopards from their prey have been recorded (Pocock 1941, Prater 1965).

We present two different observations of leopard and striped hyena interaction. We located an adult nilgai kill of a tigress in the morning of 4 April 2015 in Sariska Tiger Reserve (76°17' to 76°34' E / 27°5' to 27°33' N), which is situated in the semi-arid region of western India. The tigress consumed hardly 20% of the kill and left it. We deployed camera traps to understand visitation by other co-predators at the kill. A leopard, possibly a female and a striped hyena have been camera trapped feeding together on the same carcass. The leopard came first to the kill and started feeding on it. The striped hyena appeared at 19:56 h encircling the kill, which hyenas often do when they approach a conspecific at a feeding site (Supporting Online Material SOM Figure F1a). They fed on the carcass for 10 minutes without showing any kind of aggression (Fig. 1a & SOM F1b).

Kleptoparasitism has been reported in leopards. However, striped hyena and leopard feeding together has been recorded for the first time to our knowledge. We continued camera trapping for a few days and searched for any evidence of aggressive interaction, but we did not find anything. Later the tigress came back to the kill and consumed it (Fig. 1b).

In another incident, a leopard with two cubs killed a striped hyena in Sariska Tiger Reserve on 24 December 2014. The killed hyena was from a breeding clan. The clan consisted of a breeding female, two sub-adult helpers and three pups. Sub-adult striped hyenas babysit for their mother at dens and ensure the sur-vival of young pups (Jhala 2013). They can be fatal for young leopards. Their den site was inside the leopard's home range. The leopard detected the den and later killed the helper striped hyena possibly to protect her cubs from any potential danger (Fig. 2a, b & SOM F2). We found the carcass of the striped hyena next to the den. Initial examination of bite marks and indirect evidence such as pugmarks revealed that the hyena was killed by a leopard. However, the carcass was left untouched. Consequently, the clan left the den site after the loss of the female sub-adult helper hyena.

Sariska Tiger Reserve has a healthy population of both leopard (Mondal et al. 2012) and striped hyena (Gupta et al. 2009) and a reintroduced tiger population. The reserve has an excellent prey base to sustain its carnivore population (Gupta et al. 2009). Both leopard and striped hyena can survive in human-dominated landscapes (Athreya 2010), and their body weight and ecological requirements are similar. Direct observations of interspecific interaction between leopards and striped hyenas are rare. Our observation will certainly add to the limited existing knowledge of this subject. We recommend further detailed studies for the conservation of these two large carnivores.

**Acknowledgement**

We would like to thank Rajasthan Forest Department for necessary permissions for the project. We thank the Director, Dean and Research Coordinator of the Wildlife Institute of India for facilitat-ing the project work and for their support. We also thank Parag Nigam and P. K. Malik for their encouragement. Sariska Tiger Reserve staff and our field assistants Ratan, Rajesh, Mamraj and Jairam are also thanked for their help in the field.

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Supporting Online Material Figures SOM F1a, b and F2 are available at www.catsg.org.

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**Fig. 1.** Camera trap photographs showing (a) leopard and striped hyena feeding together and (b) tigress approaching her kill after the leopard and the striped hyena left.

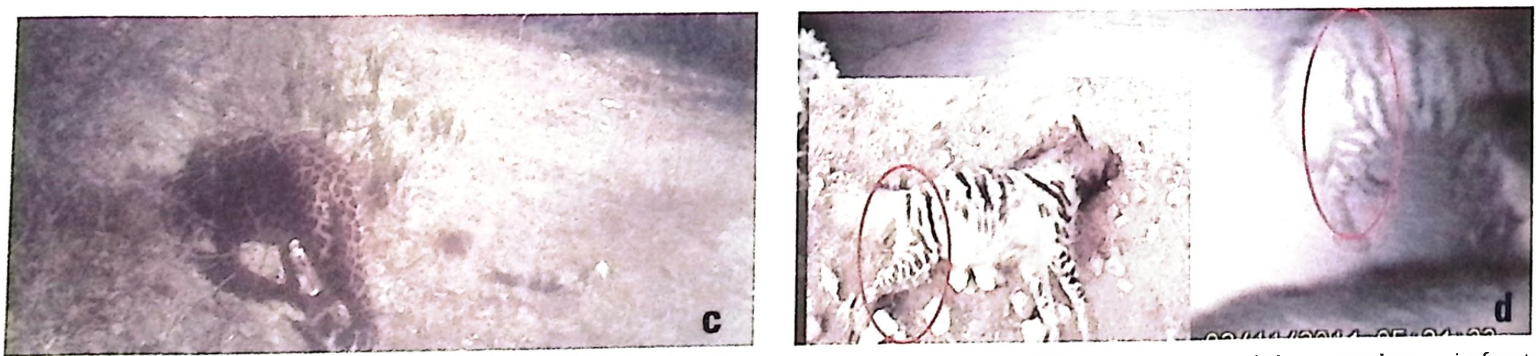

**Fig. 2.** a) leopard investigating the den-site of striped hyenas, b) female sub-adult striped hyena carcass and the same hyena in front of the den.

**Mandal D., Chatterjee D., Qureshi Q. & Sankar K. 2018. Behavioural observations on interaction of leopard and striped hyena, western India. Cat News 67, 20-21. Supporting Online Material.**


**SOM F1**. Camera trap photographs showing a) leopard at and striped hyena approaching the kill and b) feeding together.


**SOM F2**. Leopards close to the densite (indicated by red circle) of triped hyenas.

# The Striped Babysitters

FOLLOW THE RESEARCH

## Often regarded as solitary animals, the fascinating social life of striped hyenas at Sariska is also astonishing.

TEXT: DIBYENDU MANDAL

Ten years ago, I would have described striped hyenas as 'nocturnal solitary scavengers'! My sources would have been Prater's *The Book of Indian Animals* – the bible for Indian mammals, Google and regular doses of National Geographic broadcasts. Prater describes striped hyenas as lone scavengers. A simple Google search shows images that support the theory that this species is a loner, while NatGeo often shows hyenas to be mighty scavengers with strong jaws, snatching another predator's kills. However, there's more to their ecology.

Why are some species solitary and others social? Most (85%–90%) terrestrial mammalian carnivores are solitary, interacting exclusively with their mates and offspring or other individuals at territorial boundaries, the rest are gregarious. A typical example of solitary and social carnivores would be tigers and lions. Conventional ecological theory suggests that sociality evolved to take down large-bodied prey and for protection. However, there are animals such as the European badger and red fox that forage individually but live communally. A seminal study by Dr. David MacDonald published in Nature in 1983 tried to explain the underlying reasons of such social behaviour, citing resource heterogeneity to have allowed animals to share space and form groups at low costs. Co-operation may arise secondarily in these circumstances, but a lot can be understood about the evolution of group formation by studying these loosely social animals.

The hyena family is remarkably diverse in their degree of sociality and food habits providing a unique opportunity to study carnivore social evolution. Although the aardwolf *(Proteles cristata)* remains solitary during the non-breeding season, it forms monogamous pairs during the breeding season and feeds on termites. The brown hyena *(Hyaena brunnea)* lives in groups of up to 14 individuals and are scavengers like the striped hyena. Spotted hyenas *(Crocuta crocuta)* are pack hunters who lives in complex, hierarchically ordered, female-dominated groups containing up to 90 animals. Such diverse range of social complexity and feeding habits is unparalleled to most animal families. However, all these three species are confined to the African continent. Only striped hyenas are distributed outside Africa, giving us a perfect opportunity to study them in diverse habitats from the savannah to the outskirts of villages or big cities. Striped hyenas are tolerant

Semi-arid striped hyena habitat with human settlements visible along the valley

Pups waiting for the babysitter ... (Camera Trap I...

Babysitter arrives with food (chital fawn) for the pups at the den (Camera Trap Image: Dibyendu Mandal/ WII)

Babysitter ... (resting) along with pups at the den ... Dibyendu Mandal/ WII)

and often live in close human proximity. They have an amazing ability to survive in landscapes dotted with settlements despite the fact that they often get killed on roads or come into conflict with humans. But why should we study them in different habitats?

Seminal studies in Kenya first showed that striped hyenas have complex social organisation. A comparative study from two areas in Kenya shows that their sociality is influenced by patterns of food resources across the landscape. However, striped hyenas do not interact much with their hyena neighbours in Kenya. On the contrary, research in India has discovered that striped hyenas regularly interact with others at the dens. This finding is of profound importance. Greater food availability coupled with patchy space for den-building devoid of disturbance may have influenced striped hyena sociality in the risky human-dominated landscapes of India. However, further focused research is necessary.

My doctoral work aims to find out their resource availability, sociality and survival rate in the semi-arid reserve of western India – specifically at Sariska Tiger Reserve – to shed light on the underlying reasons of group formation in a comparative context. Unlike their African counterparts, our findings suggest that Indian hyenas form den-centric clans that consist of a breeding female, multiple adult females and pups. These adults or sub-adults, mostly females, babysit the pups. We have recorded 11 individuals, including three pups, at one den during our six-month-long monitoring. They were highly interactive at their dens, engaging in social play, grooming, greeting, proximity resting, feeding, food provisioning behaviour, and vigilance over pups. Interactions mostly occur during the twilight hours with a peak during dawn when adults returned from foraging. Adults, other than the breeding female, play a crucial role in rearing and survival of pups. Male tenure-ship or role in the clans is still to be looked into. However, males seem to be nomadic and don't help in rearing pups.

This may be due to the greater food resource availability in Sariska. Striped hyenas in Sariska not only scavenge on ungulate and livestock carcasses, but also hunt smaller prey at times. Given their daily food requirement (1 kg/ day), greater food availability might have reduced competition and allowed them to share space with conspecifics. However, their requirement for inviolate areas to build dens may have led to such complex social systems. Presence of adults/ sub-adults as helpers or protectors may be the reason for higher survival rate of striped hyenas in Sariska. Discover more about hyenas and evolution of sociality by following my research in the upcoming years.

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I sincerely thank the Director and Dean of Wildlife Institute of India for their support and encouragement throughout the study. I also thank Dr. Parag Nigam and Dr. P. K. Malik for their continuing encouragement and help during the study. I thank Rajasthan Forest Department for necessary permissions and field support.

Supervisors: Dr. K. Sankar and Shri. Qamar Qureshi

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May 18, 2018

Dibyendu Mandal
Research Fellow
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dibyendu@wii.gov.in

Dear Dibyendu:

We are pleased to invite you to the Society for Conservation GIS 21st annual conference in Monterey, CA, USA from July 15 - 18, 2018 to present your scientific work: '***Influence of traffic regulations on striped hyena (Hyaena hyaena) population dynamics in a semi-arid protected area of North-Western India***'. This conference is part of your scholarship award from SCGIS and all travel, food and lodging related to this conference are included in your award.

This letter of invitation may be used to support applications for permission to attend the conference, for purposes of obtaining independent financial support for your participation, and in support of an application to the US Embassy in your country of residence for a visa to enter the United States for attending the SCGIS conference of 2018. This letter is specific to the person named in the address field and may not be transferred.

The venue is Asilomar Conference Center, located on a marine sanctuary in a state park of California. We are pleased to offer you this additional experience as part of your scholarship award.

Sincerely yours,

Sandra Coveny

SCGIS Conference Committee

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May 7th, 2018

Mr. Dibyendu Kumar Mandal
Wildlife Institute of India
Chandrabani, Dehradun
Uttarakhand, India
248001

Dear Mr. Mandal

We are writing to invite you to participate in the biennial meeting of the International Society for Behavioral Ecology (ISBE 2018) to be held at the Minneapolis Convention Center in Minneapolis, Minnesota USA from the 11th to the 16th of August 2018.

We have received and processed your registration for the meeting. We are pleased to invite you to make a presentation at the ISBE 2018 entitled "**Solitary but social: Resource heterogeneity governs sociality of striped hyena in India.**" You can check the details of your registration at our conference website z.umn.edu/isbe2018.

The International Society for Behavioral Ecology (www.behavecol.com) was founded in 1986, and is the pre-eminent learned society in the field. The society publishes the journal *Behavioral Ecology* (https://academic.oup.com/beheco) and organizes an international meeting every other year. The Minneapolis meeting will be the society's 17th international meeting.

Faculty from the University of Minnesota are organizing this event on behalf of the society. The organizers expect that 800 to 1000 scientists from at least 20 different countries will participate. Your participation in this scientific conference will provide the opportunity to learn of the latest developments in our field and to interact with your fellow behavioral ecologists from all over the world.

Sincerely

Marlene Zuk

David Stephens

Marlene Zuk
Professor & Chair of the Organizing Committee

David Stephens
Professor & Department Head