RESOURCE PARTITIONING AMONG SYMPATRIC UNGULATES IN KANHA TIGER RESERVE, MADHYA PRADESH, INDIA

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IN
WILDLIFE SCIENCE

Submitted by

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I declare that the thesis titled **"RESOURCE PARTITIONING AMONG SYMPATRIC UNGULATES IN KANHA TIGER RESERVE, MADHYA PRADESH, INDIA"** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from January 2014 to June 2020 Under the guidance of Dr. Yadvendradev Jhala Senior Professor and Prof. Qamar Qureshi, and has not formed the basis for the award of any degree, diploma, associate ship, fellowship, titles in this or any other University or other institution of higher learning. I further declare that the material obtained from other sources has been duly acknowledged in the thesis. I shall be solely responsible for any plagiarism or other irregularities, if noticed in the thesis.

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Executive summary 1. Ungulates as a group exhibit a complex yet predictable suite of life- history characteristics. They are characterized by long lives, low adult mortality, delayed reproduction, small litter size, high maternal investment in young and high, but variable, survival rates of young. As a result of those life history characteristics, ungulates exhibit striking competitive abilities. Competition is considered to be a major selective force causing the differential use of resources such as food and space and the consequent morphological and behavioral difference between species. The tropical forest of India supports rich and multi-species assemblages of sympatric ungulates without clear evidence of how communities are likely to be shaped by competitive forces. Moreover, limited studies have addressed population ecology, habitat use and resource partitioning among ungulates in India. Therefore, understanding the mechanism that permits coexistence of ungulate assemblages will help in their conservation and subsequently of large carnivores that subsist on them. In this thesis, I explore the potential mechanisms of how the community of sympatric ungulates in Kanha might partition resources by evaluating i) habitat-specific seasonal densities and spatial co-occurrence of ungulates; ii) demographic parameters; iii) temporal activity and food habits of ungulates, and; iv) factors affecting their group size. 2. My study area was ~ 2074 km2 Kanha Tiger Reserve comprising inviolate Kanha National park (core zone devoid of human settlements and use) and the multiple-use area (buffer zone; consisting of forest and ix revenue land, used by rural communities for farming and livestock rearing). The Kanha National Park is formed by the catchments of two rivers, Banjar and Halon. Since, its inception as a national park in 1955, the Banjar catchment gained considerable conservation investment in terms of village relocation and habitat management compared to Halon catchment, which was later added to the National Park in 1976. Kanha is a tropical moist mixed deciduous forest dominated by Terminalia alata, Lagerstroemia parviflora, Anogeissus latifolia ,Madhuca indica., Diospyros melanoxylon, Butea monosperma etc., bamboo (Dendrocalamus strictus) forest, dense stands of sal (Shorea robusta) interspersed with grassland of anthropogenic origin. Ungulates were studied in this area between 2013 to 2018, and the major study species were chital (Axis axis), sambar (Rusa unicolor), gaur (Bos gaurus) while

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Organization of thesis

The thesis is organized into the following chapters:

Executive summary: Synthesizes and concludes the key findings of the objective chapters.

Chapter 1. Introduction and study area: Introduce mechanism of resource partitioning among sympatric ungulates. Gives a brief overview of ungulate ecology and the background of the study. Discusses and reviewed literature about the species biology, status and distribution, demography and food habits. Elucidates the major questions posed in the dissertation and the hypotheses behind each of those ecological queries. Also discusses the primary objectives of the thesis. Informs about the area where the study was conducted, its vegetation and climatic factors, its faunal and floral assemblages and anthropogenic relationships.

Chapter 2. Habitat use of ungulates: This chapter represents habitat specific seasonal densities and biomass of ungulates; their habitat use and status in different management regimes.

Chapter 3. Demographic parameters of ungulates: This chapter deals with population trend, sex ratio, age structure and body condition of ungulates in different conservation investment areas of Kanha.

Chapter 4. Factors affecting group size of ungulates

This chapter represents the factors how group size of ungulates is formed.

Chapter 5 Resource partitioning among sympatric ungulates

This chapter deals with resource partitioning among sympatric ungulates in the context of space, time and food.

Executive summary

1. Ungulates as a group exhibit a complex yet predictable suite of life-history characteristics. They are characterized by long lives, low adult mortality, delayed reproduction, small litter size, high maternal investment in young and high, but variable, survival rates of young. As a result of those life history characteristics, ungulates exhibit striking competitive abilities. Competition is considered to be a major selective force causing the differential use of resources such as food and space and the consequent morphological and behavioral difference between species. The tropical forest of India supports rich and multi-species assemblages of sympatric ungulates without clear evidence of how communities are likely to be shaped by competitive forces. Moreover, limited studies have addressed population ecology, habitat use and resource partitioning among ungulates in India. Therefore, understanding the mechanism that permits coexistence of ungulate assemblages will help in their conservation and subsequently of large carnivores that subsist on them. In this thesis, I explore the potential mechanisms of how the community of sympatric ungulates in Kanha might partition resources by evaluating i) habitat-specific seasonal densities and spatial co-occurrence of ungulates; ii) demographic parameters; iii) temporal activity and food habits of ungulates and; iv) factors affecting their group size.
2. My study area was ~ 2074 km^2 Kanha Tiger Reserve comprising inviolate Kanha National park (core zone; devoid of human settlements and use) and the multiple-use area (buffer zone; consisting of forest and

revenue land, used by rural communities for farming and livestock rearing). The Kanha National Park is formed by the catchments of two rivers, Banjar and Halon. Since, its inception as a national park in 1955, the Banjar catchment gained considerable conservation investment in terms of village relocation and habitat management compared to Halon catchment, which was later added to the National Park in 1976. Kanha is a tropical moist mixed deciduous forest dominated by *Terminalia alata, Diospyros melanoxylon, Lagerstroemia parviflora, Anogeissus latifolia, Madhuca indica, Butea monosperma* etc., bamboo (*Dendrocalamus strictus*) forest, dense stands of sal (*Shorea robusta*) interspersed with grassland of anthropogenic origin. Ungulates were studied in this area between 2013 to 2018 in the subset, and the major study species were chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*) while status, population trend and habitat-specific densities were obtained for all ungulates (barasingha (*Rucervus duvaucelii branderi*), wild pig (*Sus scrofa*), barking deer (*Muntiacus vaginalis*), chousingha *(Tetracerus quadricornis*) and nilgai (*Boselaphus tragocamelus)* that co-occur in Kanha Tiger Reserve except mouse deer (*Moschiola indica*) and blackbuck (*Antelope cervicapra*) (which were reintroduced and too few for quantitative analysis). Line transect based distance sampling, camera trap-based photo captures, and scan and focal animal sampling were conducted to derive information on habitat-specific densities, population trend over the years, other demographic parameters (age and sex structure and body condition), habitat use, food habits and temporal activity patterns of different ungulates.

3. Conservation practitioners require habitat-specific seasonal species densities for habitat management. Herein, we used habitat-specific stratified distance sampling in Kanha Tiger Reserve (KTR) with 200 spatial transects and an effort of 1200 km walk in the combined year 2013 and 2014. The analysis was done to examine a) impact of anthropogenic use and b) effect of seasonal habitat on ungulate densities in KTR. While a single detection function for each species was used for estimating density within the human-restricted core and multiple-use buffer of KTR, species-specific seasonal detections were modelled for each habitat. Habitat type was determined by remote sensing classification and ground validation.
4. Four habitat types could be easily distinguished by Remote Sensing as well as on the ground; these were a) Grasslands (9%), b) Sal (24%), c) Bamboo-mixed (19%), d) Miscellaneous forests (48%). Ungulate biomass was 4.8 times higher in the inviolate core area compared with the buffer zone. The core supported herbivore density and biomass (mean ± standard error) of 50 ± 4.80/km^2 and 26,806 ± 2573 kg/km^2, respectively. Chital was found to be most abundant, having a density of 30.1 ± 4.34/km^2 and contributing 33 % of the biomass with a habitat preference for grasslands (106 ± 39/km^2). Sambar had the highest density (15.4 ± 3.34/km^2) in bamboo-mixed habitat. Gaur contributed 39 % of the ungulate biomass and showed a seasonal shift in density from sal forests (9.65 ± 3.55/km^2) in summer to miscellaneous forests (8.13 ± 1.94/km^2) in winter. Barasingha was restricted to grasslands with a density of 1.56 ± 0.76/km^2. Chousingha was rare (0.1 ± 0.04/km^2), found

mostly in miscellaneous forests and plateau grasslands. Grassland and bamboo-mixed forests (28% of the KTR) supported 58 % of the total ungulate biomass. Management should strive to create an optimal habitat mosaic that maintains ungulate diversity and density while addressing the specific needs of endangered species.

5. Identifying primary predictors of population productivity and changes in abundance constitute challenges for effective conservation and management of ungulates. Demography studies help us to understand the drivers of changes in abundance over space and time, more specifically related to how underlying vital rates (such as survival, growth, and reproduction) structure populations. Demographic parameters of wild ungulates would differ with respect to conservation investments within the park. I obtained long term data (2013-2018) on ungulate seasonal density to estimate population trends using line transect based distance sampling in Banjar (high conservation investment area) and Halon catchments (low conservation investment area). Age and sex structure, female-fawn ratio, and body condition of ungulates were evaluated in both Banjar and Halon catchments of KNP. Chital and sambar showed significant growth in Banjar catchment (chital; $r=0.09$, $SE=0.01$, $P<0.01$ and sambar; $r=0.06$, $SE=0.02$, $P<0.05$) while gaur showed significant growth in Halon catchment ($r=0.25$, $SE=0.07$, $P<0.01$). Sex ratio of chital and gaur were skewed towards females while sambar in Halon catchment showed male biased sex ratio. Though Banjar catchments had higher growth rate, ungulates had better body

condition in Halon catchment, suggestive of ungulate populations nearing carrying capacity in Banjar.

6. Theory suggests that group size in ungulates is determined by tradeoffs between forage availability, intraspecific or interspecific competition for food, and predation risk. I investigate the probable factors of group formation in ungulates (chital, sambar and gaur) in Kanha National Park. I hypothesized that grouping in ungulates depends on season, habitat type, ungulate density, predator density or a combination of these factors. To test this postulate, I modelled ungulate group size as a function of their density, carnivore density, habitat type and season. Spatially Explicit Capture Recapture models (SECR) for carnivores and Density Surface Modelling (DSM) for ungulates were used to determined their spatial densities. Pearson's correlation coefficient analysis was done to explore relationships between group size and ecological variables. Factors influencing the mean group size such as season and habitat were analyzed using two-way Analysis of Variance (ANOVA) to understand the individual effect and interactive effect of these factors on group size. Since both tiger density and ungulate group sizes were highly correlated to ungulate density, I first removed the variation explained in both group size and tiger density attributed to ungulate density by partitioning out the effect of food availability (density) and subsequently tested for influence of predation on group formation. I found a significant relationship ($P=0.07$ for chital and $P=0.05$ for sambar) that explained 7-8% variation in group sizes of chital and sambar accounted for by tiger density. Larger group size of chital were found in open habitat of

grasslands within high tiger density area. Group size of sambar also showed positive correlation with tiger density but in closed habitat, while grouping of gaur in different habitat was more of a function of resource requirements than a response to higher perceived predation risk from tiger. Results of this study highlight that ungulates do respond to food availability as well as to predator density by forming larger groups.

7. Understanding how species partition resources to coexist is integral to understanding ungulate resource ecology. I studied chital (65 kg), sambar (205 kg), and gaur (800 kg) of different body size and digestive strategy for understanding resource partitioning at three different scales (space, time, and food). I investigated seasonal variation in space use using density surface modelling. Seasonal food habits, diet niche breadth and diet niche overlap of ungulates in different habitats were derived using focal animal sampling where observations were quantified as bite counts (number of bites of a particular food item). Proportional use of different habitats for foraging was estimated in both summer and winter. Apart from chital, sambar and gaur, temporal activity pattern of barasingha, wild pig and barking deer in Kanha was also analyzed through photo-captures. Gaur and sambar co-occur at high densities in areas with low chital densities for both summer and winter season. All ungulates showed bimodal activity patterns with crepuscular peaks in activity. Chital primarily used grassland habitat for foraging. *Desmotachya bipinnata* and *Chloris barbata* contributed 15.35% and 13.03 % to the annual dry matter intake, respectively. Sambar and gaur primarily used bamboo-mixed habitat for foraging. *Dendrocalamus*

strictus contributed 49.57% for sambar and 27.51% for gaur annual diet. The diet niche breadth of sambar and gaur were relatively narrower than chital in both summer and winter. During winter in Kanha, food resources are abundant and diverse, and hence less overlap (15%) was observed between chital and gaur. However, during summer, food in general is dry and scarce and of low nutritional value, dietary overlap increases (46%) between chital and gaur overlap in grassland (55%) and miscellaneous forest (31%). Gaur grazing is likely to result in grazing facilitation for chital. The term “facilitation” is well established in ungulate literature in Gwyne and Bell’s research on Serengity (1968) between large and small bodied ungulates. In contrast, gaur and sambar showed high overlap in winter (76%) than summer (9%), especially in bamboo-mixed (94%) and miscellaneous forest (76%). Surplus resources, abundance of a preferred food type and use of high elevation areas in these habitats in winter, allow both species to coexist in harmony, by avoiding competition.

8. In this study, I document and investigate resource use in ungulate systems and how those resources are partitioned across space and time. My study revealed that ungulates in Kanha are habitat specialists except gaur which showed differential seasonal use of habitats. Maximum diversity and ungulate biomass were supported by grasslands followed by bamboo-mixed habitat. Grasslands account for 9% of the Kanha National Park, and is managed as an arrested successional stage by woody plant removal and fire. Enhancing grassland habitat along with its appropriate management would help maintain ungulate diversity and

increase ungulate biomass. My study stresses the importance of human free core areas and the need for conservation investments for achieving high ungulate densities and biomass that are essential to sustain source populations of tigers and other endangered carnivores in this landscape. Habitat specific demographic responses of ungulates guide managers to invest in appropriate conservation strategies. My results indicate that when species have evolved together, like chital, sambar and gaur, the observation of overlap in resource use in different seasons is likely to be indicative of the absence of food limitation and thus of the absence of competition. Although I did not explicitly test the hypothesis whether or not shared resources are limiting, generally good physical condition (estimated visually) even at the end of the summer season showed no apparent indication of limited resources. My study provides insight into the importance of resource partitioning, conservation investments, seasonality of habitats use and diet composition amongst sympatric ungulates, that in turn determine their demographic response. The above information will be useful for the conservation management.

Chapter 1. Introduction & study area

1.1 Mechanism of coexistence: Resource partitioning among sympatric ungulates

One of the vital goals in community ecology is to unveil the structuring drivers of multi-species assemblages (Connor & Simberloff 1979; Hopf et al. 1993; Amarasekare 2003). It helps in understanding the conditions allowing species coexistence and determining species spatial distribution, identifying how sympatric species use and share space and resources, interspecific interactions and relative roles of environmental factors (Redfern et al. 2006; Ritchie et al. 2009).

Resource partitioning among sympatric ungulates can help scientists understand how aggregate ecological processes impact species extinction (Giller 2012). Competition is causation in the evolution of adaptations that enables resource partitioning by coexisting species. Competition should be minimal to non-existent for species pairs that diverge the most in their physiological and behavioural characteristics resulting in the selection of different habitats and foods. Still, competition would be intense for sympatric species with similar niches which compete for common resources that are in short supply. (Schoener 1974 & 1986; Schaller 1977).

Resource partitioning amongst African ungulates has been widely studied (Jarman, 1979; Jarman & Sinclair 1979; Hanley & Hanley 1982; Gordon & Illius 1989; Voeten & Prins, 1999; Forsyth 2000). Characteristics that influence the potential for competitive interactions among species are multidimensional and relate to the various axes that describe the niche of a species. These characteristics include feeding adaptations, physiology (Hofmann 1989), body size (Demment & Van Soest 1985), and season (Thill et al. 1987). Hofmann (1989) categorized ruminants into three categories based on gastrointestinal anatomy; concentrate selector or browser, intermediate feeder, and grazer or roughage feeder. Four morphological characteristics of ungulates influence forage preferences. They can help in the assessment of interspecific interactions: body size, type of digestive system, rumino-reticular volume to body weight ratio, and mouth size (Hoffman 1989). Considering these four factors, Hanley and Hanley (1982) highlight that understanding selective foraging patterns of ungulates provides insight on the dietary overlap and subsequently, food resource partitioning in sympatric ungulate species.

1.2 Ungulate ecology

Ungulates are an integral component of most terrestrial ecosystems (Scholes & Archer 1997; Dharani et al. 2008; Dobson 2009); regulating nutrient recycling (McNaughton et al. 1997; Augustine 2003; Murray et al. 2013); modifying vegetation community structure (Milchunas et al. 1988); composition (Augustine & McNaughton 1998); biomass production (McNaughton 1976) and reducing the incidence of fire with the removal of flammable biomass (McNaughton et al. 1988; Van de Vijver et al. 1999). Ungulates also impact the ecology of large carnivores (Sinclair et al. 2003). Ungulates are distributed worldwide (except Australia and Antarctica) and exhibit a remarkable diversity in body sizes ranging from the 3-kg chevrotain to the 4-tonne elephant. Diversity of ungulates is particularly rich in Indian subcontinent representing 39 species from 23 genera, seven families and two orders (Prater 1980; Wilson & Reeder

2005), which constitute nearly 15% of the extant ungulate species globally today (Wilson & Reeder 2005).

Free-ranging large ungulates have disappeared from many parts of Asia. Their populations are dwindling globally in terms of distribution and abundance (Schipper et al. 2008), specifically in India (Madhusudan 2004). While much of India's tropical forest habitat has shrunk due to human activity, the rapid spread of invasive species like *Lantana camara* and *Pogostemon* species in wildlife habitats does not bode well for ungulates in India either (Ahrestani 2009). Moreover, today less than 5% of their landscape is available as natural and undisturbed habitat (Ahrestani 2009), which is mostly confined to Protected Areas (Karanth et al. 2009, 2010).

1.3 Background of the study

Forested habitat in India is different from the open sparsely wooded savanna landscape in Africa from which much of the understanding of large herbivore ecology has emerged. However, due to the difference in forest structure, prey availability and biogeographical realm, we cannot generalize findings same for Indian scenario. The tropical forest of India sustains species-rich and high abundance ungulate assemblages without clear evidence of competition for resources. Therefore, it is necessary to incorporate spatial dimension into our thinking on resource partitioning of ungulates. Despite historical interventions of man (hunting and illegal fire) in the elimination of many of the large mammals, many terrestrial systems in tropics especially Kanha Tiger Reserve still supports rich and varied large herbivore species coexistence (Ahrestani et al. 2011).

Kanha Tiger Reserve is accustomed to intensive habitat management practices such as burning practices and village relocation, which creates a need for better understanding of ungulate-habitat relationships. Past annual burning practices from 1903-1972 resulted in decrease/ shrinkage of grasslands in Kanha. Although annual burning if properly controlled and managed, favours the availability of young grass to ungulates but continuous burning over the years in Kanha grasslands without controlling measures, brought an adverse situation. However, after observing the regression of grasslands, burning practices were stopped by the management authorities in Kanha after 1972. Complete protection from fires resulted in encroachment of coarse, unpalatable and weedy plants for e.g. *Pogostemon* species and *Desmotachya bipinnata* and encroachment of woody species such as *Butea monosperma, Lagerstroemia parviflora* and *Diospyros melanoxylon*. Due to its anthropogenic nature and climatic climax, these woody species colonized in grassland and gradually created favourable conditions for other tree species to grow. This causes drastic changes in the habitat structure of Kanha.

Kanha management had also taken a major initiative to relocate villages from the park and hence reclaimed more than 10,000 hectares of land. This proved to be a crucial measure for ungulates, especially for barasingha and chital in the conservation history of Kanha. Since 1969, many scientific studies were mostly focussed on barasingha to recover their population in Kanha. Therefore, a shift in management practices favourable for barasingha survival resulted in the decline of Kanha’s small population of blackbuck, an endemic Indian species and the only true Indian antelope, which thrive in extensive meadow habitats. Blackbuck also got extinct from terai area of Dudhwa National Park when their habitat was declared protected against anthropogenic pressure (Qureshi et al. 1994). The extinction was because of the increase in grass height altering predation regime on this species. Compared to studies of community ecology of Africa, Europe and North America, there is little understanding of mechanisms of habitat and resource partitioning of large mammalian herbivores in Asia and how they differ in their seasonal habitat selection and diet, in order to coexist (Ahrestani et al. 2012). Studying, understanding and documenting the mechanism that permits the coexistence of the ungulate assemblages is critical in Kanha especially in the presence of two equal density top predators; Tiger (*Panthera tigris*) and Leopard (*Panthera pardus*) in the Reserve.

1.4 Review of literature

1.4.1. Study species biology

There are nine ungulate species coexist in Kanha Tiger Reserve **(Table 1.1)**. I have studied three major ungulates, differing in body size and diet to understand habitat use and resource partitioning among them. The study species are chital, sambar and gaur. However, we also gathered information on habitat-specific densities, population trend and temporal activity pattern of barasingha, wild pig, barking deer and chousingha. The body size of the study species ranged from 18 kg barking deer to an 800-kg gaur (Karanth & Sunquist 1992), and they also occupied a wide range of habitat niches ranging from dense forests to open woodland and forest-edge habitats.

Before doing any study on ungulate-habitat relationship, an understanding of individual species biology is required.

a. **Chital *(Axis axis)*:** Chital (family Cervidae; commonly known as spotted deer) was once historically the most common ungulate distributed nearly throughout India, but now its distributional range is contracted drastically to about 36%, limited mostly to protected areas (Karanth et al. 2009, 2010). However, they are locally abundant in some protected forests. They live in social groups and may even form temporary herds of 100-200 individuals during periods of high forage abundance. Their body sizes generally range between 40 to 60 kg although large well-grown stags may weigh > 90 kg. Chital prefers open forests and grasslands (Mishra 1982) and avoids steep terrains and evergreen forests (Mishra and Wemmer1987). Chital are preferential grazers (Dinerstein 1980; Tak & Lamba 1984; Mishra & Wemmer 1987). Schaller (1967) found grasses to constitute >60% of their diet in Kanha, Central India. However, chital also readily browse on leaves from many numbers of trees, shrubs and vines and seasonal fruits (Dinerstein 1979; Johnsingh & Sankar 1991). Rodgers 1988 has categorized chital as a generalist feeder, which takes grass, forbs and woody plants in its diet while Hofmann 1985 classified chital based on morpho-physiological ruminant feeding types as an intermediate /mixed feeder. Chital drink water regularly and are known to be intolerant to heat, preferring to rest in the shade. The ecological densities of chital range from 3 to 50 animals km^2 (Dave 2008; Karanth & Nichols 2000; Awasthi et al. 2016).

b. **Sambar (*Rusa unicolor*):** Sambar (family Cervidae) is predominantly a forest ungulate adapted to a variety of habitats throughout India (Karanth et al. 2009). However, nearly one-third of its distributional range has contracted in the past 100 years (Karanth et al. 2010). Its body size varies between 100 to 250 kg, and fully-grown adult stags may weigh ~ 320 kg. Sambar is a large intermediate selective feeder (Hofmann 1989) that prefers dense cover and steep terrain. Schaller (1967) found sambar to subsist on a wide variety of plants in central India. Sambar is also known to feed on various browse such as twigs, bark, wild fruits, shoots and leaves of trees (Sankar 1994). It is known to drink water regularly, and it typically lies up in thickets, when it is not foraging. The ecological densities of sambar range from 1.5 to 10.7 per km^2 (Karanth & Nichols, 2000; Awasthi et al. 2016).

c. **Gaur *(Bos gaurus)*:** Gaur (family Bovidae) is the largest bovid species in the world with adult body masses between 500 to 900 kg, although large bulls may exceed 1000 kg. Gaur was once found widely in the forests of central and south India, but now has one of the most restricted distributional ranges among herbivores (Karanth et al. 2009) with an estimated range contraction of ~60% in the past 50 years (Karanth et al. 2010). Gaur is predominantly a forest grazer and a bulk feeder (Hofmann 1989). It lives in social groups, although adult bull gaurs are usually solitary. It is common to see agglomerations of gaur numbering about 20-40 in feeding groups during monsoon season. It is primarily a grass-roughage eater, and its diet includes coarse and dry grasses, bamboo, leaves and twigs of shrubs, forbs and trees. It occasionally feeds on tree bark as well (Pasha et al. 2002; Ahrestani 2009). Gaur typically lies up in forest clearings. Gaur moves widely compared to other ungulates and is known to drink water at least once a day (Schaller 1967). Gaur populations can undergo severe fluctuations due to disease outbreaks. The ecological densities of gaur vary from 0.6 to 11.3 per km^2. (Awasthi et al. 2016; Karanth et al. 2008). Gaur is absent in arid and semi-arid forests (Karanth et al. 2009).

d. **Swamp deer *(Rucervus duvaucelii branderi):*** The swamp deer or barasingha (family Cervidae) is endemic to the Indian subcontinent. Stags weigh 170-280 kg, and hinds weigh 130-145 kg (Schaller 1967; Prater 1980; Gopal 1995). Central subspecies are present along the grasslands bordering Sal forest and rivers of central Indian highlands (Brander 1923; Spillet 1966; Schaller 1967) which survives only in Kanha. Schaller (1967) in 1965 observed fewer than 100 barasingha in Kanha which increased to 200 in 1974 (Martin 1977) and reached a maximum of 500 in 1988 (Kotwal & Parihar 1992; Gopal 1995). The smallest groups (5-15) were formed during winter, followed by monsoon (10-25) and summer (10-50). Barasingha utilizes a variety of habitat types including open forest where grasses are present mainly marshy, and sandy grasslands observed maximum abundance (Schaller 1967; Martin 1977; Schaff 1978; Singh 1984, Gopal 1995; Qureshi et al. 1995; Khan & Ahmad 2004).

e. **Wild pig *(Sus scrofa*):** Wild pig (family Suidae) is a generalist ungulate widely distributed throughout India (Allwin et al. 2016). It is a social non-ruminant that lives in small groups. Wild pig body size ranges between 25-100 kg. Their food includes root, tubers, bulbs, bark, flowers, fruits, seeds, sedges and soil invertebrates as well as carrion (Spitz 1986). Although wild pig prefers swampy areas, they readily take shelter in thick shrubs and grass thickets. They need water regularly for drinking and may cover considerable distances to do so (Prater 1980). They raid crops periodically and are one of the most widely and illegally hunted ungulates in India (Madhusudan & Karanth 2002). Although prolific breeders, wild pigs are generally found in low to medium densities ranging between 0.4 to 8.0 animals km^2 (Awasthi et al. 2016). Wild pig populations are known to undergo a lot of fluctuations due to disease outbreak (Santiapillai & chambers 1980).

f. **Barking deer *(Muntiacus vaginalis):*** Barking deer (family Cervidae) is a small (< 25 kg body mass) ungulate distributed throughout India, although its historical range has contracted by 40% now. It is a non-social cervid. It is a specialist concentrate feeder and a nibbler, which selectively feeds on nutritiously rich plant matter such as tender grass shoots, leaves, fruits and berries (Hoffman 1989, Ilyas & Khan 2003). It drinks water regularly, with increasing frequency during dry seasons (Putman 1988). It is a forest edge species favouring forest clearings and gap. Barking deer typically live in dense cover but mostly feed in open areas associated with gaps in the forest canopy (Mishra and Wemmer 1987). It is not found in most arid and semi-arid forests and seen in low density in alluvial grasslands (Eisenberg & Seidensticker 1976). Barking deer density estimates range from 0.6 to 7.7 km^2 (Awasthi et al. 2016, Wegge and Storaas 2009).

g. **Chousingha *(Tetracerus quadricornis*):** Chousingha (family Bovidae) is also known as four-horned antelope. It is endemic to the Indian subcontinent. Approximately 95% of its current global population occurs in India (Rahmani, 2001). It weighs around 20-25 kg. It tends to be a solitary species but also occurs in small groups up to three. Existing literature suggests that species prefer 'open' habitats (Chundawat et al. 1999). Species prefer tree- savanna open deciduous habitat (Krishna et al. 2008). Primarily a browser and concentrate feeder (Sharma 2009). It mostly occurs at low densities (usually less than 1/ km^2). They defecate at a particular location coupled with markings with their preorbital glands which are the means of marking territories (Prater 1980, Sharma et al. 2009).

h. Nilgai *(Boselaphus tragocamelus*): Nilgai (family Bovidae) commonly called blue bull and is Asia's largest antelope. They evolved in peninsular India during the Tertiary geological period (Leslie & Sharma 2009). It prefers open grasslands and savannas. It is also locally a significant agricultural pest in India. The premaxillary shape of nilgai suggests them as a mixed feeder (Solounias & Moelleken 1993). Nilgai is less gregarious as compared to other group-living ungulates and occur in small groups throughout the year. The density of nilgai in India varies widely depending on habitat condition, interspecific competition with cattle, predation and degree of protection. Their densities range from 0.23 to 11.36 individuals /km^2 (Khan et al. 1996; Bagchi et al. 2004; Awasthi et al. 2016).

1.4.2. Density and Habitat use

Understanding ungulate habitat use is important in the management of increasing ungulate populations and in assessing the potential for interspecific competition. Habitat selection is strongly influenced by quantity and quality of food (Sinclair 1975; White 1978; Murden & Risenhoover 1993) as well as foraging opportunities (Masse & Cote 2009; Burkepile et al. 2013), the behavioural process by which animal actually chooses habitat (Johnson 1980).

Different field techniques have been employed to assess the habitat use by wild animals which include, radio tracking (Johnson 1980; Thomas & Taylor 1990; McShea et al. 2001) or direct observations (Biggins & Pitcher 1978) or indirect evidence like track counts (Litvaitis et al. 1985; Thompson et al. 1989) and pellet counts (Collins & Urness 1981; Loft & Kie 1988) and line transects based ungulate density (Buckland et al. 2001). A review of the current literature on Asian ungulates shows that following factors may typically influence the ungulate distribution and abundance: habitat type; quality and quantity of forage; shade; water availability; topography; predation pressure and degree of hunting and other anthropogenic pressures. At the global level, several studies have linked ungulate biomass to rainfall (East 1984), soil fertility (Coe 1980) and the primary productivity of the forests (Du Toit & Owen-Smith 1989; McNaughton et al. 1996). Thus, the gradient of plant abundance and nutrient quality often shapes ungulate abundance and community structure (Olff & Prins 2002). History of past human disturbances and consequent creation of secondary habitats (e.g. grassy meadows, eco-tones) through processes such as shifting cultivation, fire, logging also influence both ungulate diversity and abundance. Recent studies have clearly documented the overwhelmingly negative effects of hunting (Madhusudan & Karanth 2002), intensive livestock grazing (Madhusudan 2004), forest biomass extraction (Kumar & Shahabuddin 2006; Karanth et al. 2006) and forest fires (Hiremath & Sundaram 2005) at a local scale in India. At a broader scale, biophysical factors (e.g. water, terrain feature) and eco-climatic features (e.g. deciduousness of the habitat) are also likely to influence forest vegetation (Krishnaswamy et al. 2009; Vaidyanathan et al. 2010), which in turn will influence ungulate abundance and distribution. Furthermore, ecological traits such as body size and diet also impose limits to species abundance levels (Eisenberg 1980; Hudson 1985). Recent studies (Karanth et al. 2008) and empirical observations at a few sites (Khan et al. 1996; Karanth et al. 1999) have shown that management interventions such as relocation of human settlements and effective patrolling could potentially enhance ungulate habitat quality, enabling their increased abundance. Thus, an array of local as well as broad-scale factors linked physical environment, habitat ecology and management will drive spatial variation in ungulate abundance. Only some preliminary studies by Schaller (1967), Eisenberg & Lockhart (1972), and, Berwick (1974) were available until the 1970s. The study of population biology of ungulates gradually increased in South Asia after the 1970s (Seidensticker 1976; Eisenberg & Seidensticker 1976; Martin 1977; Dinerstein 1979, 1980; Mishra 1982; Johnsingh 1983; Karanth & Sunquist 1992; Khan et al. 1996; Bagchi et al. 2004; Karanth et al. 2008; Ahrestani 2009; Wegge & Storaas 2009; Steinmetz et al. 2010; Wang 2010). These studies have reported overall ungulate densities and biomass estimates from different parts of South Asia. Moreover, very few of these have examined the patterns of ungulate abundance in relation to body size, diet and habitat use in different conditions (Schaller 1967, in Sal forests; Dinerstein 1979 and Mishra 1982, in swampy grasslands; Karanth & Sunquist 1992; Khan et al. 1996, in the dry deciduous forest; Bagchi et al. 2004, in semi-arid forests; Wang 2010, in temperate forests, Namgail 2009 in Trans- Himalayan region of Ladakh and Ahrestani 2009 in the moist deciduous forest of south India. Ungulate population densities and biomasses in well-protected sites of the Indian subcontinent are comparable to some of the best African savanna habitats (Eisenberg & Seidensticker 1976; Karanth & Sunquist 1992; Khan et al. 1996). However, the community structure, habitat relationships and habitat use patterns of ungulates in the Indian subcontinent have not been well-explored (but see Shrestha and Per Wegge 2008) as they have been in quantitative studies of African ungulates (Peters & Raelson 1984; Du Toit & Owen-Smith 1989).

1.4.3. Demographic factors

Wildlife conservation and management interest lie in understanding the ‘population trends’, which is being defined as a statistic reflecting average direction and magnitude of change over a specified period of time (Droege, 1990). Rate of increase is described as the annual change in density or abundance of a wildlife population (Hone 1999). Many authors (Caughley & Birch, 1971; Harris 1986; Eberhardt & Simons, 1992; Johnson, 1994) explored aspects of the estimation of the rate of increase and biases. Numerical response (Caughley, 1976, 1980) and demographic parameters such as birth and death rate help us in determining the rate of increase of wildlife population (Caughley 1976; Johnson 1994; Sibly & Smith, 1998).

Environmental stochasticity and sometimes, density dependence play a vital role in herbivore population dynamics in such conditions (Caughley & Gunn, 1993). The study of population dynamics involves the changes that occur over time and the causes of those changes (Johnson, 1994). A very few studies in the subcontinents have been carried out to understand the population dynamics and the demography of ungulates (Graff & Nichols, 1966; Schaller, 1967; Sidensticker, 1976; Ables 1974; Barrette 1991; Khan & Vohra 1992; Shankar Raman 1997). A simple non-invasive field technique to assess the physical condition of ungulate was devised by Riney (1960), which involves the scoring of various body parts of an ungulate individual in the field.

1.4.4. Food habits

The knowledge of the feeding habits of wild animals is critical to effective wildlife management and many phases of ecological research (Talbot & Talbot, 1962). Besides that the studies of food habits have intrinsic value because they are important components of an animal’s life history (Litvaitis et al. 1996) and substantial information has been collected on the diets of many terrestrial vertebrates in Africa (e.g. Talbot & Talbot, 1962; Gwynne & Bell, 1968; Leuthold, 1977; Bell, 1971; Jarman & Sinclair, 1979) in North America (Martin et al. 1961; Tueller, 1979) and Europe; (Mann & Putman 1989; Putman et al. 1993).

Food habits study of different ungulates in India is quite a few as compared to other countries. The food plants of wild ungulates were listed in Kanha (Schaller 1967). Food habits of ungulates in Kedarnath Wildlife Sanctuary was studied by faecal analysis (Green 1985). Haque (1990) studied wild ungulate food habits by direct feeding observations and by pellet analysis. Johnsingh & Sankar (1991) studied the food plants of wild ungulates in Mundanthurai while, Berwick (1974) and Khan (1994) studied the food habits of the ungulates in the dry tropical forest of Gir, these studies were mostly based on opportunistic direct observations.

1.4.5. Activity patterns

Many problems in conservation biology rely on a detailed understanding of species natural history. Many previous studies have shown the importance of studying activity patterns of various wildlife species (Green, 1985; Newton, 1984; Isvaran, 1995). Some studies have that been carried out on ungulates include Schaller (1967) in India, Graff & Nichols (1966) in Hawaii and Fuchs (1977) in Texas, Semiadi et al. 2003 in New Zealand. Apart from this, very little has been done in studying activity pattern and time budget of ungulates (but for chital see, Sharatchandra & Gadgil, 1980; Shrestha, 1982; Bhat, 1993; for gaur see Manjrekar et al. 2017).

Wild ruminants spend most of their day (>90%) foraging, resting/ruminating or walking between bedding and feeding sites (Renecker & Hudson, 1993). The forage quality, distribution and abundance in time and space influence the activity pattern and time investment of ungulates in various activities (Lucas, 1987; Bunnell & Harestad, 1990; Dove, 1996). Spatial distribution of forage affects the ungulate movement for food search which might, in turn, expose them to high predation risk and therefore need to invest more time on vigilance (Owen-Smith, 2002; Caro, 1994). Parker & Robins (1985) explained the role of ambient temperature on the daily activity patterns of ungulates. The time spent in various activities is influenced by energy requirement and the constraints they encounter, i.e. food distribution, predators and thermal stress (Lucas, 1987; Bunnell & Harestad, 1990; Dove, 1996).

Energy demands in animals are indicated by the amount of time spent on foraging (Bunnell & Gillingham 1985). Survival and reproduction depend on how this energy is obtained, and time spent (Bunnell & Harestad, 1990). Thus, time spent in foraging is an insight into the strategies that animals adapt to survive and reproduce (Bunnell & Gillingham, 1985). Allocation of time spent in foraging by various mammals is influenced by a number of factors such as body size, diet, digestive system capabilities and mode of locomotion (Bunnell &

Harestad, 1990). Most studies have noted that rest and rumination occur periodically when not feeding.

Major limiting factors in foraging by ruminants is gut fill and passage time which depends on forage quality and time spent in rumination. Schaller (1967) found chital resting around midnight until shortly before dawn almost as a routine. On overcast days, chital tends to remain more active on grasslands and do not seek the shade of trees during mid-day (Schaller 1967; Tak & Lamba 1984).

1.4.6. Factors affecting group size of ungulates

The group sizes are a function of the social (Jarman 1974, Wilson 1975, Dinerstein 1980), reproductive behaviour (Fuchs 1977) and food availability (Wilson 1975; Sharatchndra & Gadgil, 1975, Khan et al. 1996). Besides the availability of food, the pattern of food distribution in a foraging area dictates the group sizes in ungulates (Jarman, 1974; Mishra, 1982; Johnsingh, 1983; Karanth & Sunquist, 1992). Dinerstein (1980) considered the predation risk as a governing factor for determining chital group size.

The effect of open or closed habitat on chital group size was shown by Barrette (1991) and Khan (1995). Chital exhibits open membership social structure and hence group-sizes show diurnal as well as seasonal variations (Sharatchandra & Gadgil, 1975, Barrette, 1991). Generally, in chital, a matriarchal family unit comprises of an adult female, her yearling and a fawn. Due to the loose aggregation in chital herd, sometime chital herds are composed of two or more of these family units and can be accompanied by other individuals of mixed sex and age class (Fuchs, 1977). The mixed-age and sex groups are frequent in the rutting season (Khan & Vohra, 1992). Two additional associations commonly seen among chital are all-male herds and nursery herds, the latter consisting of only females with fawns (Fuchs, 1977). In India, average monthly herd size of chital varies from 5-38 individuals (Schaller 1967; Khan 1995), whereas in Texas 2-15 (Fuchs 1977) were noted.

1.5. Questions and objectives

Research Questions

1. **What are the effect of human use, season, and habitat on ungulate densities?**

Ungulates likely respond to different vegetation types and protection regimes (such as the core zone, devoid of human settlements and buffer zone, also known as a multiple-use area having human settlements and livestock grazing). Ungulates meet their food and cover requirements from a wide range of habitats. Food quality and forage productivity vary in availability with seasons which often force ungulates to shift their use of habitats in different seasons.

Hypothesis: Ungulates would be low in densities in human use area in comparison to the inviolate core zone, and they would exhibit a seasonal shift in their habitat-specific densities as food availability changes.

2. **What are the demographic parameters of ungulates in different protection regimes?**

Ungulates are likely limited by direct hunting (poaching) and competition for resources with livestock. Therefore, demographic parameters of wild ungulates would differ with conservation investments. This difference in demographic parameters would also be species-specific, i.e. species that are preferred as bushmeat or compete more with livestock will have higher differences. It is generally believed that the low conservation investments areas are detrimental to ungulate populations, and it subsequently affects the population demography, i.e. population density growth, body condition, group size and composition etc. If management investments are so much essential for ungulates, then ungulates should have low population density and poor body condition in areas with low conservation investments.

Hypothesis: Low conservation investments areas results in poor population performance of ungulates.

3. **What are the factors affecting group size of ungulates?**

   Cost and benefits related to predation and feeding determine the effective group size in different species (Caraco & Pullium 1984). Moreover, each habitat type is subject to seasonal changes that can affect group formation for different species (Krebs & Davies 2009).

   Hypothesis: Grouping in ungulates depend on a) season, b) habitat type, c) ungulate density d) predator density and/or combination of these factors.

4. **How ungulates share their resources and are distributed in space and time?**

   Different species may specialize on distinct resources (Tilman 1982) or limited by same resources but differ in terms of when they exploit the resources (Armstrong & McGehee 1980) and where they experience and respond to limiting factors. Ecological difference between species leads to niche partitioning.

   Hypothesis 1: There would be an ecological separation between sympatric ungulates (chital, sambar and gaur) at a spatial density level in both summer and winter but would be less pronounced when resources were limited (i.e. in summer).

Hypothesis 2: There would be temporal segregation between sympatric ungulates in which different ungulates would be active during different parts of the diel cycle if the interspecific overlap in space use is high.

Hypothesis 3: Published studies on ungulates suggest that diet overlap generally increases with a decrease in food abundance (Schwartz & Ellis 1981). There would be interspecific differences in diets that would maintain low seasonal overlap. The overlap would be highest during dry summer months (when resources in Central Indian forest would be most limiting, and competition for nutritional food were expected to be accentuated) and lowest in the winter season.

Hypothesis 4: Habitat use would be influenced by body size and digestive physiology. Therefore, small ungulates would be more selective (i.e. have wider diet niche breadth) than large ungulates.

Hypothesis 5: Coarse, semi-dry to dry grass form the bulk of gaur's diet (85% by volume) in summer season (Schaller 1967), thus permitting regeneration of the annual grass, replenishing and exposing the quality of grass swards for the other ungulate in the guild especially for small-bodied ruminant chital who entirely depend on more nutritious, short and high-quality grasses in the dry season of summer. Hence, facilitation may exist between larger and smaller species (gaur and chital in Kanha) if they co-occur together and when they have the same feeding strategies in the summer season.

To explore the aforementioned questions, my study objectives are as follows:

I: To evaluate seasonal habitat use by different ungulate species.

II: To estimate the demographic parameters of ungulates in Kanha

III: To understand the influence of different factors on the group size of ungulates.

IV: To estimate the space use, temporal activity and diet of sympatric ungulates.

1.6. Study area

Kanha Tiger Reserve is located in the state of Madhya Pradesh (latitudes 22^0 7'N and $22^0$27' N and longitudes 80^0 26' E and 81^0 3' E) in the Maikal chain of hills in the eastern Satpura mountains of the Central Indian Highlands. The Tiger Reserve, situated administratively in the Mandla and Balaghat districts of Madhya Pradesh. It comprises of two distinct management strata; the core which covers an area of 940 km^2, devoid of human settlements and has the prime objective of biodiversity conservation and an 1134 km^2 of a buffer zone which is a multiple-use area, having human settlements where tourism-based resorts and hotels, small scale industries like rice mills, agriculture practices, infrastructure development for village people are permitted. Although, activities adverse to conservation such as mining and large polluting industries are not permitted in the buffer zone. The area of forest or wild ungulate habitat available within the buffer zone is 585 km^2, and thus the conservation unit totals an area of 2,074 km^2 and is designated as a Tiger Reserve **(Figure 1.1)**. The Kanha National Park (core area) is formed by the catchments of two rivers, Banjar and Halon. Since, its inception as a national park in 1955, the Banjar catchment gained considerable conservation investment in terms of village relocation and habitat management compared to Halon catchment, which was later added to the National Park in 1976. As per the biogeographic classification of India (Rodgers & Panwar 1988), the area lies in zone-6E – Deccan Peninsula – Central Highlands. Kanha is a significant geographical region of our country, as far as the occurrence and distribution of flora and fauna are concerned. Floristically, the Kanha Tiger Reserve is part of the Indo-Malayan Realm, and, zoo-geographically, a member of the Oriental Region. The floral diversity represents around 850 species of angiosperms and 22 species of Pteridophyte and two species of Gymnosperm (Pandey & Namdeo, 2009). The flora of the protected area also includes around 50 species of aquatic plants and 18 species of rare plants. The richest family in the Poaceae family with 109 species indicates the presence of heterogeneous grassland in reserve.

Kanha is a tropical moist deciduous forest interspersed with grasslands of anthropogenic origin, arrested in succession by management activities of annual burning and woody plant removal. The undulating terrain and variation in the altitude (450- 950 m above mean sea level) has resulted in a diversified floral composition (Champion and Seth 2005). In general, four different habitat types' viz. grassland, pure sal forest, miscellaneous forest and bamboo-mixed forests are present in reserve. The higher elevation sites consist of extensive plateau-capped hills supporting sparse or little tree growth of miscellaneous forest and are primarily grasslands. The depressions, gorges and streams, just below these plateaux, support bamboo (*Dendrocalamus strictus*), while the low altitude sites comprise valleys with grassy meadows interspersed with groves of sal (*Shorea robusta*) and the lower slopes carry dense stands of sal with bamboo which also occur in miscellaneous stands in the upper slope. The grassland habitat, the mainstay of thousands of ungulates, constitutes around 8% of the total area of the core zone. Such rich habitat diversity is intrinsically capable of meeting all the food, and other life stages requirement for ungulate species that coexist together in reserve.

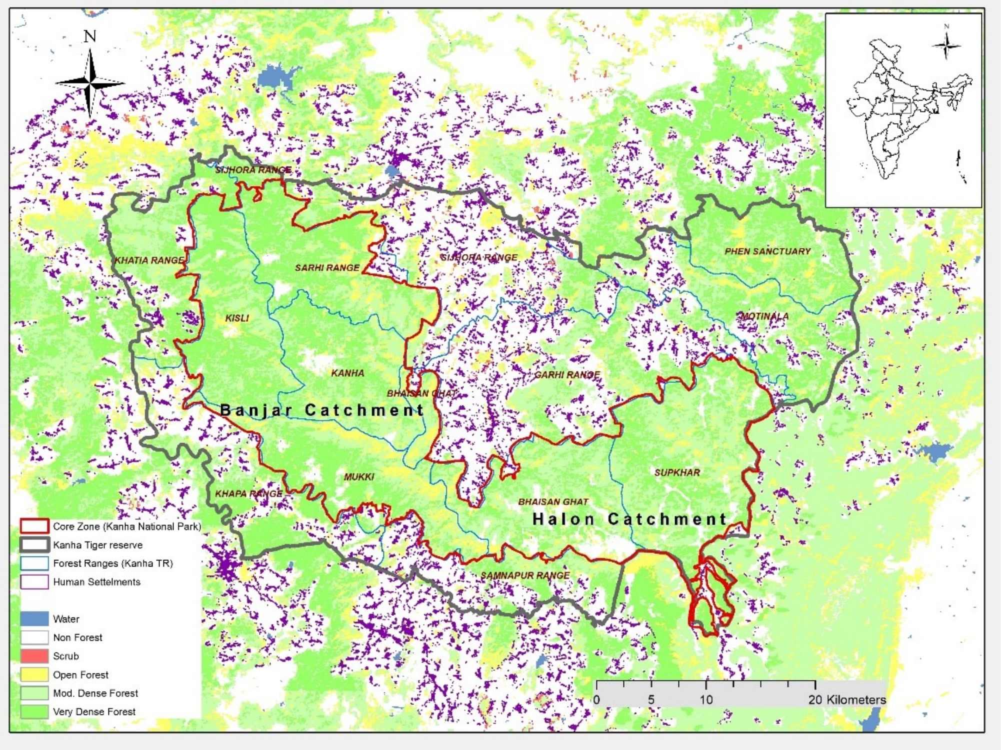

Figure 1. 1 Study area of Kanha Tiger Reserve, Madhya Pradesh, India. The map inset shows outline map of India with location of the Kanha Tiger Reserve.

There are 43 species of mammals and 27 species of reptiles and over 300 species of birds. The faunal assemblage consists of endangered carnivores like a tiger (*Panthera tigris*), leopard (*Panthera pardus*), wild dog (*Cuon alpinus*) and sloth bear (*Melursus ursinus*), and nine species of ungulates such as hard ground barasingha (*Rucervus duvaucelii branderi*), chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*), barking deer (*Muntiacus vaginalis*), wild pig

(*Sus scrofa*), chousingha (*Tetracerus quadricornis*), nilgai (*Boselaphus tragocamelus*) and mouse deer (*Moschiola indica*). Recently blackbuck (*Antelope cervicapra*) also got re-introduced in the National Park. Among small carnivores, jungle cat (*Felis chaus*) and rusty-spotted cat (*Prionailurus rubiginosus*) are present in reserve. The climate is monsoon-type with marked seasonal variations in temperature and rainfall. The mean annual rainfall is 1623 mm, most of its arriving during the monsoon months (Negi & Shukla 2011). Three seasons are observed in Kanha, namely winter (December to February), summer (March to May), and the rainy season (June to September). October and November are a transition period from monsoon to winter.

The present Kanha core zone used to be a typical Indian forest landscape dotted with many villages and settlements with their inhabitants and cattle populations. The village life had a touch of aboriginality as the majority of populations in these villages belonged to the Scheduled Tribes, mainly the Gonds and the Baigas, and these villages always depended on the nearby forests for their needs and demands of grass, fuelwood, timber and a wide range of minor forest produces.

This automatically resulted in a perceptible biotic pressure on the forests and wildlife of the vicinity of these forest villages. Besides, such humanized backdrop also ran counter to the philosophy of managing protected areas effectively (Shukla 2005). The hard ground barasingha was the species that suffered most in this background, and its population declined sharply in its habitats. Location of Sonf village was initiated to reclaim a substantial area of additional land for the barasingha in 1969 (Panwar 1973). Village relocation proved to be a most crucial measure and was the turning point in the conservation history of wildlife in general and barasingha in particular in Kanha (Panwar 1973; Gopal & Shukla, 2001; Gopal, 2012). The Park Management has successfully relocated completely 35 forest villages outside the National Park between 1969 to 2018. The relocation has helped the Park Management reclaim more than 10,000 hectares of wildlife habitat.

Table 1. 1 Ungulates in moist deciduous forest of Kanha Tiger Reserve.

Serial no	species	scientific name	body mass (Kg)	foraging strategy	home range (sq km)	breeding season	gestation period (months)	fawning/calving season
1	Chital	*Axis axis*	65	grazer	3.5 for stag and 2.5 for female	MARCH-JUNE	7	Seasonal (dry) January-March
2	Sambar	*Rusa unicolor*	205	browser	4 for stags and 1.7 for hinds	APRIL-DEC	8	Seasonal (wet) Late may-early July
3	Gaur	*Bos gaurus*	800	intermediate feeder	135 to 142 for male and 32 to 169 for female	PERRENIAL	9.5	Perennial August to March
4	Barasingha	*Rucervus duvaucelii branderi*	170	grazer	10-30 annually	SEP-OCT	8	Seasonal (wet) September-October
5	Barking deer	*Muntiacus vaginalis*	24	nibbler	Not more than 1 sq km *	ALL MONTHS	7	Perrenial
6	Nilgai	*Boselaphus tragocamelus*	195	intermediate feeder	3.6 seasonal and 7.3 annual	OCT-FEB	8	Seasonal (wet)
7	Chousingha	*Tetracerus quadricornis*	19	browser/nibbler	Not more than 1 sq km*	FEB-APRIL	8	Seasonal (wet)
8	Wild pig	*Sus scrofa*	80	omnivorous	13.4-20.19 range for male and 2.14-5.16 for female	NOV-DEC	4	Seasonal (wet)
9	Mouse deer	*Moschiola indica*	3	frugivorous	0.24 sq km	FEB-APRIL	5	Post monsoon season

References: Brander 1923, Schaller 1967, Berwik 1974, Martin 1977, Harestad and Bunnel 1979, Prater 1980, Santiapillai and Chambers 1980, Johnsingh 1983, Geist & Bayer 1988, Sankaran 1989, Sankar 1994, Qureshi et. al. 1995, Spitz and Janeau 1995, Khan 1994, Ahrestani 2009, Sharma et al 2009, Sankar et. al. 2013.

(*)- indicates Body weight Home Range (HR) equation from Harestad and Bunnel 1979.

Chapter 2. Habitat use of ungulates in Kanha Tiger Reserve

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1. Introduction

Tropical deciduous forests are capable of supporting high density of ungulates due to their high productivity and nutrient availability (Field et al. 1998; Melillo et al. 1993). Subsequently, due to a high prey abundance, these forests are important refuges for conserving large carnivores. Land for conservation comes at a high premium in tropical countries with burgeoning human populations (Dinerstein et al. 2010). Severe biotic pressure such as bush meat consumption, use of non-timber forest products, and livestock grazing has likely resulted in an unprecedented reduction of ungulate abundance in these forests. Protected areas in the tropics are relatively small compared to other biomes (Schmitt et al. 2008). Often large carnivore populations in the tropics, such as those of tigers, are primarily restricted to Protected Areas (Jhala et al. 2014). Rarely does a single reserve harbour a tiger population of sufficient size required for its long-term persistence (Yumnan et al. 2014). Density of large carnivores are primarily dictated by the density of their prey (Hayward et al. 2007). Therefore, managing them optimally to serve both the purpose of conserving biodiversity as well as harbouring viable large carnivore populations becomes crucial. The Tiger Reserves in India are legally mandated to delineate a core area where large investments by the Government are made to resettle human settlements from within the core area through an incentivised, voluntary, relocation scheme (Wildlife (protection) Amendment Act 2006). The core is subsequently declared 'inviolate' with extremely restricted human activity (Gopal et al. 2007). Scientific data that document the effectiveness of these investments in achieving the desired conservation objectives would encourage Governments to invest further in such schemes that benefit both the local communities through better livelihood options and biodiversity conservation (Secretariat of the Convention on Biological Diversity 2008).

Ungulates meet their food and cover needs from a wide range of resources and habitats. Food quality, plant productivity and water regime vary in availability with seasons (Prins and Loth 1988; Beever et al. 2000), which often force ungulates to expand their home ranges, or shift their use of habitats in a seasonally predictable fashion. Distance sampling (Buckland et al. 2001) has opened up the field of estimating forest dwelling ungulate abundance. However, current application of distance sampling has been done on random foot transects that typically traverse multiple habitat types. Although estimates from such studies are unbiased to the region of inference, they fail to provide information on how ungulate abundance responds to different habitats, a vital requirement for management. Precision of estimates from distance sampling on foot transects depends on variability of Effective Strip Width (ESW), encounter rate and cluster size (Buckland et al. 2001). For a given sample size, habitat specific distance sampling would provide more precise density estimates compared to the same number of transects that traverse habitat mosaics (Thomas et al. 2010). Estimating abundance by habitat stratification is a sensible approach to improve the precision of estimates and ensure proper coverage of habitats (Sutherland 2000).

Herein, I use stratified line transect sampling in Kanha Tiger Reserve (KTR), Madhya Pradesh, India and analyze our data with conventional distance sampling to assess the effect of a) human use and b) habitat and season on ungulate densities. My results showed that ungulate densities were significantly depressed in “multiple use" forests of the buffer zone compared to the “human restricted" core area of KTR. Some ungulates of KTR showed significant seasonal shifts in their habitat specific densities, while others seemed to be habitat specialists and maintained high habitat specific densities in summer and winter. I attempt to interpret my results in the context of nutritional and cover requirements of ungulates and thereby provide management options for specific ungulate species and for the overall conservation objectives of KTR.

2. Materials and Methods

2.1. Study area

The Kanha Tiger Reserve comprises of two distinct management strata; the core which covers an area of 940 km^2 , devoid of human settlements and has the prime objective of biodiversity conservation and a 1134 km^2 of buffer zone which is a multiple use area, having human settlements where tourism based resorts and hotels, small scale industries like rice mills, agriculture practices, infrastructure development for village people are permitted. Although, activities adverse to conservation such as mining and large polluting industries are not permitted in the buffer zone. The area of forest or wild ungulate habitat available within the buffer zone is 585 km^2 and thus the conservation unit totals an area of 2,074 km^2 , and is designated as a Tiger Reserve. Kanha is a tropical moist deciduous forest interspersed with grasslands of anthropogenic origin, arrested in succession by management activities of annual burning and woody plant removal (Kanoje 1999). In general, four different habitat types' viz. grassland, pure sal forest, miscellaneous forest and bamboo-mixed forests are present in the reserve. Ten species of ungulates coexist in Kanha such as hard ground barasingha (*Rucervus duvaucelii*), chital *(Axis axis)*, sambar (*Rusa unicolor)*, gaur *(Bos gaurus)*, barking deer *(Muntiacus vaginalis)* ,wild pig (*Sus scrofa)*, chousingha *(Tetracerus quadricornis),* nilgai (*Boselaphus tragocamelus)*, mouse deer (*Moschiola indica*) and recently reintroduced Blackbuck (*Antelope cervicapra*). Three seasons are observed in the area, namely winter (December to February), summer (March to May), and rainy season (June to September) (for detailed information regarding study area see **Introduction chapter 1**).

2.2 Habitat mapping and validation

Extensive ground truthing was done by sampling 900 vegetation plots of 707 m^2 size in the field by trained personnel. Each vegetation plot was classified to its dominant vegetation community to record major habitat types (**Supplementary information S7**). Plots 1) with > 70% sal were considered as "pure sal"; 2) having < 70% sal and > 30% other tree species were considered as "miscellaneous forests"; 3) with miscellaneous forests having > 20% bamboo were considered as "bamboo-mixed forests"; 4) having < 10% tree cover and ground vegetation dominated by grasses were defined as “grasslands”. The other habitat categories were 5) agriculture/fallow fields, 6) barren areas and built-up human habitation area and 7) water bodies. I used 70% of ground plots for modelling vegetation classification while 30% were used for model validation to assess the performance of image classification. Unsupervised classification of LANDSAT-8 satellite imagery (pixel size=30 metres; acquisition date; April and November 2013) was carried out. The results of the unsupervised classes were merged by supervised classification to adhere to field identifiable classes mentioned above. Digital image processing, geo-referencing and digital classification of remotely sensed data was done using ERDAS imagine 2010 (Earth Resources Data Analysis System, Leica Geosystems, Atlanta, Georgia, USA).

I built an error matrix that compared the habitat classes identified in the field for independent, randomly selected 450 vegetation plot locations against their corresponding classified pixels on the image using kappa coefficient (Cohen 1960). Kappa indicates to what extent classification accuracy is due to the true agreement of the field data and classified data (Lillesand et al. 2004). Its values generally range from 1 for perfect agreement to 0 for no agreement (Rosenfield and Fitzpatrick-Lins 1986). Habitat classification was assessed as accurate if kappa coefficient was greater than 0.6 (Landis and Koch 1977).

2.3 Sampling design and data collection

Ungulate density is likely to respond to regimes of protection as well as to vegetation types. Hence, I used a stratified design in the core area of the Tiger Reserve, where the number of transects in each habitat were approximately in proportion to the area of the habitat. Thus, grassland had 12 transects, sal forest: 36 transects, bamboo-mixed forest: 29 transects and miscellaneous forest had 73 transects. Based on management zones, the core area had 150 transects, while the forest of buffer zone had 50 transects (**Figure 2.1**). Line transects of 2 km were marked within each strata and walked during early morning (6:00 am to 8:00 am), for three consecutive mornings in summer and winter of 2013. In each season, sampling was completed within 30 days. The total transects survey effort comprised 1200 km of the walk along 200 spatial replicates in both seasons. Radial distance, animal bearing and group size were recorded with an encounter of each ungulate species. I surveyed the entire reserve with observers who were well versed with field craft and species identification. I trained and tested each observer in the use of laser range finder (Bushnell RX 1000), see through compass (Suunto KB-20) and GPS (Garmin eTrex 10).

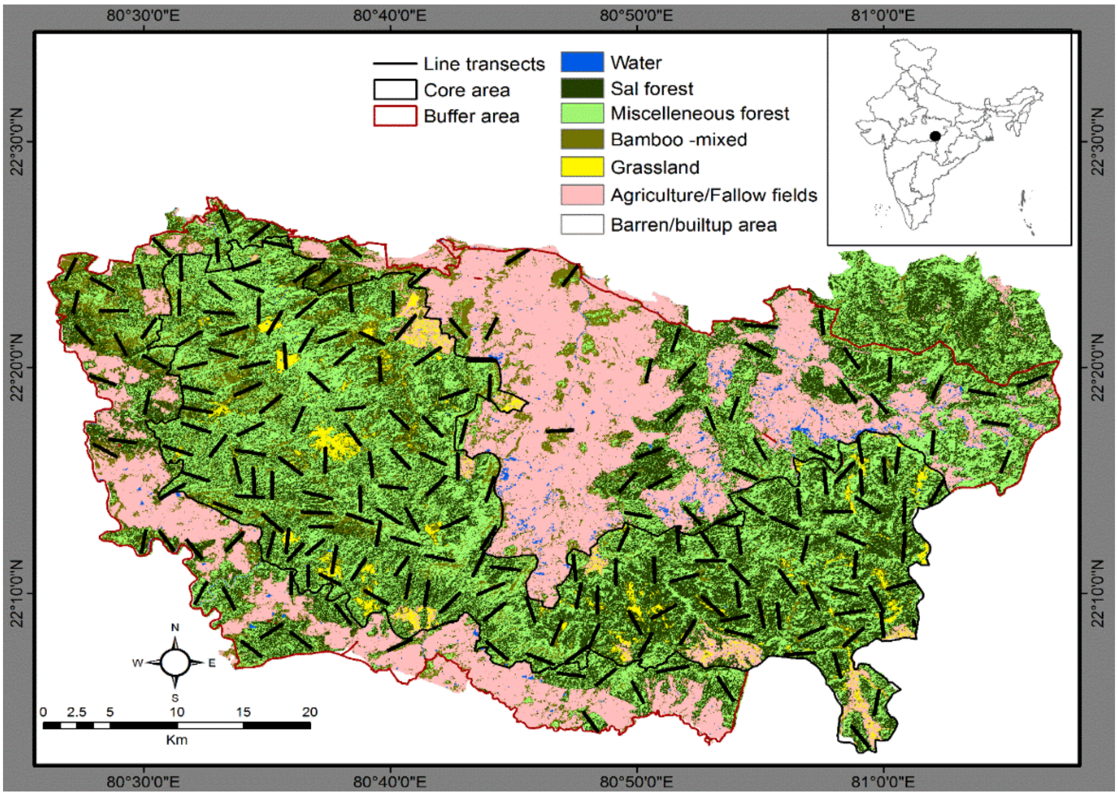


Figure 2.1 Vegetation cover map of Kanha Tiger Reserve showing the spatial distribution of habitat specific line transects.

2.4 Data analysis

Ungulate abundance estimates were derived from 200 line transect samplers placed across 1945 km^2 of the study area using Conventional Distance Sampling (CDS) approach (Buckland et. al. 2001) in program Distance (version 6.2; Thomas et. al. 2010). Densities of six major ungulates (chital, sambar, gaur, wild pig, barasingha, and barking deer) were recorded for each management and habitat strata. Chousingha and nilgai, were analysed only for management strata as the number of observations recorded for these species was insufficient to separately estimate detection functions and densities for each habitat type.

For the first analysis, I was interested in finding out if a density of specific species differed between two regimes of management i.e. the core area, devoid of human settlement and the buffer zone, a multiple use area with extractive use by local communities. For this analysis, I developed detection functions for each species from all transects pooled across management zones and subsequently estimated density for each species for each management zone by post stratification. Since habitat types between core and buffer areas were similar, I did not expect detection functions for each species to differ between the core and buffer zones. I tested this premise for species that had a large number of detections in both management strata (chital and barking deer), by comparing the effective strip width (ESW) and detection probability obtained from independent fitting of detection functions for core and buffer habitats (**Supplementary information S1 and S2**). Since ESW's and detection probability did not differ between core and buffer, we pooled data separately for individual species between core and buffer zones to obtain a more robust and precise estimate of ESW for each species and estimated density separately for core and buffer using a common detection function.

In our second analysis, I was interested in the effect of habitat type and season on ungulate densities. I restricted our analysis to the core of the tiger reserve since transects in the buffer area were not habitat specific. This was because habitat patches in the buffer were too small to lay a transect of reasonable length. Since there were few detections of sambar, gaur, and wild pig in grassland for both seasons and few detections of gaur within sal forests and bamboo mixed forests for winter season to permit the modelling of detection functions, I pooled individual species detection data for these species from our transect walks in these habitats for the years 2013 and 2014. A detection function was then modelled for each species for a particular habitat in a specific season by combining the two years' data. This detection function was then used to obtain the species density for the year 2013 by post-stratification by years, for a particular habitat in a specific season. Shape criteria were examined for heaping and any outliers were right-hand truncated where necessary (Buckland et al. 2001). Three key functions (uniform, half-normal and hazard rate all with cosine series adjustment) were considered for each analysis. Model selection was evaluated using Akaike's Information Criteria (AIC) while Kolmogorov Smirnov statistics were used to assess the goodness of fit of each model (Buckland et al. 2004).

Considering ungulate abundance in a habitat type to be the use by that species, I computed Ivlev index of electivity (1961). Ivlev index measures the utilization of habitat types (U) by species in relation to their availability (A) in the landscape (Dyke 2008). Ivlev index of selection is determined as U-A/U+A. It is an algorithm for identifying the strength of selection for habitats (Yeo and Peek 1992). The selection index will be zero whenever animals use the habitat in the same proportion as its availability. It will approach the value of one when use is proportionately much higher than availability suggesting the strong preference for that habitat. Alternatively, it will approach a value of negative one when use is less than availability (Dyke 2008). Ivlev index were only used for graphical representation **(Figure 2.2).** Following Byers et al. (1984) I first tested for overall seasonal habitat preference by an ungulate species through a Chi square test, and subsequently we used simultaneous Bonferroni confidence intervals that control for an overall experiment wise error rate, to check for preference of each habitat type. I computed ungulate biomass for each habitat in each season by multiplying species density with the 3/4th of the adult female body mass (Schaller 1972) **(S8 and S9)**.

3. Results

A Kappa statistics value of 0.8 ($p < 0.001$) suggested good agreement of validation plots with the vegetation map **(Supplementary information S7)**. As per the habitat classification map prepared in this study, the area under 1) pure sal was 426 km^2, 2) miscellaneous forests was 648 km^2, 3) bamboo mixed forests was 425 km^2, 4) grassland was 88 km^2, 5) agriculture/fallow fields was 268 km^2, 6) barren and built up areas was 218 km^2, and 7) water bodies was 16 km^2. Chital was the most commonly sighted ungulate followed by sambar, barking deer, gaur and wild pig **(Tables 2.1, 2.2 and 2.3).**

3.1 Human use and ungulate density

Species densities differed between core and buffer zones **(Table 2.1).** The results showed that among all ungulates, chital was the most abundant with much higher density in the core area (30.1 ± 4.34) compared to the buffer zone (8.45 ± 2.37) of the Tiger Reserve. The next most abundant were sambar and gaur, with a consistent trend between core and buffer areas, in both summer and winter season. Only in the case of wild pig and barking deer, densities were comparable between both management strata and seasons. Only nilgai had higher densities in buffer zone compare to core zone **(Table 2.1).** While barasingha and chousingha were not detected in the multiple use buffer zone. Group size of all ungulates except nilgai were larger in the core zone **(Table 2.1).** Detection probabilities and ESW's for chital and barking deer did not differ between core, buffer, and combined analysis **(S1 and S2).**

3.2 Habitat specific densities and preference by ungulates

All species of ungulates showed preference for certain habitats ($\chi^2 > 7.85$, $P < 0.05$). Chital was most abundant amongst all ungulates, across all four habitats and in both summer and winter season. Chital densities were highest in grassland followed by bamboo-mixed forest with little seasonal variation **(Table 2.2 and 2.3).** Chital consistently showed a high preference for grassland in both summer and winter season (**Figure 2.2 a and b; S10 and S11**). Sambar had the highest densities in the bamboo-mixed forest in summer followed by sal forest and miscellaneous forest. The seasonal densities of sambar show a little habitat shift from bamboo-mixed in summer season to miscellaneous forest in winter (**Table 2.2 and 2.3**). Sambar exhibited the preference for bamboo-mixed habitat in both summer and winter season (**Figure 2.2 c and d; S10 and S11).** Gaur densities were highest in sal forest in summer and miscellaneous in winter. Gaur showed a major seasonal shift in density from bamboo-mixed and sal forest in summer to miscellaneous forest in winter **(Table 2.2 and 2.3).** They preferred sal in summer whereas in winter, gaur showed preference for miscellaneous forests **(Figure 2.2 e and f; S10 and S11).** Wild pig density was also found to be higher in bamboo-mixed habitat and the seasonal densities were similar across all habitats **(Table 2.2 and 2.3).** Wild pig showed preference for bamboo-mixed habitat in both summer and winter **(Figure 2.2 g and h; S10 and S11**). Barking deer had highest densities in bamboo-mixed and miscellaneous forests **(Table 2.2 and 2.3)** and also showed preference for these habitat types **(Figure 2.2 i and j; S10 and S11**). Barasingha being obligate to grassland were only detected in grassland habitat **(Table 2.2 and 2.3**) while chousingha were detected on transects in miscellaneous forests and plateau grasslands. Detection probabilities were highest for grassland habitat and lowest for bamboo forests for all species in both seasons **(S5).**

Table 2. 1 Density of ungulates in the core and buffer area of Kanha Tiger Reserve in 2013.

Species	season	Management site	Best model	Detection probability $\hat{P}$ (SE)	KS test p value	Observation (n)	Mean Cluster size E(s)(SE)	Group density $\widehat{DS}$(SE)	Density $\hat{D}$ (SE)
Chital	Summer	Core	HRC	0.25 (0.01)	0.892	357	9.62(0.52)	3.14 (0.48)	30.3 (4.9)
		Buffer				51	5.8(0.65)	1.35(0.28)	7.9(1.88)
	Winter	Core	HNC	0.18(0.01)	0.823	326	8.35 (0.47)	3.59 (0.40)	29.9 (3.7)
		Buffer				55	5.93 (0.66)	1.51 (0.43)	9.0 (2.79)
Sambar	Summer	Core	HRC	0.29(0.01)	0.727	250	2.86(0.10)	2.76 (0.33)	7.90 (0.99)
		Buffer				15	2.58(0.43)	0.49 (0.13)	1.29 (0.42)
	Winter	Core	HNC	0.13(0.01)	0.721	258	2.33 (0.08)	3.58 (0.36)	8.38 (0.89)
		Buffer				18	2.24 (0.37)	0.54 (0.17)	1.22 (0.43)
Gaur	Summer	Core	HRC	0.21(0.03)	0.712	102	5.25(0.63)	0.92 (0.21)	4.83(1.25)
		Buffer				10	2.75 (0.82)	0.30 (0.15)	0.83(0.49)
	Winter	Core	HRC	0.28 (0.02)	0.810	98	3.59 (0.42)	1.18 (0.17)	4.27 (0.81)
		Buffer				8	4.9(1.12)	0.29 (0.14)	1.44 (0.76)
Wild pig	Summer	Core	HRC	0.21 (0.01)	0.858	91	4.94 (0.53)	1.0 (0.15)	5.29 (0.95)
		Buffer				17	7.66 (2.92)	0.53 (0.14)	4.11 (1.92)
	Winter	Core	HRC	0.21(0.02)	0.772	90	4.74 (0.55)	1.31 (0.22)	6.22 (1.27)
		Buffer				19	9.44 (4.07)	0.53 (0.14)	5.07 (2.58)
Barking deer	Summer	Core	HRC	0.20(0.01)	0.821	124	1.22 (0.03)	1.36 (0.16)	1.66(0.20)
		Buffer				51	1.25 (0.06)	1.68(0.30)	2.11 (0.40)
	Winter	Core	HRC	0.23 (0.03)	0.897	127	1.12 (0.02)	1.99 (0.22)	2.23 (0.26)
		Buffer				56	1.31 (0.08)	1.80 (0.35)	2.37 (0.49)
Barasingha	Summer	Core	UC	0.3(0.02)	0.810	32	15.9 (3.54)	0.10 (0.03)	1.59 (0.70)
		Buffer	-	-		--	--	--	--
	Winter	Core	UC	0.6 (0.08)	0.882	40	7.5 (1.42)	0.20 (0.10)	1.52 (0.81)
		Buffer	-	-		--	--	--	--
Chousingha	Summer	Core	HRC	0.25(0.01)	0.892	8	1.39 (0.26)	0.06 (0.02)	0.09 (0.04)
		Buffer				--	--	--	--
	Winter	Core	HNC	0.18 (0.01)	0.823	10	1.37(0.07)	0.08 (0.03)	0.11 (0.04)
		Buffer				--	--	--	--
Nilgai	Summer	Core	HRC	0.20 (0.01)	0.727	4	1.41 (0.45)	0.04 (0.03)	0.06 (0.05)
		Buffer				16	2.69 (0.45)	0.19 (0.10)	0.52 (0.28)
	Winter	Core	HNC	0.13(0.01)	0.721	12	5.08 (1.13)	0.06 (0.03)	0.33 (0.20)
		Buffer				14	2.5 (0.38)	0.17 (0.05)	0.44 (0.16)

Notes: A single global detection function was modelled for each species by pooling data from the entire study area, while density for each management strata was estimated subsequently in Program DISTANCE. SE-Standard Error. KS -Kolmogorov Smirnov test. Best Model are UC, Uniform Cosine; HNC, Half Normal Cosine; HRC, Hazard Rate Cosine.

Table 2. 2 Habitat specific summer densities and biomass of major ungulates in Kanha Tiger Reserve in 2013.

Habitat type	species	Best model	KS test p value	No of observations (n)	Effective strip width (ESW)[SE]	Encounter rate(n/l)	Detection probability $\hat{P}$ (SE)	Group Density $\widehat{DS}$ (SE)	Mean Cluster size E(S)](SE)	Density $\hat{D}$ (SE)	Biomass Kg/km^2 (SE)
GRASSLAND	Chital	UC	0.831	82	122.5(14.2)	1.13	0.56 (0.05)	4.64 (1.63)	23.7 (2.99)	110.09(41.15)	5174.23(1934.0)
	Sambar*	UC	0.869	36	86.08 (6.62)	0.20	0.55 (0.04)	1.21 (0.39)	2.93 (0.26)	3.55 (1.22)	482.8 (165.9)
	Gaur*	UC	0.869	21	86.08 (6.62)	0.11	0.55 (0.04)	0.57 (0.22)	7.5(1.88)	3.88 (1.91)	2176.68(1071.5)
	Wild pig*	UC	0.831	20	122.5 (14.2)	0.11	0.56(0.05)	0.88 (0.37)	5.12 (1.35)	3.01 (1.52)	81.27(41.0)
	Barasingha	UC	0.882	32	182 (24.4)	0.40	0.6(0.08)	1.10 (0.35)	14.34 (2.19)	15.8 (5.59)	2512.2(888.8)
	Barking deer	----	-----	----	-----	----	-----	-----	----	-----	-----
SAL FOREST	Chital	HRC	0.619	91	74.05 (8.56)	0.42	0.41 (0.04)	2.84 (0.75)	7.94 (0.61)	22.61 (6.24)	1062.67(293.2)
	Sambar	HRC	0.963	56	41.32 (5.81)	0.25	0.40 (0.05)	3.13 (0.83)	2.86(0.25)	9.0 (2.52)	1224(342.7)
	Gaur	HNC	0.795	29	48.44 (9.56)	0.13	0.42 (0.08)	1.38 (0.45)	6.96 (1.11)	9.65 (3.55)	5413.65(1991.5)
	Wild pig	HNC	0.623	21	43.8 (5.90)	0.09	0.47 (0.06)	1.10(0.34)	4.88 (1.26)	5.42(2.17)	146.34(58.5)
	Barking deer	HNC	0.829	24	39.37 (6.74)	0.11	0.69 (0.11)	1.41(0.39)	1.41 (0.09)	1.99(0.57)	35.82(10.26)
BAMBOO-MIXED FOREST	Chital	HNC	0.615	71	46.72 (6.67)	0.4	0.18 (0.02)	4.36(1.08)	8.04 (1.00)	42.56 (12.3)	2000.32(578.1)
	Sambar	HRC	0.916	90	39.8 (5.09)	0.5	0.40 (0.05)	6.49(1.34)	2.76 (0.16)	17.9(3.88)	2434.4(527.6)
	Gaur	HNC	0.675	22	47.22 (13.03)	0.12	0.20 (0.05)	1.33 (0.53)	4.52 (0.99)	6.05 (2.76)	3394.05(1548.3)
	Wild pig	HRC	0.685	23	48.3 (13.2)	0.13	0.29 (0.08)	1.36(0.53)	7.78(1.90)	10.64(4.89)	287.28(132.0)
	Barking deer	HRC	0.939	34	28.6 (4.67)	0.19	0.22 (0.03)	3.4(0.85)	1.33 (0.07)	4.55(1.16)	81.9(20.8)
MISCELLANEOUS FOREST	Chital	HRC	0.601	115	54.5 (8.2)	0.26	0.35 (0.05)	2.41 (0.6)	9.08 (0.88)	21.97(6.04)	1032.59 (283.8)
	Sambar	HRC	0.871	89	46.9 (5.09)	0.20	0.38 (0.04)	2.17(0.47)	2.87(0.19)	6.25(1.42)	850(193.1)
	Gaur	HRC	0.923	32	48.1 (14.6)	0.07	0.29 (0.01)	0.76(0.30)	4.61 (1.04)	3.51(1.62)	1969.11(908.8)
	Wild pig	HRC	0.629	50	46.6 (3.62)	0.11	0.57 (0.04)	1.23(0.23)	4.93 (0.73)	6.07(1.47)	163.89(39.6)
	Barking deer	HRC	0.670	62	48 (5.78)	0.14	0.38 (0.04)	1.47(0.28)	1.14 (0.04)	1.69(0.33)	30.42(5.94)

*** Indicates that we used pooled detection data for 2012 and 2013 to fit a detection function but report density, group density, cluster size and biomass only of 2013. UC-Uniform Cosine; HNC-Half Normal Cosine; HRC- Hazard Rate Cosine; KS test- Kolmogorov Smirnov test; SE-Standard Error.**

Table 2. 3 Habitat specific winter densities and biomass of major ungulates in Kanha Tiger Reserve in 2013.

Habitat type	species	Best model	KS Test p value	No of observations(n)	Effective strip width (ESW) (SE)	Encounter rate (n/l)	Detection probability $\hat{P}$ (SE)	Cluster size Density $\widehat{DS}$ (SE)	Mean Cluster size E(S) (SE)	Density $\hat{D}$ (SE)	Biomass (kg/km2) (SE)
GRASSLAND	Chital	UC	0.679	84	81.7 (6.74)	1.16	0.40 (0.03)	7.15 (2.36)	14.74 (2.02)	103.5 (36.9)	4864.5(1734.3)
	Sambar∗	UC	0.909	26	67.68 (10.31)	0.18	0.22 (0.03)	1.33 (0.43)	2.38 (0.28)	3.18 (1.10)	432.48(149.6)
	Gaur*	HNC	0.909	20	88.8 (20.95)	0.06	0.75 (0.17)	0.39 (0.20)	5.0 (1.30)	1.95 (1.13)	1093.95(633.9)
	Wild pig*	UC	0.679	23	81.73 (6.74)	0.12	0.39 (0.09)	0.49 (0.18)	9.55 (1.47)	4.7 (1.8)	126.9(48.6)
	Barasingha	UC	0.932	40	115.4 (17.09)	0.51	0.71 (0.10)	2.22 (1.06)	7.97(1.37)	17.7 (9.0)	2814.3(1431)
	Barking deer	….	….	……..	…….	……	…..	……….	……..	……	…….
SAL FOREST	Chital	HRC	0.708	60	53.04 (12.54)	0.27	0.38 (0.09)	2.61 (0.93)	6.58 (0.60)	17.23 (6.33)	809.81(297.5)
	Sambar	HRC	0.711	62	42.5 (39.23)	0.28	0.26 (0.02)	3.71 (0.7)	2.08 (0.14)	7.73 (1.66)	1051.28(225.7)
	Gaur*	HNC	0.711	22	44.99 (11.71)	0.05	0.34 (0.08)	0.56 (0.23)	3.36 (1.40)	1.90 (1.11)	1065.9(622.7)
	Wild pig	HNC	0.624	21	33.2 (8.11)	0.09	0.18 (0.04)	1.46 (0.47)	4.64 (1.27)	6.78 (2.9)	183.06(78.3)
	Barking deer	HNC	0.764	31	36.9 (4.05)	0.14	0.59 (0.06)	1.94 (0.44)	1.01 (0.05)	1.97 (0.46)	35.46(8.28)
BAMBOO-MIXED FOREST	Chital	HNC	0.611	75	47.09 (7.20)	0.43	0.25 (0.03)	4.57 (1.09)	7.6 (0.57)	34.74 (8.74)	1632.78(410.7)
	Sambar	HRC	0.620	72	42.6 (15.9)	0.41	0.26 (0.09)	5.8 (1.16)	2.22 (0.15)	12.97 (2.7)	1763.92(367.2)
	Gaur*	HRC	0.620	34	37.46 (7.93)	0.08	0.22 (0.04)	1.07 (0.39)	2.26 (0.68)	2.43 (1.15)	1363.23(645.1)
	Wild pig	HRC	0.712	21	26.3 (10.7)	0.11	0.24 (0.09)	2.18 (1.15)	4.82 (1.26)	10.53 (6.24)	284.31(168.4)
	Barking deer	HRC	0.670	20	51.2 (13.26)	0.10	0.46 (0.12)	1.0 (0.3)	1.0 (0,05)	1.01 (0.40)	18.18(7.2)
MISCELLANEOUS FOREST	Chital	HRC	0.744	103	51.8 (3.77)	0.23	0.47 (0.03)	2.29 (0.44)	10.15 (0.91)	23.33 (4.98)	1095.10(233.7)
	Sambar	HRC	0.722	110	34.2 (2.91)	0.25	0.43(0.03)	3.72 (0.64)	2.49 (0.14)	9.29 (1.69)	1263.44(229.8)
	Gaur	HRC	0.747	68	47.9 (6.11)	0.15	0.40 (0.05)	1.64 (0.32)	4.95 (0.65)	8.13 (1.94)	4560.93(1088.3)
	Wild pig	HRC	0.685	40	36.07 (7.13)	0.09	0.55 (0.11)	1.28 (0.39)	5.82 (1.02)	7.47 (2.63)	201.69(71.0)
	Barking deer	HRC	0.600	69	31.22 (2.77)	0.15	0.61 (0.05)	2.55 (0.38)	1.60 (0.04)	4.07 (0.50)	73.26(9.0)

*** Indicates that we used pooled detection data for 2012 and 2013 to fit a detection function but report density, group density, cluster size and biomass only of 2013. UC-Uniform Cosine; HNC-Half Normal Cosine; HRC- Hazard Rate Cosine; KS test- Kolmogorov Smirnov test; SE-Standard Error.**

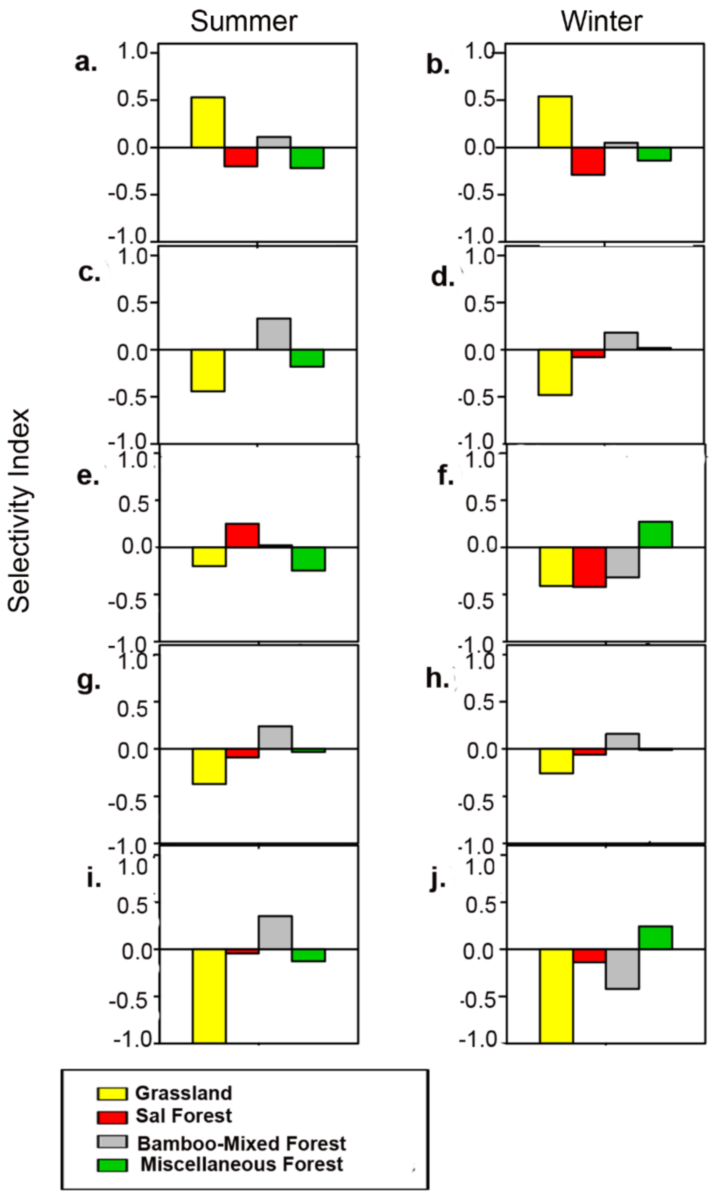


Figure 2. 2 Seasonal habitat selection by chital a) summer b) winter; sambar c) summer d) winter; gaur e) summer f) winter; wild pig g) summer h) winter and barking deer i) summer j) winter in Kanha Tiger Reserve depicted by Ivlev's selectivity index.

4. Discussion

By sampling habitats in proportion to their availability, my sampling design permits the conventional global analysis as well as habitat wise analysis. The precision of density estimates depends on the variability in effective strip width, encounter rates, and the cluster size (Thomas et al. 2010; Ogotu et al. 2005). I believe that by laying habitat specific transects and subsequently analysing the data separately for each habitat type I can minimize the variability contributed by ESW. However, sample size and encounters obtained in each habitat strata were small in comparison to the global analysis. The stratified analysis provides more ecologically meaningful results. Unfortunately, homogenous habitat patches of sufficient size to mark independent transect line within each habitat patch were not available in the human dominated buffer zone. I, therefore, could not extend the habitat specific analysis to the buffer zone.

4.1. Core and buffer densities

Our study unambiguously demonstrates the impact of even low human use on wild ungulate densities. The core area, where there were no human habitations and had minimal use by humans had higher densities of all ungulates except wild pig, barking deer and nilgai. The core had 4.8 times higher wild ungulate biomass compared to the buffer zone. This higher biomass density in the core area was due to both increased encounter rate as well as larger cluster size. It is well known that larger cluster sizes are found in resource rich areas (Pullium and Caraco 1984), suggesting that habitat quality was better in the core area for most ungulates. More importantly, barasingha and chousingha were found only within the core area of the Tiger Reserve and were either absent or occurred in very low densities in the multiple use buffer zone forests, highlighting the importance of undisturbed areas for endangered and rare ungulates. The depression of wild ungulates in the forests of the buffer zone were likely due to competition with livestock (Loveridge et al. 2010), extraction of minor forest produces and biomass, and subsistence level poaching (Steinmetz et al. 2010). In countries like India, with high human densities and associated high demand for land, protected areas are small by global standards (Lopoukhine et al. 2012). Harbouring viable populations of apex carnivores such as tigers in such small reserves is a major conservation concern. My study lends support to the conservation strategy of relocating human habitation by incentivised voluntary relocation from core areas of tiger reserves, as such areas would then support a much higher density of prey and subsequently the carnivore community, including tigers.

4.2. Habitat specific seasonal densities

Seasonal habitat selection by ungulates is influenced by metabolic and nutritional requirements for maintenance, growth, rut, gestation and lactation (Owen Smith 1994). These physiological needs combined with predation risks vary across habitat types (Kie 1999) and determine animal distribution. Tropical India is highly seasonal due to the effect of monsoon. Ungulate densities are likely to respond to varying seasonal nutrient availability in different habitats.

Grasses grow during monsoon (July to September), mature and flower in October and November, and become senescent in summer (March to June). However, due to high soil moisture and management practice of late winter burn, most grasses produce a fresh flush of new shoots during early summer.

Thus, protein and nutrient availability are maximum in monsoon and in a month of early summer after the annual late winter burn (February to March) in grasslands. In forested habitats, new flush of leaves, flowers and fruits emerge prior to monsoon in the peak of the dry summer season (May and June). Bamboo *(Dendrocalamus strictus)* produce new shoots at the beginning of summer and growth declines by October and November (Liese and Kohl 2015). Patterns of ungulate distribution may change in different times of the year because plant growth and, thus food availability changes between the seasons. In my study, chital used grassland habitat throughout the year and maintained large herd size and high densities over other habitat types. Due to smaller mouth parts, chital could possibly obtain the required nutrients by selective foraging (Schaller 1967) even when the nutrient quality of grasslands declined in summer. Chital fawns have a "lying out" stage wherein they remain hidden in tall grass clumps and bushes for the initial few weeks of their life in winter (Schaller 1967). Thus, the requirement of food and cover by chital could potentially be achieved by living within grassland and bamboo-mix forests in both the seasons.

Maximum densities of sambar were recorded in bamboo-mixed habitat throughout the year and sambar also showed a high preference for this habitat type. Sambar are primarily browsers and prefer undulating to steep terrain (Hoffman 1989). Bamboo-mixed forests provide the maximum diversity of browse species, and this habitat type occurs on hill slopes, explaining the high density and preference shown by sambar for this habitat mainly in summer. The cluster size of sambar were small and similar across habitats.

Gaur are known for their seasonal movements (Imam 1985). Unlike other ungulates, there was a distinct difference in their seasonal densities between different habitats. During the summer, their density, as well as preference was higher for sal forest. Plants such as *Flemingia spp*. and *Mallotus philippinensis* sprout in sal forest during this season and are a significant source of food for gaur. During winter season, gaur mainly shift to areas with more browse and having dense plant cover. Gaur herds were observed to be larger in summer compared to winter in all habitats. During summers, water becomes a limiting factor in the higher elevations and gaur descend to valley habitats where they calve and rut (Schaller 1967). This results in larger aggregations of gaur in summer.

My study stresses the importance of inviolate core areas for achieving high wild ungulate densities and for maintaining populations of endangered and rare species. We show the relevance of different habitat types for differential seasonal use by ungulates and attempt to interpret these in the context of nutrition and cover needs by wild ungulates. Much of the Kanha forest was worked for enhancing timber production in the past, and the current stands of sal forests are a result of selective thinning of non-timber species (Blakesley1905). Now the thrust of management within protected areas is for the conservation of diversity, endangered species, and ungulate biomass to sustain viable populations of large carnivores. Maximum diversity and ungulate biomass was supported by grassland followed by bamboo-mixed habitat. Furthermore, endangered species like barasingha and blackbuck were found only in the grassland habitat. Grasslands accounts for 9% of the KTR core area, most of which originated due to the anthropogenic activity of agriculture and livestock grazing. Most grasslands of KTR are currently maintained by management of woody plant removal and fire in this arrested stage of succession. Enhancing this habitat along with its appropriate management would help maintain ungulate diversity, cater to the needs of the only surviving population of the endangered hard ground barasingha and increase ungulate biomass so as to sustain a source population of tigers in this landscape.

Chapter 3. Demographic parameters of ungulates in Kanha Tiger Reserve

1. Introduction

Ungulates are known as “potential initiators” of interaction chains, significantly influencing ecosystem processes (Augustine & McNaughton 2006). They impact plant community structure and forest dynamics directly through grazing and browsing (Chase et al. 2000), as well as indirectly through seed dispersal (Duncan et al. 2006). Ungulates also influence primary productivity, nutrient cycling, and soil fertility, both positively (McNaughton et al. 1997) and negatively (Ritchie et al. 1998). Ungulates as prey, play an essential role in maintaining populations of carnivores (Wolf & Ripple 2018). When sufficient prey is unavailable, carnivore populations decline and can become locally extinct (Brugiere et al. 2015). Therefore, monitoring changes in population size of ungulates over time is critical for effective conservation and management of protected areas. Long-term monitoring helps us in deciphering population dynamics and is of great help in prioritizing conservation efforts (O’Kelly et al. 2012).

Ungulates are an excellent model for long-term studies. Ungulates can be observed or sampled repeatedly within a year or seasons and over multiple years. It is because of their longevity and philopatric nature (Bowyer et al. 2014). Therefore, by monitoring ungulates over a life span, we can study changes in age structure, body condition (long-term fitness consequences of changes in internal states) as well as the effect of predation and human disturbance (Festa-Bianchet et al. 2017). Trends in age and sex ratio of ungulates over the years can additionally provide relevant information for population management (Dreiss et al. 2010). Thus, a single demographic parameter “growth” summarizes the collective action of the environment, both biotic and abiotic, on the status and performance of the species population (Caughley 1977).

During the last five decades, considerable ecological changes have taken place within the Kanha ecosystem. Villages from within the Protected Area have been relocated since 1961 coupled with intensive grassland management for barasingha conservation. It has resulted in enhancing habitat conducive for other grassland ungulates. Tiger centric management initiated by Project Tiger since 1972 has proved particularly favourable to other ungulates in the Reserve as well. In Kanha, high conservation investments have been made in Banjar catchment (Kanha-Kisli-Sarhi-Mukki landscape) compared to Halon catchment (Supkhar-Bhaisanghat landscape), which is more prone to poaching. Against this background of ecological change, it is of interest to know how ungulates within the two management units (Banjar and Halon) of Kanha National Park have been affected, where also three predators (tiger, leopard and dhole) are found in high densities. The objective of this chapter is to assess trends in ungulate abundance and other demographic factors with respect to management investments. The analysis uses population estimates from line transect surveys conducted during the past six years (2013- 2018) in both seasons, summer and winter, to determine the population trends of six ungulates in Kanha National Park, Madhya Pradesh, India.

2. Materials and Methods

2.1 Field design and data collection:

Study of demographic patterns of ungulates was carried out at two spatial scales. At the landscape scale; the entire National Park of Kanha (940 km^2) was sampled for ungulate densities. While, at a local scale, I used stratified design in the National park in two zones; Banjar (539 km^2) and halon (402 km^2) catchments, which differed in terms of conservation investments **(Figure 3.1).**

Line transects of 2 km were marked randomly within each stratum (Banjar catchment had 88 transects while halon catchment had 62 transects) within National Park **(Figure 3.1).** Each transect was walked during the early morning (6:00 am to 8:00 am), for three consecutive days in summer (from the year 2013 to 2017) and winter (from the year 2014 to 2018). Total transects survey effort comprised 900 km of the walk along 150 spatial transects in both seasons for each consecutive year. Radial distance, animal bearing and group size were recorded with an encounter of each ungulate species. I surveyed the entire National Park with well-trained field staff and wildlife researchers.

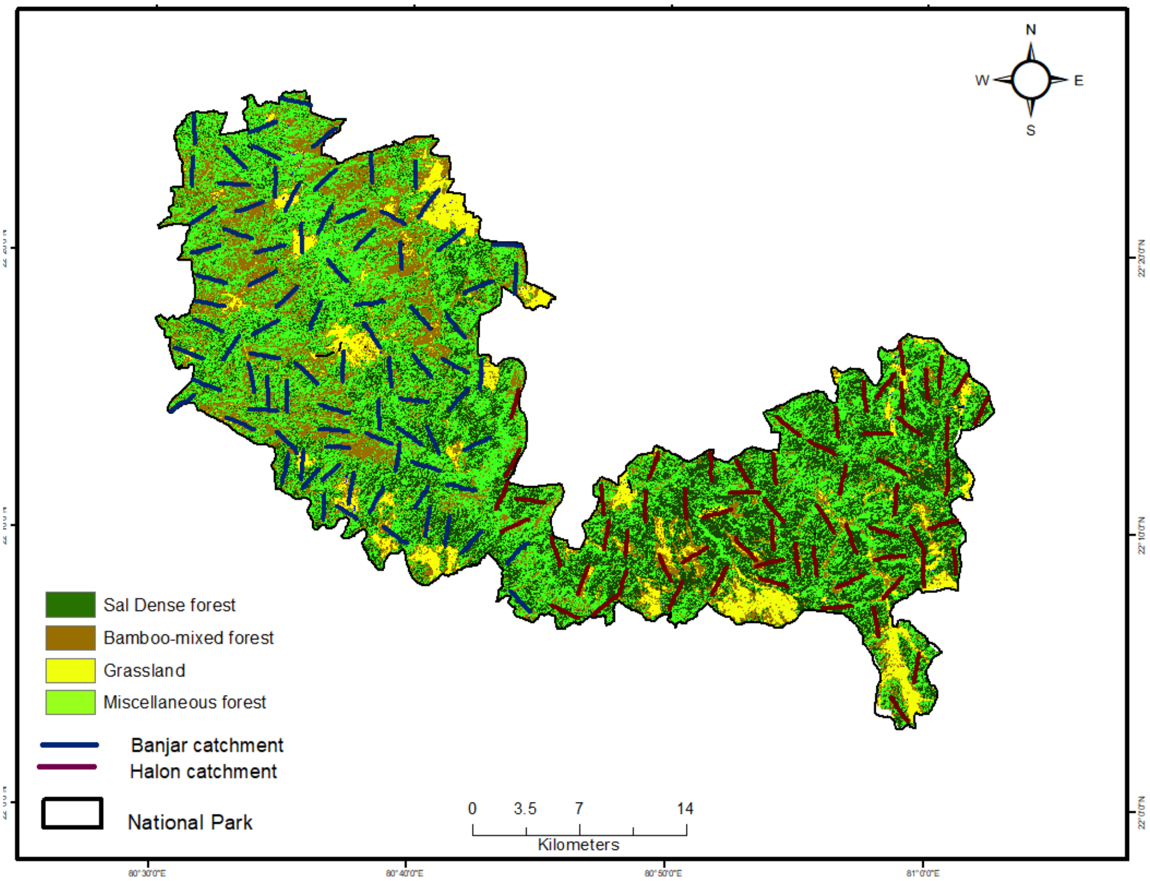


Figure 3. 1 Map showing line transects (n=150) in Banjar and Halon catchments of National Park.

2.2 Demographic parameters (population structure, sex ratio, female: fawn ratio, fawn: yearling ratio and body condition):

Intensive surveys on group size and composition were conducted and recorded throughout Kanha National park for chital, sambar and gaur. I collected data on age-sex group structure using direct sampling without replacement (Skalski et al. 2005) by traversing a study area with widely spaced and non-overlapping travel routes where each individual animal or group were sighted once during each survey season. Each group was distinguished into identifiable age and sex categories (Schaller 1967). The age categories were 1) fawn or calf (< or equal to 6 months) 2) juvenile or yearling (< or equal to 1 year but > 6 months)

3) sub-adult male and female (< 2 years but > 1 year) 4) Adult male and female (> 2 years). A detailed description of age categories discerned in the field is given in **Figure 3.2 a, b.**

Population management data for ungulates were collected to facilitate information relative to biologically meaningful period. The biological years for large ungulates include birth, preweaning and post-weaning periods for juveniles, and same period and breeding/ fawning period for adults. Therefore, I collected age-sex structure data in two consecutive years of 2018 and 2019 for estimating adult sex ratio and adult female: fawn ratio in the biologically meaningful period between December to June (which represents the crucial period for breeding and fawning season of major ungulates, i.e. chital, sambar and gaur).

The nutritional pinch period in Kanha is prior to monsoon and before burning season in February-March. During this period (December to June), I sampled throughout Kanha National Park and scored a minimum of three animals for each ungulate (chital, sambar and gaur) in each group encountered for body condition. The index consists of scoring different regions of an ungulate body, i.e. rump, tail, pelvic girdle, pectoral girdle and ribs, on a score of 1 to 5, 1 being excellent condition while 5 being extremely poor (Riney 1960). The body condition of gaur was also assessed visually by scoring an area of depression around the lumbar and pelvic region **(Figure 3.3).**

Fawn (< or equal to 6 months)

Small, square bodies, square and flat heads and large ears, their bodies and legs are thin and have not built any significant muscle definition.

Yearling (< or equal to 1 year but > 6 months)

Bigger than fawn. Shorter faces/muzzles than mature female deer. Males are identified by single spiked antlers.

Subadult (< 2 years but > 1 year)

Shorter than mature adult in height. Thinner necks than adult deer. Legs are thinner and longer in compare to its body. Flattish belly, antlers tend to be less heavy and simpler in structure, antlers do not protrude in front of the male deer’s face. Rump is more angular in its feature. Depth of chest seems less than length of legs.

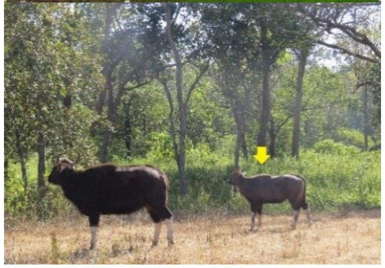
Adult Male and female (> 2 years)

Belly sags and rump becomes bigger and rounder with age. Antlers shows triangular profile and complex structure. An older buck antler will stick about as far as deer’s nose. Greater apparent depth of chest, may seen more than length of legs especially in male adults. Most of the enamel worn away at fully matured.

Figure 3. 2a Criteria to distinguish different age categories of cervids (chital and sambar) in field following Schaller et. al. (1967).

Calf (< 15 months)

Light orange-brown body coat; horn appears as a bump on the head or if visible are only 10-15 cm long; 50% in body mass.



Juvenile (15-24 months)

Reached more than 2/3rd adult female shoulder height; white stocking visible.

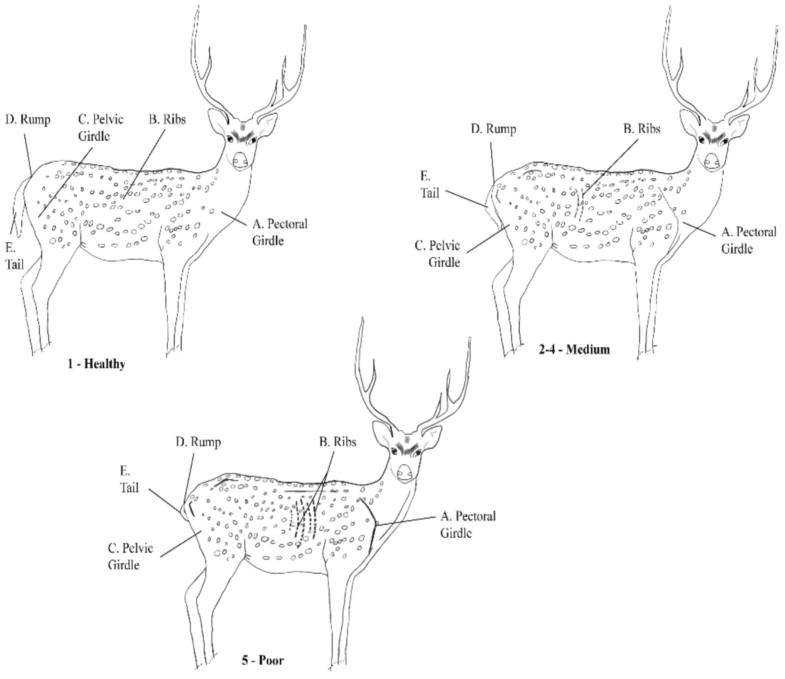
Subadult (2-3 years)

Dark Brown in colour; horn curve inwards; amount of white in female horns exceed 40%.

Adult (> 3 years)

Females remain dark brown and do not turn black, while males are called as blackbulls; horn curve more inwards and closer to each other; amount of white on female's horn exceed 80%, height and mass increase and dewlaps get bigger.

Figure 3.2b Criteria to distinguish different age categories of bovid (gaur) in the field following Ahrestani et. al. (2011).



Score 1: Shiny coat, spinal process and ribs well covered, rump rounded at the base of the tail, pelvic and pectoral girdle pin bones well covered

Score 2-4: less shiny coat, ribs visible faintly, body outline bony, rump less rounded

Score 5: Scruffier and harsher appearance of coat, spinal process very apparent, pin bones and base of tail very obvious

Figure 3. 3 Body condition score of ungulates (chital as an example) in field following Riney (1960).

2.3 Data analysis:

2.3a Ungulate Density and its Trend:

Ungulate density estimates were estimated for each season (summer and winter) for each year (2013-2018) from 150 line transect samplers placed across 900 km^2 of the study area using conventional distance sampling approach in Program Distance (Version 7.0). I analyzed population trends of 5 ungulate species: chital, sambar, gaur, barking deer and wild pig, in the National Park as well as for each management strata (Banjar and Halon catchment). Since there were very few sightings of chousingha, I developed detection functions for chousingha from all transects pooled across years and subsequently estimated density for each year in summer and winter for National Park by post-stratification. I also estimated global density for chousingha for summer and winter using a common detection function as it was difficult to assess population trend.

It is preferable to fit a separate detection function to each year of data when sample sizes are reasonably large, to avoid confounding any changes in density with possible changes in detection probability (Buckland et al. 2004). I tested this premise for species that had a large number of detections in each year (2013-2018) stratum such as chital by comparing the effective strip width (ESW) and detection probability obtained from independent fitting of detection functions for each year **(Figure 3.4).** Since ESWs and detection probability differs between years, I used separate detection functions for each year, and separate analysis was done for each conservation investment zone (Banjar Catchment and Halon Catchment) to get density estimates for each zone, for each year, season and for each species. Shape criteria were examined for heaping, and any outliers were right-hand truncated where necessary (Buckland et al. 2001). Three key functions (uniform, half normal and hazard rate all with cosine, simple polynomial and hermite polynomial series adjustment) were considered for each analysis **(Table 3.1 to 3.6).** Model selection was evaluated using Akaike's information criteria (AIC), while Kolmogorov–Smirnov statistics were used to assess the goodness of fit of each model (Buckland et al. 2004).

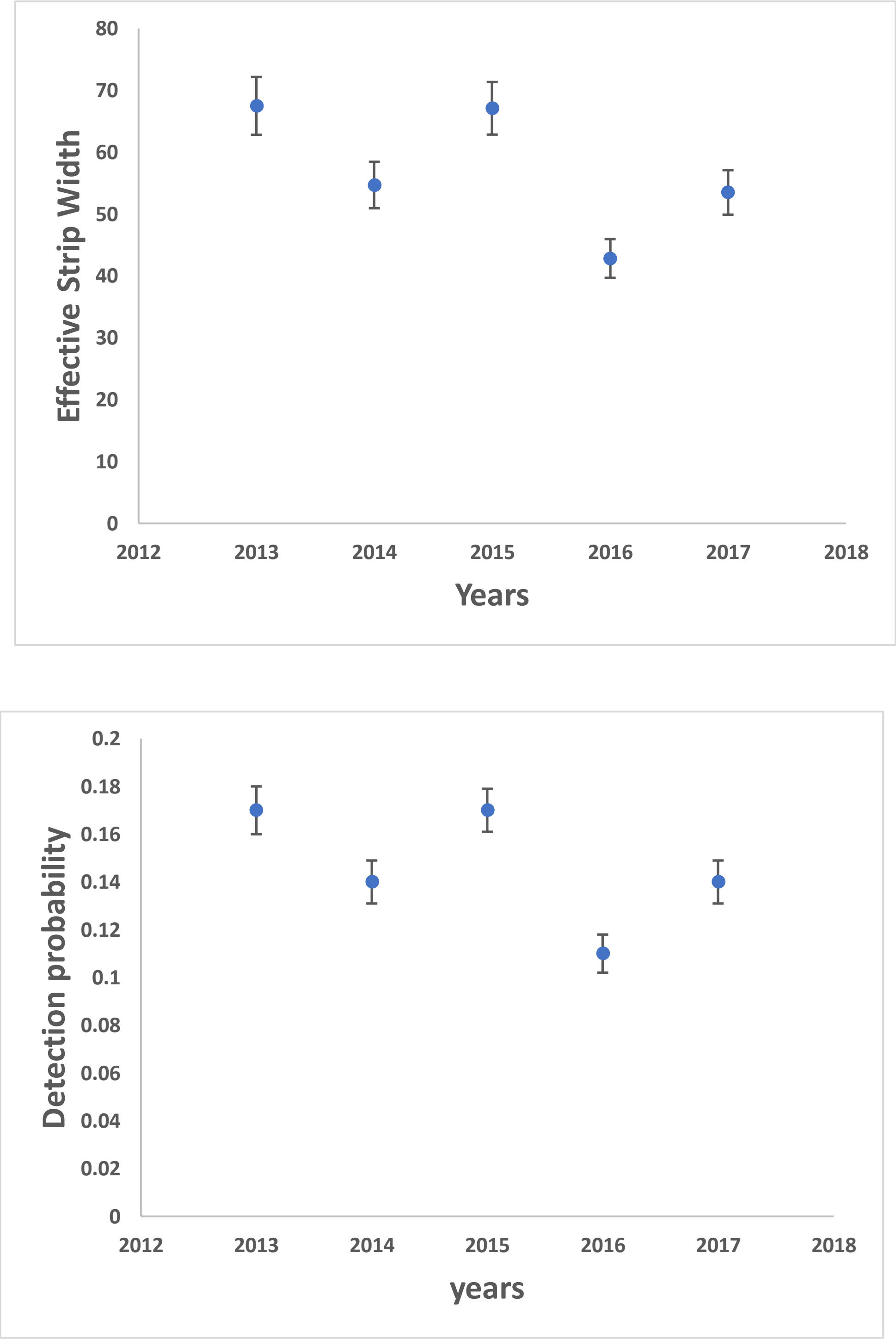


Figure 3. 4 Effective Strip Width and Detection probabilities of chital in National park from year 2013 to 2018 (Error bars are standard error).

I estimated annual growth rate (r) for ungulates by regressing Natural log of density against years (Skalski et al. 2005) to identify trends; whether population increased, decreased or was stable over time. This analysis allows researchers and managers to access annual recruitment pulses in the population. Time periods of population estimates were graphed and examined visually through scatter plots and subsequently analyzed using formal hypothesis testing (Zar 1999).

2.3b Population structure, sex ratio, fawn:female ratio and body condition:

The age structure of chital, sambar and gaur populations were computed from the data pertaining to percentage contributions of each age-sex class to total population for summer and winter season for Kanha National Park as well as Banjar and Halon catchments. Sex ratio was computed to evaluate the population structure (Schaller 1967). The sex ratio of the population was estimated by the maximum likelihood estimator (MLE) as ($R_{F/M}$=f/m, where f = number of adult females recorded in a sample of size n and m = a number of adult males recorded in a sample of size n) using single sample survey without replacement (Skalski et al. 2005). I traversed an area with non-overlapping travel routes each day and sighted the animals of that area once during the survey; therefore, sampling would be considered as a survey without replacement. The fawn to female ratio and fawn to yearling ratio was also calculated to estimate recruitment (Schaller 1967; Caughley 1977; Jhala 1991). The variance for the sex ratio estimator, $R_{F/M}$ and fawn to female ratio is derived using the delta method (Skalski et al. 2005).

Body condition of chital, sambar and gaur were evaluated to understand the population status and health of ungulates (Harder & Kirkpatric 1996). The scores on various body parts were likely to be correlated amongst themselves. Hence, to reduce the dimensionality and redundancy of the data, a principal component analysis (PCA) was conducted (McGarigal et al. 2000) in SPSS version 21 software (SPSS 2012). Principal component scores of ungulate body condition were statistically compared (using one-way Anova) between seasons (summer and winter) and Banjar and Halon catchments.

2.4 Estimation of carrying capacity of tigers based on available prey density and their biomass

Individual prey densities of chital, sambar, gaur and wild pig obtained from DISTANCE were multiplied with 3/4th of the adult female body mass of individuals of prey species (Schaller 1972) to obtain biomass of prey species. Tiger carrying capacity of our intensive study area was then estimated by using Hayward et al. (2007) equation model for preferred prey species, who applied the same model to lions in South Africa. This model is as follows: **$y = 2.158 + 0.377x$**; where y= log10 of maximum carrying capacity of predator density for the available prey and x = log10 of prey biomass per unit area/sq.km. Based on field data from lions, Hayward et al. (2007) assessed b as 0.377 (**Supplementary information S12).**

3. Results

3.1 Density estimates and Population trend of ungulates

A total of 150 transects **(Figure 3.1)** with an effort of 900 km were walked during the winter and summer season from the year 2013-2018 in Banjar and Halon catchments within Kanha National Park. Among wild ungulates in the National Park, chital was the most abundant species followed by sambar, gaur, wild pig, barking deer and chousingha in both summer and winter of 2013-2018 **(Table 3.1 & 3.4).**

Chital and sambar density (mean ± standard error) was highest in Banjar catchment compared to Halon catchment in both summer and winter seasons **(Table 3.2, 3.3, 3.5 & 3.6).** Gaur density was relatively higher in Banjar catchment compared to Halon catchment in both the seasons **(Table 3.2 & 3.5).** In contrast, wild pig and barking deer density were high in Halon compared to Banjar catchment **(Table 3.3 & 3.6).** Chousingha was the least abundant species among wild ungulates in Kanha and patchily distributed in the park. The density of chousingha could be computed only for National park as there were very low sightings in Banjar and Halon separately **(Table 3.1 & 3.4).** The global density of chousingha in Kanha National Park was found to be 0.12 (SE ± 0.03) in summer and 0.16 (SE ± 0.04) in the winter season.

Ungulate density showed stable trends over the years in National Park as well as in their local catchments: Banjar and Halon, in both summer and winter seasons **(Figure 3.5 to 3.7).** Amongst all ungulates, the only chital showed a significant increase in density (realized rate of increase, r=0.09, SE ± 0.02; P value=0.00) over the years in National park **(Figure 3.5).** Chital also shows significant growth rate in local catchment, Banjar catchment (r=0.09 SE ± 0.01; P value=0.00) when compared to Halon catchment **(Figure 3.6 & 3.7).** Sambar showed significant growth in Banjar (r=0.06, SE ± 0.02; P value= 0.03) **(Figure 3.6)** while gaur showed significant growth in Halon catchment (r= 0.25, SE ± 0.07; P value= 0.00) **(Figure 3.7).**

Table 3. 1 Density Parameters based on best model selection of ungulates in summer season in Kanha National Park.

Species	Year	n	D (SE)	DS (SE)	E(S) (SE)	ESW (SE)	P (SE)	n/l	KS test	Best fit model
Chital	**2013**	359	28.84(3.02)	2.95(0.25)	9.83(0.53)	67.5(4.67)	0.17(0.01)	0.39	0.812	HZ SP
	2014	371	33.38(3.6)	3.76(0.32)	8.94 (0.46)	54.7(3.75)	0.14(0.009)	0.41	0.932	HZ SP
	2015	328	34.49(3.86)	2.72(0.22)	12.81(0.75)	67.1(4.25)	0.17(0.009)	0.36	0.821	HZ COS
	2016	277	35.1(4.12)	3.60(0.34)	9.63 (0.63)	42.83(3.13)	0.11(0.008)	0.30	0.765	HZ SP
	2017	370	42.9(6.12)	3.84(0.32)	13.17(0.72)	53.51(3.60)	0.14(0.009)	0.41	0.748	HZ SP
Sambar	**2013**	250	9.5(1.08)	3.42(0.36)	2.79(0.10)	47.18(2.81)	0.21(0.01)	0.27	0.788	HZ SP
	2014	225	8.03(0.91)	3.08(0.32)	2.60(0.10)	40.72(2.73)	0.18(0.01)	0.25	0.673	HZ COS
	2015	216	8.06(1.01)	2.96(0.35)	2.72(0.10)	39.69(2.44)	0.18(0.01)	0.24	0.687	HZ COS
	2016	241	9.66(0.93)	3.30(0.28)	2.92(0.12)	37.48(2.43)	0.17(0.01)	0.26	0.721	HZ COS
	2017	262	10.0 (0.98)	3.59(0.30)	2.98(0.11)	42.07(2.27)	0.19(0.01)	0.29	0.745	HZ COS
Gaur	**2013**	91	4.81(0.93)	0.93(0.14)	5.16(0.63)	45.86(6.98)	0.18(0.02)	0.10	0.621	HZ COS
	2014	86	4.13(0.82)	0.87(0.13)	4.70(0.62)	66.82(7.38)	0.26(0.02)	0.09	0.654	HZ COS
	2015	87	4.65 (0.84)	0.88(0.11)	5.23(0.66)	61.75(8.67)	0.24(0.03)	0.09	0.701	HZ COS
	2016	87	3.65 (0.63)	0.88(0.10)	3.55(0.63)	56.12(5.05)	0.22(0.01)	0.09	0.759	HZ COS
	2017	108	5.2 (0.89)	1.10(0.13)	4.77(0.56)	49.13(4.85)	0.19(0.01)	0.12	0.751	HZ COS
Wild Pig	**2013**	102	7.25(1.2)	1.35(0.17)	5.36(0.57)	51.76(4.11)	0.18(0.01)	0.11	0.897	HZ SP
	2014	125	7.68(1.19)	1.65(0.18)	4.64(0.49)	46.58(3.49)	0.16(0.01)	0.13	0.928	HZ COS
	2015	102	6.91(1.13)	1.35(0.16)	5.11(0.55)	43.06(4.37)	0.15(0.01)	0.11	0.581	HZ SP
	2016	124	7.73(1.15)	1.64(0.18)	4.71(0.47)	39.60(3.60)	0.14(0.01)	0.13	0.434	HZ SP
	2017	128	7.78(1.1)	1.69(0.17)	4.59(0.43)	41.71(3.71)	0.14(0.01)	0.14	0.429	HZ SP
Barking Deer	**2013**	124	2.64(1.08)	2.07(0.22)	1.27(0.03)	40.39(3.76)	0.11(0.01)	0.13	0.478	HZ SP
	2014	137	2.5(0.91)	2.29(0.22)	1.09(0.01)	38.09(3.27)	0.11(0.009)	0.15	0.945	HZ COS
	2015	154	2.19(1.01)	2.58(0.27)	1.16(0.02)	34.08(2.49)	0.10(0.007)	0.17	0.444	HZ SP
	2016	152	3.12(0.93)	2.54(0.26)	1.22(0.03)	36.49(2.60)	0.10(0.007)	0.16	0.959	HZ SP
	2017	164	3.32(0.98)	2.74(0.23)	1.21(0.02)	38.41(2.08)	0.11(0.006)	0.18	0.986	HZ SP
Chousingha	**2013**	8	0.14(0.06)	0.08(0.03)	1.61(0.29)	49.71(8.87)	0.16(0.02)	0.008	0.810	HZ SP
	2014	8	0.25(0.13)	0.11(0.05)	2.12(0.47)	37.29(9.45)	0.12(0.03)	0.008	0.920	HN HP
	2015	3	0.08(0.06)	0.06(0.04)	1.40(0.42)	26.36(1.07)	0.08(0.03)	0.003	0.935	HN HP
	2016	7	0.11(0.07)	0.08(0.05)	1.29(0.17)	44.7(12.08)	0.14(0.04)	0.007	0.946	HN HP
	2017	8	0.21(0.11)	0.13(0.06)	1.65(0.42)	33.84(8.61)	0.11(0.02)	0.008	0.954	HN HP

(D= Density; DS= Group size Density; E(S)=Mean cluster size; ESW= Effective Strip Width; P= Detection Probability; n/l= Encounter Rate; KS test= Kolmogorov Smirnov Test; HZ-Hazard Rate; SP- Simple Polynomial; COS- Cosine; HN -Half Normal)

Table 3. 2 Density Parameters based on best model selection of ungulates in summer season at Banjar catchment of Kanha National Park.

Species	Year	n	D (SE)	DS (SE)	E(S) (SE)	ESW (SE)	P (SE)	n/l	KS test	Best fit model
Chital	**2013**	333	45.2 (7.14)	4.59(0.67)	9.84(0.56)	68.69(5.07)	0.18(0.01)	0.63	0.685	HZ SP
	2014	323	50.15(7.64)	5.64(0.80)	8.88(0.48)	54.21(3.83)	0.14(0.01)	0.61	0.672	HZ COS
	2015	285	53.85(10.32)	4.03(0.72)	13.30(0.84)	66.94(4.63)	0.17(0.01)	0.53	0.846	HZ SP
	2016	237	56.33(10.2)	5.56(0.91)	10.13(0.75)	40.35(3.33)	0.10(0.008)	0.44	0.673	HZ SP
	2017	319	61.98(9.34)	5.02(0.68)	12.34(0.79)	53.06(4.03)	0.14(0.01)	0.60	0.855	HZ SP
Sambar	**2013**	219	13.04 (1.65)	4.47(0.53)	2.90(0.10)	46.35(2.94)	0.21(0.01)	0.41	0.682	HZ SP
	2014	182	10.9 (1.56)	4.16(0.57)	2.61(0.11)	41.34(3.13)	0.19(0.01)	0.34	0.810	HZ SP
	2015	187	12.83 (1.85)	4.62(0.63)	2.77(0.12)	38.32(2.54)	0.17(0.01)	0.35	0.900	HZ SP
	2016	193	14.95 (1.88)	5.06(0.58)	2.98(0.15)	36.09(2.71)	0.16(0.01)	0.36	0.980	HZ SP
	2017	206	15.18 (1.75)	4.78(0.71)	3.21(0.12)	40.79(2.67)	0.18(0.01)	0.39	0.784	HZ COS
Gaur	**2013**	76	7.43 (1.61)	1.69(0.40)	5.41(0.71)	42.35(7.40)	0.16(0.02)	0.14	0.984	HZ SP
	2014	64	5.68 (1.33)	0.89(0.19)	5.35(0.66)	67.63(9.67)	0.26(0.03)	0.12	0.609	HZ COS
	2015	58	5.86 (1.29)	0.98(0.22)	5.72(0.55)	55.88(9.87)	0.22(0.03)	0.10	0.941	HZ SP
	2016	57	4.6 (1.02)	0.97(0.18)	4.57(0.72)	55.34(6.89)	0.21(0.02)	0.10	0.994	HZ SP
	2017	74	6.3 (1.36)	1.52(0.27)	4.62(0.67)	45.90(4.53)	0.18(0.01)	0.14	0.892	HN COS
Wild Pig	**2013**	75	6.85 (1.34)	1.36(0.23)	5.04(0.45)	52.2(5.17)	0.18(0.01)	0.14	0.706	HZ SP
	2014	82	6.62 (1.34)	1.70(0.27)	3.88(0.47)	45.49(4.24)	0.16(0.01)	0.15	0.770	HZ SP
	2015	67	6.74 (1.59)	1.56(0.33)	4.31(0.40)	40.55(6.01)	0.14(0.02)	0.12	0.920	HZ SP
	2016	66	7.48 (1.84)	1.99(0.42)	3.74(0.46)	31.31(4.92)	0.11(0.01)	0.12	0.965	HZ SP
	2017	83	7.40 (1.44)	1.65(0.28)	4.48(0.41)	47.58(4.96)	0.17(0.01)	0.15	0.726	HZ SP
Barking Deer	**2013**	80	2.35 (0.35)	1.88(0.27)	1.25(0.04)	40.24(3.20)	0.11(0.009)	0.15	0.478	HZ COS
	2014	66	2.13 (0.35)	2.01(0.35)	1.06(0.02)	31.06(3.37)	0.09(0.009)	0.12	0.945	HZ SP
	2015	78	2.56 (0.41)	2.20(0.34)	1.16(0.04)	33.56(2.55)	0.09(0.007)	0.14	0.444	HZ COS
	2016	57	2.01 (0.39)	1.64(0.30)	1.22(0.07)	32.82(3.82)	0.09(0.01)	0.10	0.959	HZ COS
	2017	85	2.22 (0.32)	1.91(0.20)	1.16(0.04)	42.08(3.07)	0.12(0.009)	0.16	0.986	HZ SP

(D= Density; DS= Group size Density; E(S)=Mean cluster size; ESW= Effective Strip Width; P= Detection Probability; n/l= Encounter Rate; KS test= Kolmogorov Smirnov Test; HZ-Hazard Rate; SP- Simple Polynomial; COS- Cosine; HN -Half Normal)

Table 3. 3 Density Parameters based on best model selection of ungulates in summer season at Halon catchment of Kanha Tiger Reserve.

Species	Year	n	D (SE)	DS (SE)	E(S) (SE)	ESW (SE)	P (SE)	n/l	KS test	Best fit model
Chital	**2013**	26	6.01(1.86)	0.63(0.18)	9.51(1.92)	55.28(8.41)	0.22(0.03)	0.06	0.773	HZ SP
	2014	48	9 (2.97)	0.97(0.25)	10.01(1.72)	64.95(10.8)	0.26(0.04)	0.12	0.579	HZ SP
	2015	44	8.51 (2.26)	0.91(0.23)	9.27(1.41)	64.43(11.5)	0.25(0.04)	0.11	0.548	HZ SP
	2016	41	7.6 (1.49)	1.04(0.26)	6.64(0.84)	52.75(8.46)	0.21(0.03)	0.11	0.972	HZ SP
	2017	51	13.79(4.31)	1.21(0.32)	11.03(0.99)	56.42(5.11)	0.22(0.02)	0.13	0.646	HZ SP
Sambar	**2013**	31	2 (0.47)	0.77(0.24)	2.33(0.28)	53.54(13.1)	0.37(0.09)	0.08	0.996	HN COS
	2014	43	3.36 (0.68)	1.78(0.45)	2.55(0.22)	31.92(6.13)	0.22(0.04)	0.11	0.940	HZ COS
	2015	29	3 (0.57)	0.79(0.21)	2.72(0.25)	48.94(8.74)	0.34(0.06)	0.07	0.878	HZ COS
	2016	48	4 (0.73)	1.51(0.26)	2.70(0.19)	42.53(3.78)	0.30(0.02)	0.12	0.774	HN HP
	2017	56	4.29 (0.78)	1.85(0.34)	2.46(0.16)	40.0(3.98)	0.28(0.02)	0.15	0.932	HN COS
Gaur	**2013**	15	1.03 (0.66)	0.34(0.18)	2.99(0.98)	58.21(26.7)	0.35(0.16)	0.04	0.953	HZ COS
	2014	22	2.04 (0.94)	0.42(0.15)	4.78(1.43)	68.22(14.8)	0.41(0.08)	0.05	0.524	HZ COS
	2015	29	2.65 (1.06)	0.53(0.19)	4.96(0.76)	73.03(20.86)	0.44(0.12)	0.07	0.926	HZ COS
	2016	30	3.09 (1.01)	0.87(0.20)	3.53(0.82)	46.02(6.03)	0.27(0.03)	0.08	0.840	HN COS
	2017	34	6.23 (1.75)	0.95(0.23)	6.52(0.92)	47.8(7.50)	0.28(0.04)	0.09	0.574	HZ COS
Wild Pig	**2013**	27	3.17 (1.04)	0.89(0.24)	3.55(0.64)	40.63(6.21)	0.27(0.04)	0.07	0.873	HN COS
	2014	43	8.7 (2.3)	1.46(0.33)	5.95(0.76)	38.7(4.73)	0.26(0.03)	0.11	0.572	HN COS
	2015	35	8 (2.09)	1.23(0.36)	5.08(0.76)	38.19(8.94)	0.26(0.06)	0.09	0.520	HZ COS
	2016	58	11 (2.55)	1.96(0.36)	6.03(0.65)	39.7(3.60)	0.27(0.02)	0.15	0.724	HZ COS
	2017	45	9 (2.72)	2.05(0.55)	4.60(0.48)	29.38(6.65)	0.20(0.04)	0.12	0.578	HZ COS
Barking Deer	**2013**	44	1.27 (0.27)	1.10(0.23)	1.15(0.05)	53.56(4.89)	0.36(0.03)	0.11	0.683	HN COS
	2014	72	2.34 (0.36)	2.13(0.32)	1.11(0.03)	44.64(3.83)	0.30(0.02)	0.19	0.541	HZ COS
	2015	76	3.51 (0.65)	3.06(0.55)	1.14(0.04)	33.28(3.53)	0.22(0.02)	0.20	0.971	HZ COS
	2016	95	4.5 (0.68)	3.81(0.53)	1.24(0.04)	33.47(2.19)	0.23(0.01)	0.25	0.792	HN COS
	2017	79	4 (0.52)	3.07(0.42)	1.18(0.04)	34.50(2.92)	0.23(0.02)	0.21	0.847	HZ SP

(D= Density; DS= Group size Density; E(S)=Mean cluster size; ESW= Effective Strip Width; P= Detection Probability; n/l= Encounter Rate; KS test= Kolmogorov Smirnov Test; HZ-Hazard Rate; SP- Simple Polynomial; HP- Hermite Polynomial; COS- Cosine; HN -Half Normal)

Table 3. 4 Density Parameters based on best model selection of ungulates in winter season in Kanha National Park.

Species	Year	n	D (SE)	DS (SE)	E(S) (SE)	ESW (SE)	P (SE)	n/l	KS test	Best fit model
Chital	**2014**	321	24.68(3.7)	2.99(0.41)	8.24(0.47)	59.97(2.92)	0.17(0.08)	0.35	0.904	HN COS
	2015	335	26.97(3.9)	3.39(0.46)	7.94(0.41)	54.42(0.01)	0.16(0.01)	0.36	0.969	HZ SP
	2016	358	35(7.98)	4.13(0.56)	8.46(1.54)	49.74(3.4)	0.14(0.09)	0.41	0.952	HZ SP
	2017	359	34.88(4.89)	4.39(0.56)	8.09(0.40)	47.22(3.03)	0.14(0.09)	0.40	0.688	HZ SP
	2018	312	40.43(6.9)	4.44(0.53)	9.10(1.10)	46.92(1.94)	0.18(0.01)	0.42	0.832	HZ COS
Sambar	**2014**	257	9.08(1.01)	3.89(0.41)	2.33(0.08)	36.91(1.93)	0.15(0.008)	0.28	0.625	HZ SP
	2015	277	10.51(1.11)	4.13(0.40)	2.54(0.09)	36.95(1.78)	0.15(0.007)	0.30	0.582	HZ SP
	2016	235	10.98(1.33)	3.86(0.43)	2.84(0.13)	34.98(2.11)	0.14(0.008)	0.27	0.571	HZ SP
	2017	254	9.92(1.11)	3.84(0.40)	2.57(0.10)	37.43(2.30)	0.15(0.009)	0.28	0.783	HZ SP
	2018	189	9.41(1.25)	3.51(0.43)	2.67(0.13)	37.31(3.12)	0.15(0.01)	0.26	0.957	HZ SP
Gaur	**2014**	95	3.33(0.64)	1.03(0.16)	3.21(0.36)	51.23(4.83)	0.16(0.01)	0.10	0.671	HZ SP
	2015	72	4.85(1.01)	0.85(0.13)	5.68(0.77)	46.57(3.90)	0.15(0.01)	0.07	0.824	HZ COS
	2016	84	6.07(1.34)	1.42(1.24)	4.26(0.57)	33.84(3.36)	0.11(0.01)	0.09	0.804	HZ SP
	2017	92	5.72(1.15)	1.05(0.17)	5.45(0.58)	49.65(6.21)	0.16(0.02)	0.10	0.958	HZ SP
	2018	75	5.38(1.15)	1.11(0.19)	4.83(0.60)	46.77(5.54)	0.15(0.01)	0.10	0.615	HZ COS
Wild Pig	**2014**	89	6.84(1.5)	1.37(0.25)	4.97(0.59)	36.20(4.25)	0.13(0.01)	0.09	0.525	HZ SP
	2015	81	7.79(1.7)	1.25(0.22)	6.22(0.78)	36.69(4.50)	0.12(0.01)	0.08	0.610	HZ SP
	2016	84	9.69(1.89)	1.33(0.22)	7.24(0.72)	36.01(4.27)	0.13(0.01)	0.09	0.580	HZ SP
	2017	80	7.95(1.5)	1.13(0.18)	6.98(0.74)	39.82(3.72)	0.14(0.01)	0.09	0.936	HZ SP
	2018	64	5.58(1.35)	1.03(0.19)	5.40(0.82)	43.04(5.29)	0.15(0.01)	0.08	0.551	HZ SP
Barking Deer	**2014**	125	1.96(0.24)	1.74(0.21)	1.13(0.03)	40.14(2.81)	0.11(0.01)	0.13	0.722	HZ SP
	2015	117	2.54(0.35)	2.21(0.30)	1.14(0.02)	29.14(2.18)	0.11(0.008)	0.12	0.743	HN COS
	2016	118	2.73(0.39)	2.32(0.33)	1.17(0.02)	29.18(2.83)	0.11(0.01)	0.13	0.920	HZ COS
	2017	104	1.92(0.3)	1.63(0.24)	1.18(0.03)	36.02(0.01)	0.14(0.01)	0.11	0.957	HZ SP
	2018	96	2.09(0.29)	1.91(0.26)	1.09(0.02)	34.77(2.70)	0.13(0.01)	0.13	0.678	HZ SP
Chousingha	**2014**	1	---	---	---	---	---	---	---	---
	2015	0	--	--	--	--	--	--	--	--
	2016	0	--	--	--	--	--	--	--	--
	2017	0	--	--	--	--	--	--	--	--
	2018	12	0.17 (0.09)	0.11(0.05)	1.60(0.40)	74.53(22.26)	0.37(0.11)	0.01	0.902	HN COS

(D= Density; DS= Group size Density; E(S)=Mean cluster size; ESW= Effective Strip Width; P= Detection Probability; n/l= Encounter Rate; KS test= Kolmogorov Smirnov Test; HZ-Hazard Rate; SP- Simple Polynomial; COS- Cosine; HN -Half Normal)

Table 3. 5 Density Parameters based on best model selection of ungulates in winter season at Banjar catchment of Kanha National Park.

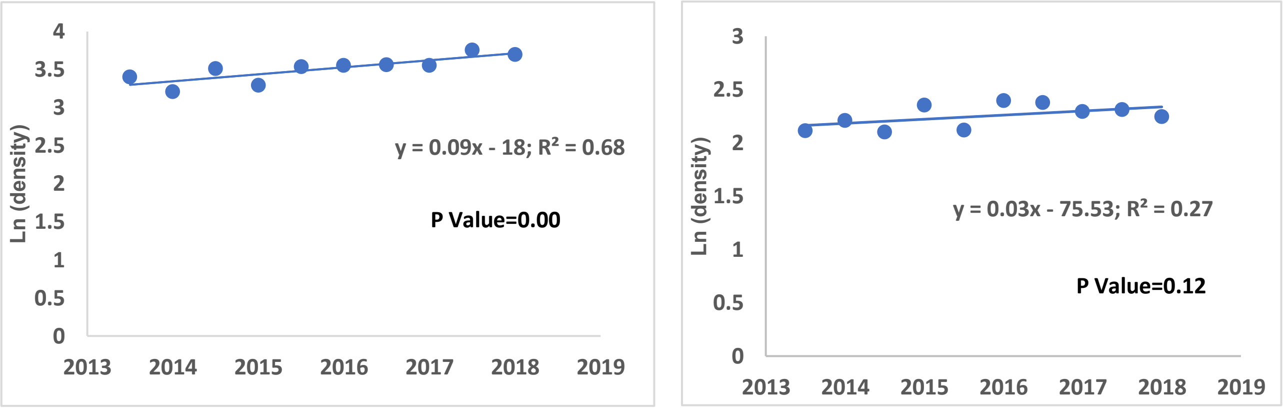
Species	Year	n	D (SE)	DS (SE)	E(S) (SE)	ESW (SE)	P (SE)	n/l	KS test	Best fit model
Chital	**2014**	288	38.56(5.95)	4.42(0.62)	8.71(0.54)	61.60(3.27)	0.18(0.009)	0.54	0.988	HN COS
	2015	297	41.88(6.37)	5.13(0.72)	8.15(0.46)	54.73(3.91)	0.16(0.01)	0.56	0.947	HZ SP
	2016	323	53.48(13.24)	6.46(0.89)	8.27(1.69)	47.84(3.38)	0.14(0.01)	0.61	0.661	HZ SP
	2017	324	54.89(7.79)	6.65(0.87)	8.24(0.42)	46.87(3.28)	0.13(0.009)	0.61	0.504	HZ SP
	2018	274	62.49(14)	6.67(0.84)	9.35(1.72)	46.82(2.84)	0.14(0.008)	0.62	0.769	HZ SP
Sambar	**2014**	207	12.87(1.55)	5.30(0.60)	2.42(0.09)	36.97(2.20)	0.15(0.009)	0.39	0.798	HZ SP
	2015	222	16.21(2.68)	5.66(0.60)	2.86(0.36)	37.09(1.99)	0.15(0.008)	0.42	0.454	HZ SP
	2016	194	16.75(2.26)	5.42(0.66)	3.08(0.17)	34.25(2.44)	0.14(0.01)	0.37	0.481	HZ SP
	2017	200	15.59(1.94)	4.78(0.51)	3.21(0.12)	36.46(2.70)	0.15(0.01)	0.37	0.934	HZ SP
	2018	156	16.87(3.51)	5.09(0.67)	3.31(0.53)	34.96(3.34)	0.14(0.01)	0.35	0.975	HZ SP
Gaur	**2014**	51	3.55(1.3)	0.97(0.23)	3.63(0.99)	49.46(7.41)	0.18(0.02)	0.09	0.551	HZ SP
	2015	49	5.94(1.42)	1.07(0.21)	5.53(0.69)	43.17(5.21)	0.16(0.01)	0.09	0.823	HZ SP
	2016	63	7.26(1.66)	1.60(0.31)	4.53(0.53)	37.70(4.89)	0.14(0.01)	0.12	0.618	HZ SP
	2017	65	5(0.96)	1.15(0.19)	4.33(0.39)	53.35(5.46)	0.19(0.02)	0.12	0.567	HZ SP
	2018	45	5.89(1.76)	1.35(0.32)	4.36(0.76)	38.03(6.09)	0.14(0.02)	0.10	0.861	HZ SP
Wild Pig	**2014**	61	8.03(2.17)	1.64(0.38)	4.89(0.65)	35.16(4.97)	0.12(0.01)	0.11	0.568	HZ SP
	2015	52	7.04(1.81)	1.29(0.30)	5.44(0.56)	38.06(6.40)	0.13(0.01)	0.09	0.574	HZ SP
	2016	51	7.77(1.81)	1.45(0.31)	5.35(0.49)	33.62(4.82)	0.12(0.01)	0.09	0.581	HZ SP
	2017	51	7.34(1.83)	1.20(0.26)	6.08(0.73)	40(5.30)	0.14(0.01)	0.09	0.865	HZ SP
	2018	46	7.43(2.14)	1.06(0.24)	6.97(1.22)	49.31(6.02)	0.17(0.02)	0.10	0.542	HZ SP
Barking Deer	**2014**	61	1.67(0.3)	1.42(0.25)	1.16(0.12)	40.44(4.21)	0.15(0.01)	0.11	0.950	HZ SP
	2015	64	2.55(0.45)	2.17(0.37)	1.17(0.04)	27.82(2.74)	0.10(0.01)	0.12	0.945	HN HP
	2016	63	2.31(0.43)	1.99(0.36)	1.15(0.04)	30.20(3.60)	0.11(0.01)	0.12	0.961	HZ SP
	2017	56	1.92(0.39)	1.65(0.33)	1.16(0.04)	31.95(3.10)	0.12(0.01)	0.10	0.981	HN HP
	2018	62	2.44(0.44)	2.13(0.38)	1.14(0.04)	33.21(3.28)	0.12(0.01)	0.14	0.958	HZ SP

(D= Density; DS= Group size Density; E(S)=Mean cluster size; ESW= Effective Strip Width; P= Detection Probability; n/l= Encounter Rate; KS test= Kolmogorov Smirnov Test; HZ-Hazard Rate; SP- Simple Polynomial; COS- Cosine; HN -Half Normal)

Table 3. 6 Density Parameters based on best model selection of ungulates in winter season at Halon catchment of Kanha Tiger Reserve.

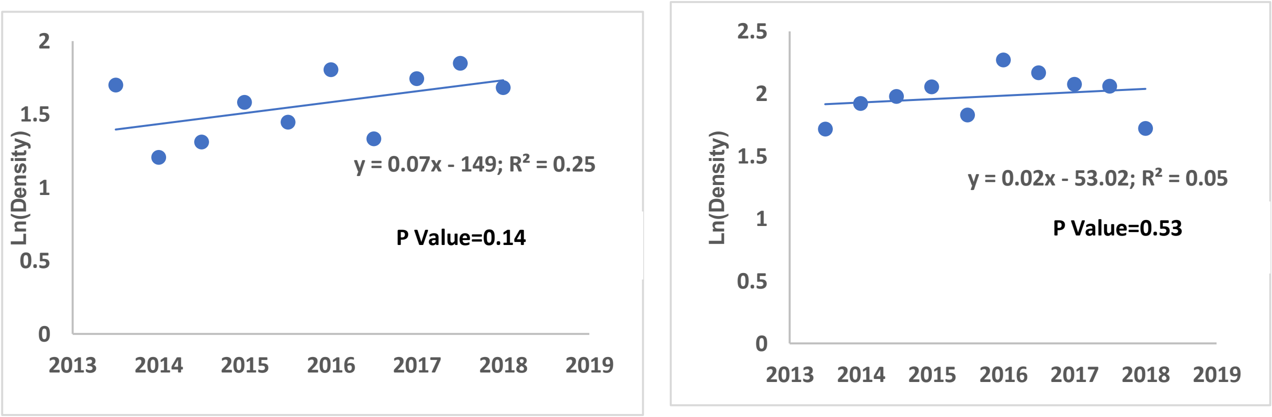
Species	Year	n	D (SE)	DS (SE)	E(S) (SE)	ESW (SE)	P (SE)	n/l	KS test	Best fit model
Chital	**2014**	33	5.87(1.71)	0.99(0.26)	5.88(0.74)	45.20(6.10)	0.23(0.03)	0.09	0.977	HN HP
	2015	37	6.86(1.78)	1.11(0.26)	6.13(0.70)	44.41(5.22)	0.22(0.02)	0.09	0.703	HN HP
	2016	35	6.59(1.77)	0.69(0.16)	9.52(1.26)	72.64(7.22)	0.37(0.03)	0.10	0.932	HN HP
	2017	35	5.85(1.7)	1.05(0.27)	5.53(0.77)	46.74(6.37)	0.23(0.03)	0.09	0.868	HN HP
	2018	38	9.84(3.3)	1.19(0.36)	8.26(1.10)	56.54(12.81)	0.28(0.06)	0.13	0.987	HZ COS
Sambar	**2014**	50	3.71(0.8)	1.87(0.38)	1.98(0.13)	36.42(4.01)	0.32(0.03)	0.13	0.814	HZ SP
	2015	54	4.58(0.87)	1.98(0.35)	2.39(0.16)	36.62(4.19)	0.32(0.03)	0.14	0.514	HZ SP
	2016	41	4.53(1.02)	2.09(0.43)	2.17(0.19)	28.16(3.92)	0.25(0.03)	0.11	0.492	HN HP
	2017	54	4.2(0.7)	1.76(0.32)	2.46(0.16)	40.53(4.17)	0.36(0.03)	0.15	0.960	HZ SP
	2018	33	1.99(0.46)	1.19(0.26)	1.66(0.14)	48.90(6.56)	0.43(0.05)	0.11	0.934	HN HP
Gaur	**2014**	44	3.76(0.95)	1.11(0.22)	3.37(0.53)	53.80(6.35)	0.17(0.03)	0.12	0.999	HZ SP
	2015	21	2.81(1.15)	0.53(0.17)	5.23(1.30)	52.38(0.03)	0.17(0.03)	0.05	0.874	HZ SP
	2016	21	3.33(1.49)	1.11(0.39)	2.98(1.30)	27(6.2)	0.08(0.02)	0.06	0.572	HZ SP
	2017	27	3.75(1.27)	0.57(0.14)	6.69(1.49)	66.8(7.97)	0.22(0.02)	0.07	0.563	HN HP
	2018	30	5.05(1.76)	0.95(0.25)	5.29(1.22)	55.17(11.25)	0.18(0.03)	0.10	0.536	HZ SP
Wild Pig	**2014**	28	4.26(1.68)	0.98(0.30)	4.32(1.07)	38.78(9.42)	0.30(0.07)	0.07	0.612	HZ SP
	2015	28	8.72(3.45)	1.20(0.35)	7.24(1.91)	31.22(6.92)	0.24(0.05)	0.07	0.715	HZ SP
	2016	33	11.06(2.97)	1.32(0.20)	8.33(1.31)	35.72(4.46)	0.28(0.03)	0.09	0.880	HN HP
	2017	29	10.6(2.98)	1.29(0.32)	7.99(1.58)	31.55(5.38)	0.24(0.04)	0.08	0.503	HN HP
	2018	18	4.05(1.41)	1.04(0.29)	4.06(1.10)	30.63(5.08)	0.24(0.04)	0.06	0.808	HN HP
Barking Deer	**2014**	64	2.45(0.43)	2.21(0.38)	1.10(0.03)	39.51(3.81)	0.26(0.02)	0.17	0.458	HZ SP
	2015	53	2.46(0.73)	2.24(0.66)	1.09(0.04)	31.69(7.39)	0.21(0.05)	0.14	0.472	HN COS
	2016	55	3.43(0.63)	2.99(0.53)	1.14(0.05)	26.36(2.44)	0.17(0.01)	0.15	0.909	HN HP
	2017	48	2.41(0.6)	1.86(0.44)	1.29(0.09)	36.32(6.37)	0.24(0.04)	0.13	0.892	HZ SP
	2018	34	1.77(0.37)	1.85(0.38)	0.96(0.02)	32.57(3.09)	0.22(0.02)	0.12	0.831	HN HP

(D= Density; DS= Group size Density; E(S)=Mean cluster size; ESW= Effective Strip Width; P= Detection Probability; n/l= Encounter Rate; KS test= Kolmogorov Smirnov Test; HZ-Hazard Rate; SP- Simple Polynomial; HP- Hermite Polynomial; COS- Cosine; HN-Half Normal)



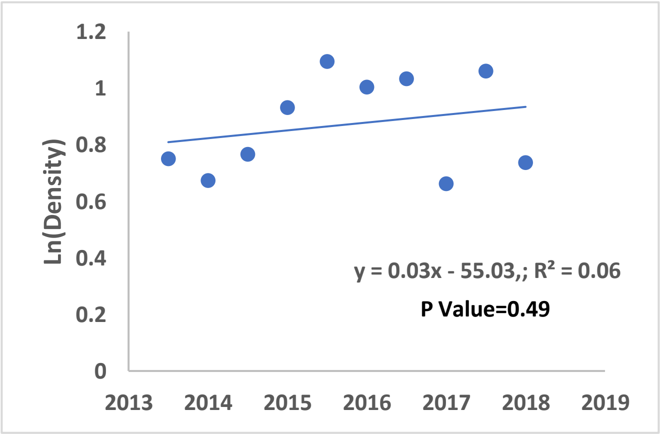
a. Chital

b. Sambar



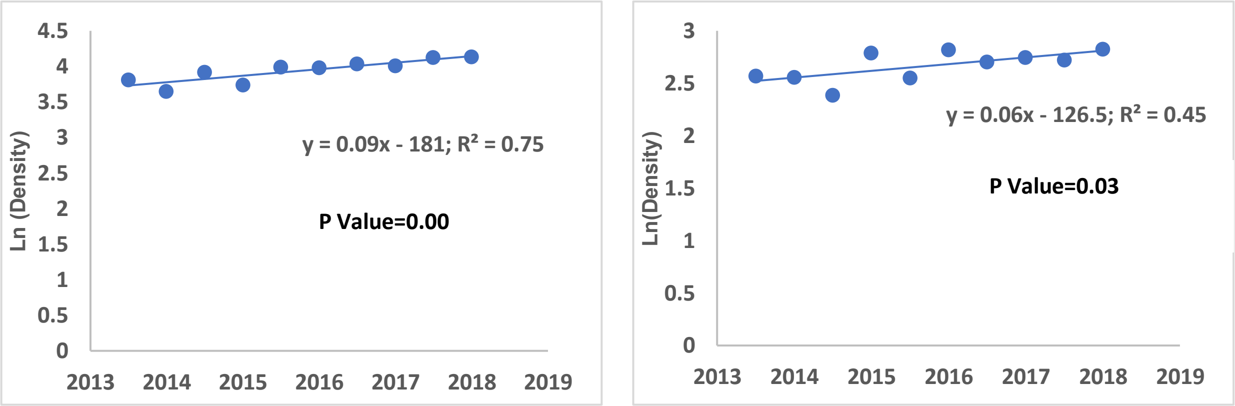
c. Gaur

d. Wild pig



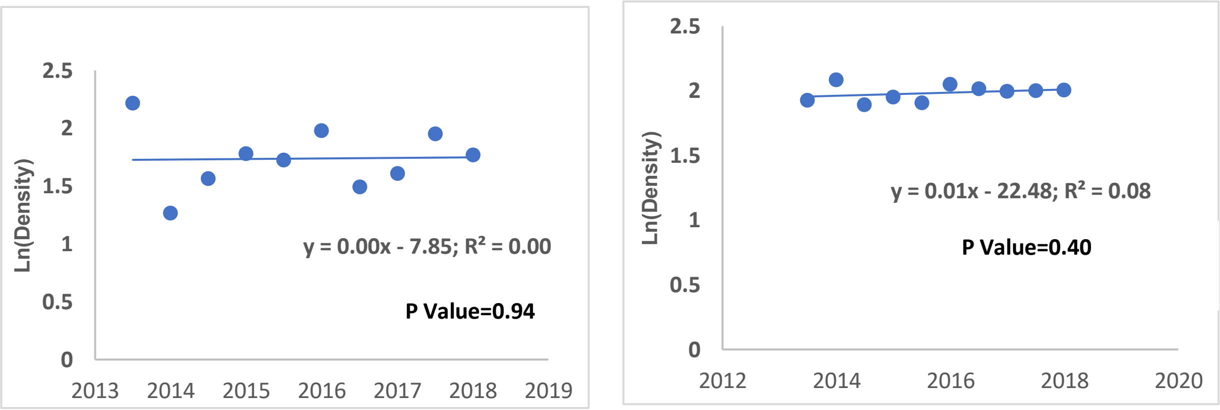
e. Barking deer

Figure 3. 5 Population growth rate depicted through seasonal abundance (log transformed) of ungulates in Kanha National Park from year 2013 to 2018.



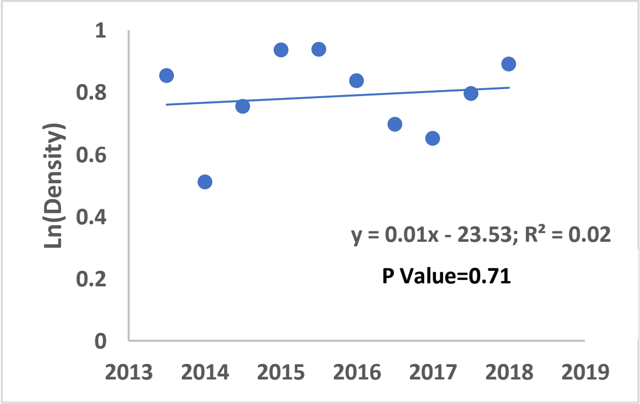
a. Chital

b. Sambar



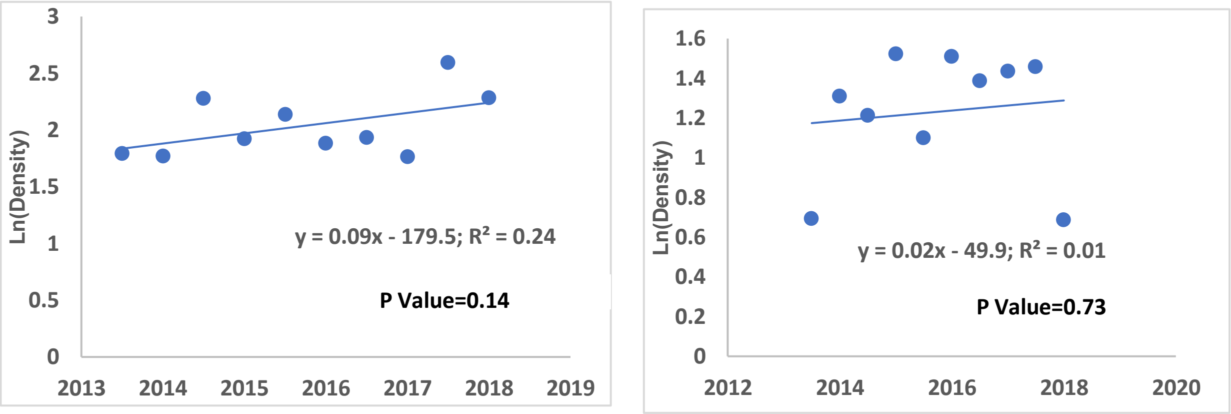
c. Gaur

d. Wild pig



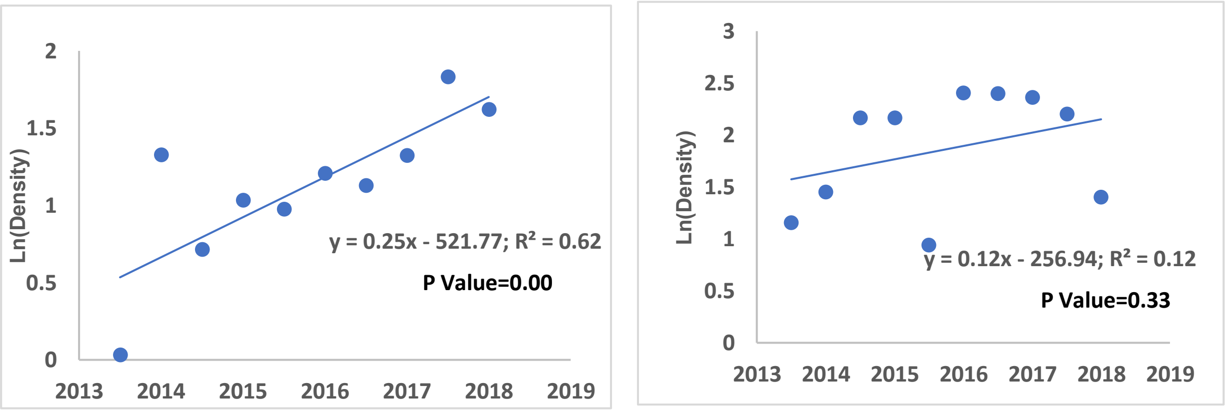
e. Barking deer

Figure 3.6 Population growth rate depicted through seasonal abundance (log transformed) of ungulates in Banjar catchment of Kanha National Park from year 2013 to 2018.



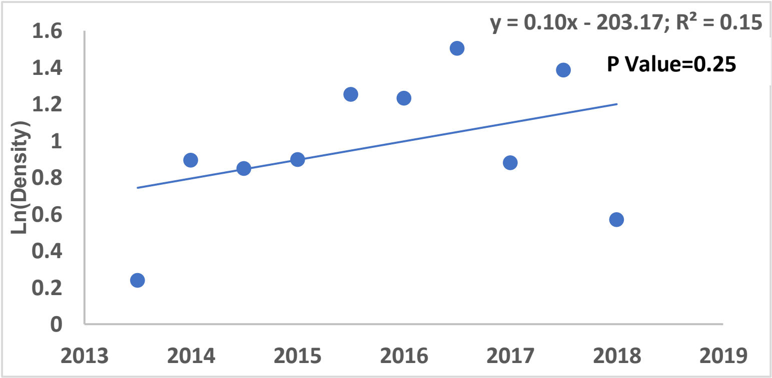
a. Chital

b. Sambar



c. Gaur

d. Wild pig



e. Barking deer

Figure 3.7 Population growth rate depicted through Seasonal abundance (log transformed) of ungulates in Halon catchment of Kanha National Park from year 2013 to 2018.

3.2 Age structure, sex ratio and fawn: adult female ratio of wild ungulates in Kanha:

The average herd composition (age-sex structure) of different wild ungulates are given in **(Table 3.7).** Except for chital, sambar and gaur, the age-sex structure could not be classified for other ungulates (wild pig, barking deer and chousingha) due to their low sightings and elusive nature. Fawns contributed more than 10% to the group composition of sambar and gaur in both summer and winter season, while in case of chital, fawns contributed less than 5% in winter (likely because fawns are not seen with females during the fawning season) and more than 5% in the summer season. The adult sex ratio male: female for chital was 1:1.2; the ratio of seasonal fawns to adult female was 1: 6 in summer and 1:12 in winter season in Kanha National park. Similarly, the adult sex ratio male: female for sambar was 1: 1.48 and seasonal fawn to adult female ratio was 1:4 in both summer and winter season. Whereas, in gaur, the adult sex ratio was 1: 3.98 and seasonal calf to adult female was 1:4 in both summer and winter season **(Table 3.8 & 3.9).**

Table 3. 7 Age-sex structure of ungulates in Kanha National Park and its Banjar and Halon Catchments in summer and winter season (Age structure was computed from the data pertaining to percentage contribution of each age-sex class to total population.

Species	Area/catchment type	Season	No. of samples (n)	Adult male % (SE)	Adult female % (SE)	Sub adult male % (SE)	Subadult female % (SE)	Yearling male % (SE)	Yearling female %(SE)	Fawn % (SE)
Chital	National Park	Summer	1698	31.49 (2.05)	55.37 (1.59)	1.27 (0.2)	0.66 (0.2)	0.61 (0.01)	0.91 (0.05)	9.69 (2.31)
	Banjar		293	39.25 (4.55)	43.00 (4.41)	3.07 (1.1)	1.37 (0.4)	1.71 (0.7)	1.71 (0.7)	9.90 (5.55)
	Halon		1405	28.19 (2.26)	60.64 (1.67)	0.50 (0.03)	0.36 (0.6)	0.14 (0.5)	0.57 (0.2)	9.61 (2.54)
	National Park	Winter	431	30.22 (4.16)	37.98 (3.89)	9.70 (4.23)	8.72 (4.16)	1.63 (0.23)	7.51 (2.3)	4.25 (1.2)
	Banjar		310	25.81 (4.89)	33.87 (4.62)	13.55 (5.28)	13.23 (5.29)	1.61 (0.3)	8.39 (2.8)	3.55 (1.5)
	Halon		121	34.71 (7.35)	42.15 (6.91)	5.79 (1.9)	4.13 (1.2)	1.65 (0.4)	6.61 (3.2)	4.96 (1.5)
Sambar	National Park	Summer	460	36.49 (4.21)	46.62 (3.11)	0.96 (0.7)	0.83 (0.5)	0.96 (0.5)	2.50 (0.7)	11.64 (4.04)
	Banjar		39	23.08 (14.04)	48.72 (11.47)	2.56 (1.7)	2.56 (1.7)	2.56 (1.7)	7.69 (4.87)	12.82 (3.8)
	Halon		421	42.95 (4.48)	45.60 (3.22)	0.19 (0.08)	---	0.19 (0.08)	---	11.07 (4.12)
	National Park	Winter	104	30.18 (8.11)	44.38 (7.33)	4.94 (3.2)	4.06 (2.6)	1.89 (1.5)	1.01 (0.9)	13.53 (9.14)
	Banjar		63	23.81 (11.0)	46.03 (9.26)	6.35 (0.4)	6.35 (0.4)	1.59 (0.1)	1.59 (0.1)	14.29 (11.6)
	Halon		41	41.46 (11.95)	41.46 (11.95)	2.44 (1.8)	---	2.44 (1.8)	---	12.20 (4.50)
Gaur	National Park	Summer	693	22.64 (3.22)	56.77 (2.48)	0.84 (0.51)	0.42 (0.32)	1.26 (0.9)	2.80 (2.4)	15.27 (3.41)
	Banjar		108	19.44 (8.64)	55.56 (6.42)	1.85 (0.23)	0.93 (0.12)	2.78 (1.5)	5.56 (3.2)	13.89 (8.93)
	Halon		585	25.30 (3.57)	57.78 (2.69)	---	---	---	0.51 (0.43)	16.41 (3.78)
	National Park	Winter	100	9.53 (4.28)	67.44 (5.72)	---	---	---	2.49 (1.5)	20.55 (9.03)
	Banjar		69	7.25 (3.2)	69.57 (6.64)	---	---	---	---	23.19 (10.55)
	Halon		31	16.13 (10.2)	61.29 (11.17)	---	---	---	9.68 (5.3)	12.90 (6.2)

SE=Standard Error

Table 3. 8 Sex ratio of ungulates in Kanha National Park and its catchments.

Ungulate species	No. of samples in National park (n)	National Park (M:F) & SE range	No of samples in Banjar (n)	Banjar (M:F) & SE range	No of samples in Halon (n)	Halon (M: F)& SE range
Chital	678	1:1.2 (SE 0.1)	563	1:1.2 (SE 0.1)	115	1:1.25 (SE 0.25)
Sambar	124	1:1.48 (SE 0.32)	88	1: 1.83 (SE 0.55)	36	1:0.89 (SE 0.27)
Gaur	254	1:3.98 (SE 1.19)	146	1: 3.7 (SE 1.39)	108	1:4.40 (SE 1.97)

SE=Standard Error

Table 3. 9 Fawn: adult female ratio of ungulates in Kanha National Park and its Banjar and Halon Catchments.

Species (fawn:female ratio)	National Park summer (SE)	National Park winter (SE)	Banjar summer (SE)	Banjar winter (SE)	Halon summer (SE)	Halon winter (SE)
Chital	1:6 (3.31) [n=1146]	1:12 (10.6) [n=219]	1:4 (0.87) [n=159]	1:13 (7.94) [n=157]	1:6 (1.52) [n=987]	1:9 (3.09) [n=62]
Sambar	1:4 (1.07) [n=322]	1:4 (3.48) [n=64]	1:4 (1.79) [n=25]	1:4 (1.96) [n=42]	1:4 (0.82) [n=434]	1:3 (1.13) [n=26]
Gaur	1:4 (0.82) [n=499]	1:4 (2.07) [n=90]	1:4 (1.94) [n=76]	1:3 (1.17) [n=64]	1:4 (0.91) [n=434]	1:4 (3.63) [n=26]

SE=Standard Error

3.3 Body condition of ungulates in Kanha

A. **Chital**: The principal component analysis (PCA) extracted a single principal component that explained 55.55 % of the variation observed in the five body condition indices, i.e. pectoral girdle, pelvic girdle, ribs, rump and tail. The first principal component had a maximum factor loading from pectoral and pelvic girdle (81%), but remaining indices too contributed to this principal component (**Table 3.10 & 3.11; Figure 3.10).** There was a significant difference in body condition of chital between seasons (One-way ANOVA, F=32.54, p=0.00) and Banjar and Halon catchments (One-way ANOVA, F=18.69, p=0.00). In the winter season, chital had better body condition than summer season **(Figure 3.9).** In Halon catchment, which is a low conservation investment area had better body condition than high conservation investment area of Banjar catchment **(Figure 3.8).**

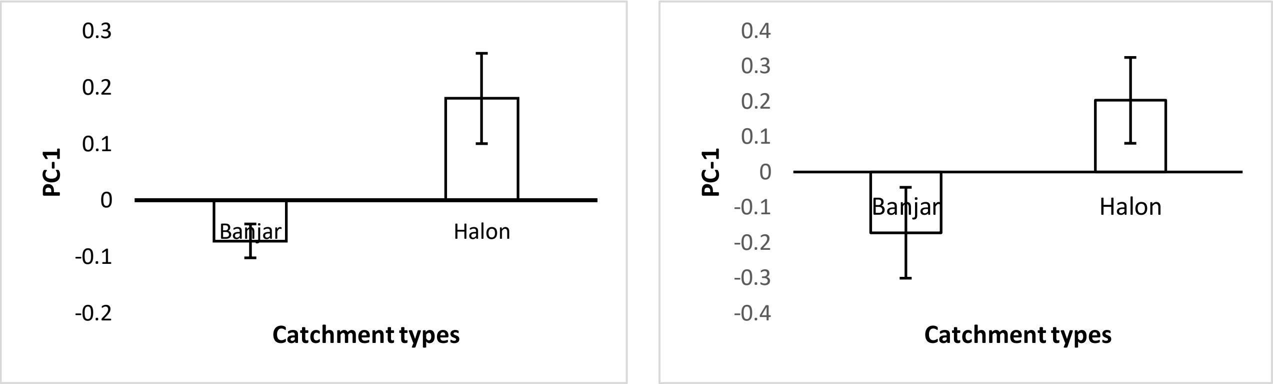
B. Sambar: The principal component analysis (PCA) extracted a single principal component that explained 77.3 % of the variation observed in the five body condition indices, i.e. pectoral girdle, pelvic girdle, ribs, rump and tail. The first principal component had a maximum factor loading from pectoral, pelvic and ribs (91%), but remaining indices too contributed equally to this principal component **(Table 3.10 & 3.11; Figure 3.10).** There was no significant seasonal difference in body conditions between summer and winter (One-way ANOVA, F=0.67, p=0.41). However, there was a significant difference in body condition of sambar between Banjar and Halon catchments (One-way ANOVA, F=4.38, p=0.02). In Halon catchment, which is a low conservation investment area had better body condition than high conservation investment area of Banjar catchment **(Figure 3.8).**

C. Gaur: The principal component analysis (PCA) extracted a single principal component that explained 87.9 % of the variation observed in the five body condition indices, i.e. pectoral girdle, pelvic girdle, ribs, rump and tail. The first principal component had a maximum factor loading from pectoral girdle (96%), but remaining indices too contributed to this principal component

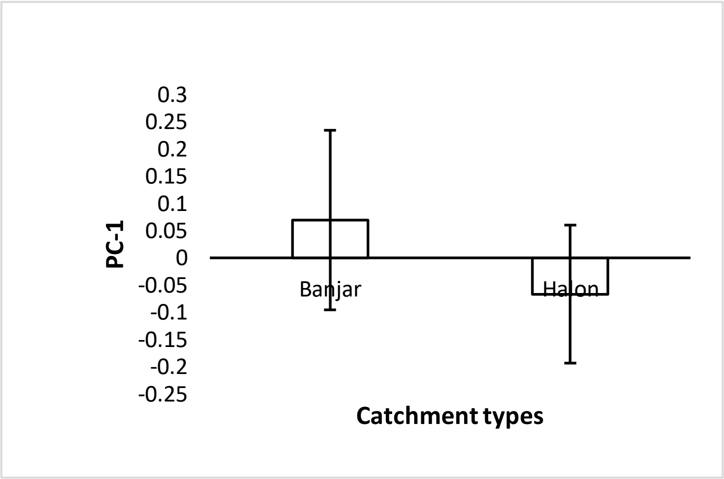
(Table 3.10 & 3.11; Figure 3.10). There was no significant difference in body condition of gaur between seasons (One-way ANOVA, F=0.01, p=0.90) and Banjar and Halon catchment (One-way ANOVA, F=0.43, p=0.25). Similar body conditions were found in both the catchments **(Figure 3.8).**

Table 3. 10 Principal component loading by different body condition indices of chital, sambar and gaur on PC-1 (Component matrix extraction method: Principal component analysis).

Index	**Component-1St Loading Chital**	**Component-1St Loading Sambar**	**Component-1St Loading Gaur**
Pectoral	0.815	0.919	0.961
Pelvic	0.808	0.919	0.930
Ribs	0.621	0.914	0.838
Tail	0.568	0.771	0.977
Rump	0.791	0.867	0.977



a. Chital **b. Sambar**



c. Gaur

Figure 3.8 Body condition of chital, sambar and gaur (scores of the first principal component) across the Kanha National Park (Bars are Standard Error).

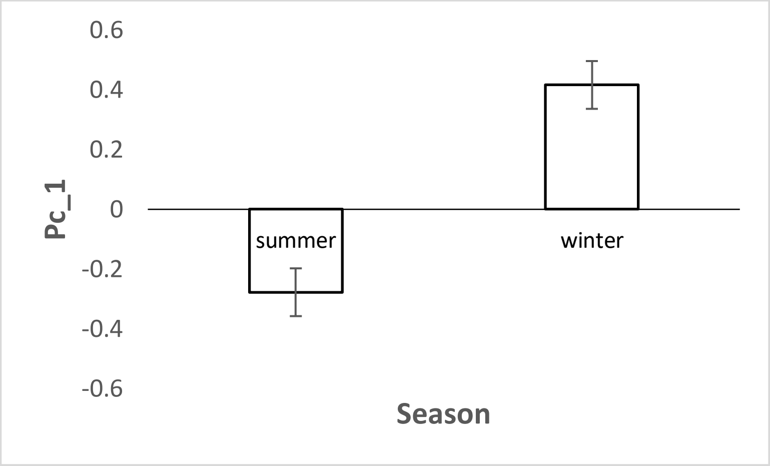


Figure 3. 9 Body condition of chital (scores of the first principal component) in different seasons across the Kanha National Park (Bars are Standard Error).

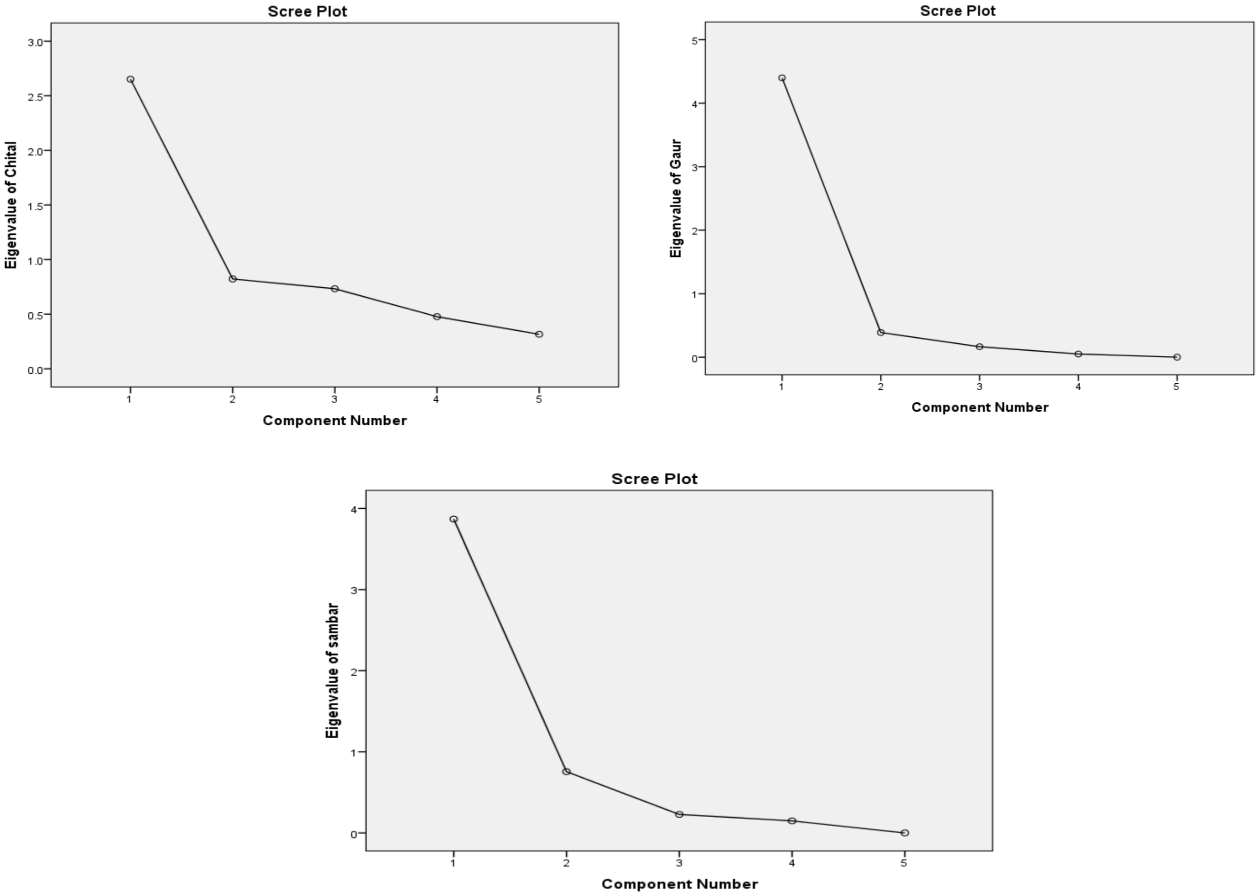


Figure 3. 10 Scree plot of chital, sambar and gaur showing eigen value of different principal component.

Table 3. 11 Initial Eigen values and total variance explained of different principal components of chital, sambar and gaur (only first component Eigen values (in bold) for all ungulates are greater than 1).

Species	**Component**	**Total Eigen Value**	**% variance**	**Cumulative (%)**
Chital	1	**2.65**	**53.03**	53.03
	2	0.82	16.44	69.48
	3	0.73	14.65	84.13
	4	0.47	9.54	93.67
	5	0.31	6.32	100
Sambar	1	**3.86**	**77.38**	77.38
	2	0.75	15.10	92.48
	3	0.22	4.55	97.03
	4	0.14	2.96	100
	5	0.01	0.01	100
Gaur	1	**4.39**	**87.96**	87.96
	2	0.38	7.75	95.71
	3	0.16	3.29	99
	4	0.05	0.99	100
	5	0.01	0.11	100

4. Discussion

4.1 Population trend of ungulates

Population trend derived from line transect based distance sampling over six years showed that all ungulates density appears to have remained relatively stable at Protected Area level in Kanha. Although, analyzing population trend in overall Protected area will not be appropriate for decision making for management interventions. The two sampling blocks, Banjar and Halon catchments were selected based on substantial differences in prey and predator densities and conservation investments to study the response of ungulates to these differences. Local-scale densities of ungulates will provide useful information on the growth rate of ungulates to wildlife managers. Separation of the study period into winter and summer season was necessary to observe the annual recruitment pulses in seasonal ungulate abundance in the National Park and its Banjar and Halon catchments. Moreover, body conditions also cycle between seasons in tropical ungulates; this is especially more pronounced in grazers such as chital in compared to browsers such as sambar and gaur.

Densities of ungulates in Kanha were compared with densities of the same species at other similar sites in Central India (see S13). From our results, we found that densities of chital and gaur in Kanha were comparable or higher than elsewhere in the moist and dry deciduous forest of Central India.

Chital, a dominant and abundant species in the Kanha National park, shows a low population growth rate but does seem to have considerably increased between 2013 to 2018 in the National park and Banjar catchment. Whereas, sambar showed a substantial increase in density in Banjar catchment from 2013 to 2018. The increase is probably related to high conservation investments in Banjar area. Government's policy of settlements and relocation leads to the human free area, together with control of illegal hunting by park authorities. Due to effective law enforcement since 1967, largely contributed to an increase of chital and sambar density in Banjar.

Gaur showed a high growth rate in Halon catchment in compare to Banjar. Unlike other species in this estimation, gaur being a migratory animal, likely move between the Kanha and Achanakmar corridors connecting protected areas (Corridor maps for gaur are available in Jhala et al. 2014). Immigration would increase population growth rates and subsequently restricted gaur populations to more protective habitat such as Kanha. Reproduction of gaur due to low predator densities and high resource availability could be also likely to be the reason for the high density of gaur in recent time in Halon. In contrast, barking deer and wild pig have shown a stable trend in between 2013 to 2018 in both the National Park and local catchments.

Resident ungulates of the Banjar and Halon catchments have either increased or remain stable between 2013 to 2018. Halon catchment, the area with maximum rainfall and less intraspecific-competition due to low densities of ungulates, chital and sambar, had better body condition in comparison to Banjar. The further increase in population will only be seen in future surveys in Halon area as there is a recent chital supplementation occurred in Halon from Banjar area, as well as the recent shift in human settlements between 2010 and 2016, together with domestic stock, and to the reduction of hunting. All these events released more land for wildlife populations and at the same time competition for food between ungulates and cattle was reduced in Halon. My study highlights the importance of conservation investments for high population performance of the ungulates. Overall stability in ungulate assemblages highlights the importance of long-term monitoring and comprehensive data in future surveys to understand ecological dynamics. The observed pattern and timing of population dynamics in combination with ancillary information may allow for the formulation of a hypothesis about the causality underlying the observed population trends (Bragina et al. 2015).

4.2 Adult Sex ratio:

The adult sex ratio for chital was intensively collected during April-June and for sambar and gaur during December-January in their respective breeding seasons. It is because it represents the time of sexual segregation of adult males and females. Thus, an unbiased estimate of actual adult sex ratio information is collected from the population (Gaillard et al. 2000). Ungulate sex ratio (male: female ratio of chital, sambar and gaur) in Kanha Tiger Reserve was skewed towards females which is quite similar from other studies (Dinerstein 1980, Johnsingh 1983, Karanth and Sunquist 1992, Sankar 1994, Acharya 2007, Ramesh 2010) (see Table S14). Adult population sex ratio was likely to be skewed and biased in favour of females. It is because males have larger bodies, proneness to injuries from intraspecific aggression, higher absolute nutrient and energy cost, lack of antlers during the rut, their dispersal behavior makes males more vulnerable to selective predation (Schaller 1967, Geist 1971, McCullough 1999, Berger and Gompper 1999). The sex ratio of chital and gaur in Banjar and Halon catchments was skewed towards females except for sambar in Halon catchment shows slightly biased sex ratio towards males.

4.3 Age ratio:

Age ratio such as fawn: adult female or calf: adult female are collected from ungulate populations during group composition survey and are widely utilized to infer demographic trends. Age ratios index recruitment, which is the product of fecundity and survival of young (White and Garrott 2005). Adult female: fawn ratio of chital in National Park is low in winter in comparison to the summer season. The major reason would be winter period (December-January) coincides with the initiation of the fawning season for most chital population; thus, data collected during this period are often termed as pre-weaning. Most mortality of juveniles during the pre-weaning period is density-independent as they are more dependent on maternal care than their own competitive ability (Cook 2002, Bender 2006) and they are not seen with an adult female during the pre-weaning period. Therefore, I also obtained data on the post-weaning period (April-May), when juveniles habitually travel and freely intermix with adults so that unbiased ratio of female: fawn could be obtained.

4.4 Effect of stable ungulate population on Predators:

Ungulates in Kanha National Park are relatively stable in population as derived from our six years population trend analysis. However, chital shows a significant growth rate of 9% at Protected area scale, which is considered as a very low growth rate of chital annually given their maximum (intrinsic) rate of natural increase Rmax is 0.33, i.e. 33% (Bipin et al. 2013). Chital and sambar also show significant growth at local catchment, i.e. Banjar catchment, which also had recorded high predator densities in this area (Kumar et al. 2019).

Top predator, i.e. tiger occupying the apex trophic position in a community and mesopredators such as leopard and dhole holding trophic positions below them influences the community structure and resource sharing between species in Kanha (Simberloff and Dayan 1991; Hayward et al. 2006). Tiger can suppress mesopredators by competing for resources, especially when the prey population becomes stable. Trophic cascades are more likely to occur if tiger density increases and reaches near carrying capacity. I used Hayward et al.

2007 equation to compute the carrying capacity of tigers in Kanha National Park considering the preferred prey of tigers to be chital, sambar, gaur and wild pig (see Negi and Shukla 2011). I believe that Hayward equation for estimating carrying capacity mainly developed for lions based on preferred prey biomass, can also and equally applicable for tigers, especially in the ecosystem with diverse carnivore community. Our results show that the current population of tiger (see Kumar et al. 2019) is below prey dictated carrying capacity that can supports 15 tigers per 100 km^2 **(See supplementary information S12).** There is still a potential for tigers to increase in density in the National park, and trophic cascade can cause extensive changes throughout the food web.

Chapter 4. Factors affecting group size of ungulates in Kanha Tiger Reserve

1. Introduction

Group formation has evolved in many species, mainly in ungulates living in larger groups in open habitats such as grasslands and savannas (Jarman 1974, Kie 1999). In contrast, in the forest few ungulates species form groups and these tend to be small (Kingdon 2015). Group size of ungulates is an adaptive response to ecological conditions (Jarman 1974) and depend on the relative cost and benefits of group living, which is expected to vary with habitat and predator presence. Individuals in larger groups gain benefits from collective vigilance and cooperative defence, reducing predation risk, optimization of resource use and avoidance of conspecifics (Treves and Chapman 1996, Krause et al. 2002). However, living in groups also presents disadvantages due to increased competition over food resources and access to space and mates (Chapman 2000).

Some of the most well-studied examples of group living are seen in gregarious ungulates such as chital in the grassland of the Indian Protected areas (Raman 1997). The main ecological factors that are hypothesized to explain the variation in the size of groups among ungulates are habitat type, predation, and resource abundance and distribution; however, their relative roles in the dense vegetation of tropical ecosystem are less well understood. Here I examine the distribution of group size of ungulate populations in a predominantly forested landscape in the Kanha National park, India. Tiger and Leopard, are the primary predators of ungulates in this multi-predator landscape.

Often, the antipredator benefits of grouping may outweigh resource acquisition and social benefits in both cervids and bovids (Jarman 1974, Krause et al. 2002, Brashares and Arcese 2002). Thus, in species where grouping is an antipredator strategy, group size should depend on key factors such as the level of predation risk and less on food availability in different habitat types and seasons. The second factor, habitat type, is thought to affect group size by modifying the antipredator benefits associated with grouping, and group sizes are predicted to increase with open habitats (Jarman 1974). The third factor, food resources affect grouping by modifying forage competition (Chapman et al. 1995). Large group sizes are not economical in those areas where resources are scarce and distributed in small patches because the cost of competing for food outweighs any benefits. Thus, group size should increase with food availability.

I test the following hypothesis: does grouping in ungulates depend on a) season, b) habitat type, c) ungulate density d) predator density or combination of these factors. Study of ungulate species in the tropical forest of Kanha is important because they show different body size, habitat preferences and predation risks. In this chapter, I investigate the probable factors of group formation in ungulates of Kanha National Park. I hypothesize that when other factors such as animal density and season are controlled, the group size should be large in open habitat such as grasslands since it is an anti-predator strategy that depends on the habitat condition and level of predation risk. It is a function of minimizing predation risk from tiger and leopard.

2. Materials and Methods

2.1 Study site and species

I studied the group size of chital, sambar and gaur in the year 2014 in the month of January -February and May and June, encompassing an area of 940 sq. Km. in the Kanha National Park, a core area of Kanha Tiger Reserve (latitudes 22^0 7’ N and $22^0$27’ N and longitudes 80^0 26’ E and 81^0 3’ E) in Madhya Pradesh, India. For the central Indian site, these sampling months correspond to winter and summer seasons (when peak fawning and breeding season of chital, the breeding season of sambar and calving season of gaur primarily occurs). Group size of chital, sambar and gaur vary widely among and within populations. Chital and gaur are usually non-permanent units like other studied cervids and bovids that often merge and split up (Estes 1991, Barrette 1991) while sambar lives in small and discrete groups. Tiger and Leopard are the main predators of these three ungulates. Chital and sambar flee when approached by predators and are thought to rely on early detection and flight to escape predation, unlike gaur. Kanha National Park is a moist mixed deciduous forest tract characterized by a tropical climate (Champion and Seth 1968) with habitats ranging from open grasslands to dense miscellaneous forest and sal dominated woodland and *Shorea spp, Dendrocalamus spp, Anogeissus spp, Terminalia spp* and *Lagerstomia spp* as the dominant vegetation (Negi and Shukla 2011). (For detailed information regarding study site and study species **see Introduction chapter 1)**.

2.2. **Vegetation map of the study area**

I measured habitat type using vegetation map of Kanha Tiger Reserve categorized into four major habitat types that differ in their vegetation density: Grassland, Sal dense, Bamboo-mixed, and Miscellaneous forest **(Figure 4.1;** Awasthi et al. 2016; **for more details see chapter 2)**. In this study, habitats were categorized into two types, open habitats (Grassland totalling 88 sq. km. area) and closed habitat (Bamboo-mixed, Sal dense and Miscellaneous forest, totalling 872 sq. km. areas). Unsupervised classification of LANDSAT-8 satellite imagery (pixel size = 30 meters; acquisition date; April and November 2013) and extensive ground-truthing (sampling 900 vegetation plots of 707 sq. m.) was carried out to derive landcover information.

2.3. Determining the group size of ungulates

I walked line transects (n=150) with other wildlife researchers and well-trained forest staff to record group size of all ungulates throughout Kanha National Park in four major habitat types in the year 2014 in both summer and winter seasons **(Figure 4.1).** During the sampling period of three consecutive days, a team of well- trained observers walked the line transects from 6:00-8:00 am in morning time (when most of the animals were actively foraging or moving) and recorded the locations (latitude/longitude coordinates) of all groups of ungulate species. Many studies considered line transect as a suitable method to detect group size (Buckland et al. 2001).

A group was defined as animals moving in a similar direction and or present in close proximity within a maximum distance of 10 meters from each other. To avoid underestimating group size in closed habitats owing to the differences in the ability to see animals in each habitat, during the transects we only counted individuals that were observed on the transects at a maximum distance of 50-100 meters from the transect line. For each observation, the following data were registered: date, species, number of observed individuals, radial distance, GPS locations and direction of deer's movement measuring through an animal bearing.

2.4. Spatial explicit Densities of carnivores and ungulates

Additionally, to assess whether group sizes vary with a population density of predator and ungulates, I used camera trap-based mark-recapture framework (Otis et al. 1978) by sampling the entire Kanha national park of 940 km^2 **(Figure 4.1)** to estimate spatially explicit densities and fine-scale density maps of tiger and leopard (Borchers and Efford 2008). I used maximum likelihood-based spatially explicit capture-recapture (SECR) to estimate densities of predators (Kumar et al. 2019). For, assessing spatially explicit ungulate densities, I used line transect based density surface modelling (DSM) in Kanha Tiger Reserve (Miller et al. 2013) (**For detailed information regarding DSM methodology see chapter 5**).

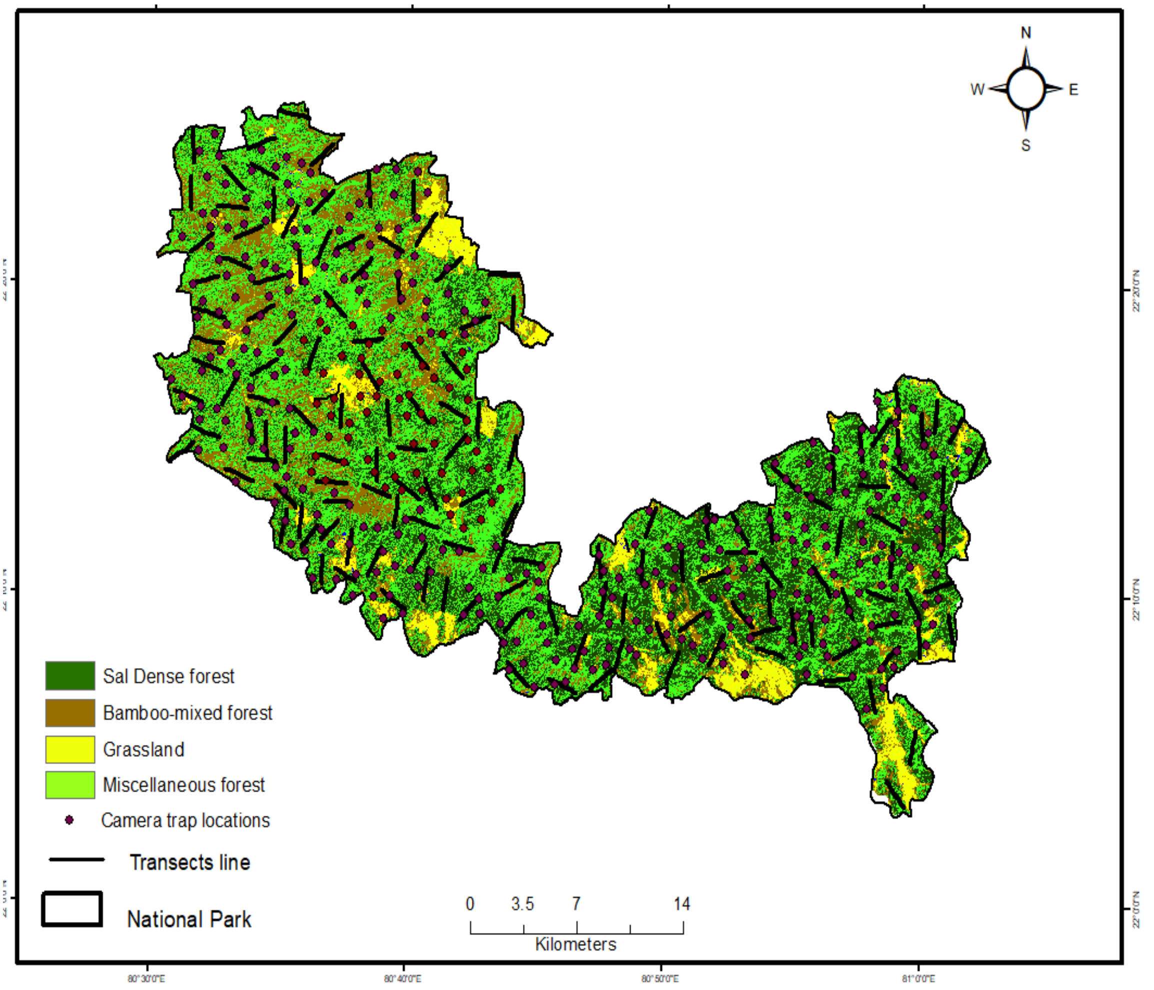


Figure 4. 1 Vegetation map showing line transects and camera trap locations in Kanha National Park.

2.5 Data analysis

Mean Group Sizes (MGS) and Typical Group Sizes (TGS) were computed for chital and other wild ungulates in both summer and winter season (Jarman, 1974). MGS represents the size of the group that an observer would encounter, on average, in a population, whereas TGS is an individual-centered measure (Jarman 1982), represents the group size of the average individual. TGS has an advantage over MGS because it is less sensitive to the number of records of solitary animals (White et al. 2012).

I estimated mean group size of ungulates by habitat, season and level of predator densities. I categorized the habitat into four distinct types based on food availability and cover a) Grasslands b) Miscellaneous c) Bamboo-mixed forest) and c) Sal forest. I extracted the mean group size of ungulates, habitat types, spatially explicit densities of both the predators (tiger and leopard) and prey (Chital, sambar and gaur) at 25 km^2 grid (based on predator female maximum home range) using Arc GIS 10.1 to understand the effect of different factors on ungulate group size at an appropriate scale.

I checked that distribution of the data was approximately normal (Shapiro-Wilk test) and that variances were homogenous (Levene test; Levene 1960). Prior to the use of any statistical model, the non-normal data variables, i.e. group size of ungulates were standardized to meet the assumptions of normality and linearity, and if needed, explanatory variables were also suitably transformed.

The results from analyzing typical group size and mean group size was very similar. Therefore, here I only present results for mean group size. Factors influencing the mean group size such as season and habitat were analyzed using two-way Analysis of Variance ANOVA (SPSS version, 11.5.) to understand the individual effect and interactive effect of these factors on group size. ANOVA was followed up with multiple range test such as Tukey's post hoc tests (Zar 1999) to examine which habitat differ statistically. Box plots were generated to understand and explore the relationship between group size and their response to different habitats, different level of predator densities and ungulate densities. Box plots were also generated for predator densities response to different habitat types to understand their effect on ungulates group size and densities. I used Pearson’s correlation coefficient analysis to explore relationships between group size and ecological variables.

As an additional way of assessing the relative importance of predator and ungulate abundance, I ran a linear regression with tiger density and group size as the response and ungulate density as the predictor. Since both tiger density and group sizes were correlated to ungulate density, I first removed the variation explained in both group size and tiger density attributed to ungulate density and then regressed the residuals of group size against the residuals of tiger density.

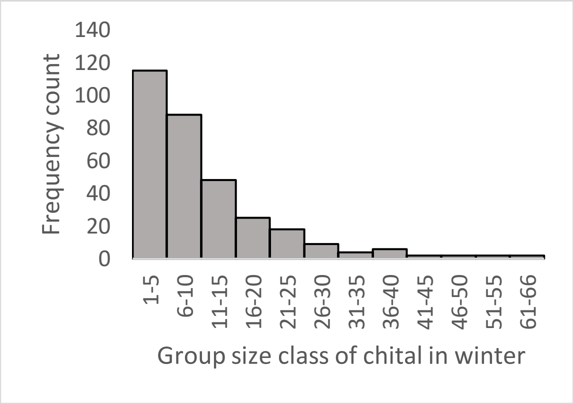
All analysis was carried out in the statistical language R, version 3.01(R Development Core Team 2013). Complete models, combining all variables were examined for the entire Kanha National park to check which models were significant and were explaining more meaningful ecological inference. Model selection was done using AIC values (Akaike 1974), R-squares, standardized B, and P-values of each model. P-values lower than 0.05 were considered significant. AIC were used to distinguish the fit of each model.

3. Results

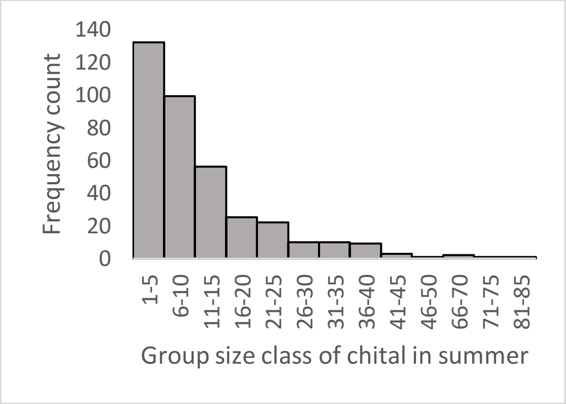
3.1 Grouping tendencies of ungulates in Kanha:

Ungulates form large groups when the food is abundant and/or to avoid predation in areas of high predator densities. All observations of chital were groups of varying sizes. Chital appears to form a more fluid group size than any other ungulate in the tropical forest. Chital showed maximum observations in group size of 1-10 (63%) while 22% of the sightings were in the size class of 11-20 individuals **(Figure 4.2 a,b).** Solitary sightings of gaur were 40%, while

32% observations in group size of 4-10 **(Figure 4.2 e, f)**. Sambar formed larger groups mostly in favoured feeding sites or near water holes or salt licks. Sambar showed maximum observations in group size of 1-3 animals (85%) while wild pig showed maximum observations in group size of 1-5 (43%) **(Figure 4.2c,d, g,h)**. Barking deer were solitary as 86% of the observations were of single animals **(Figure 4.2 I,j)**.



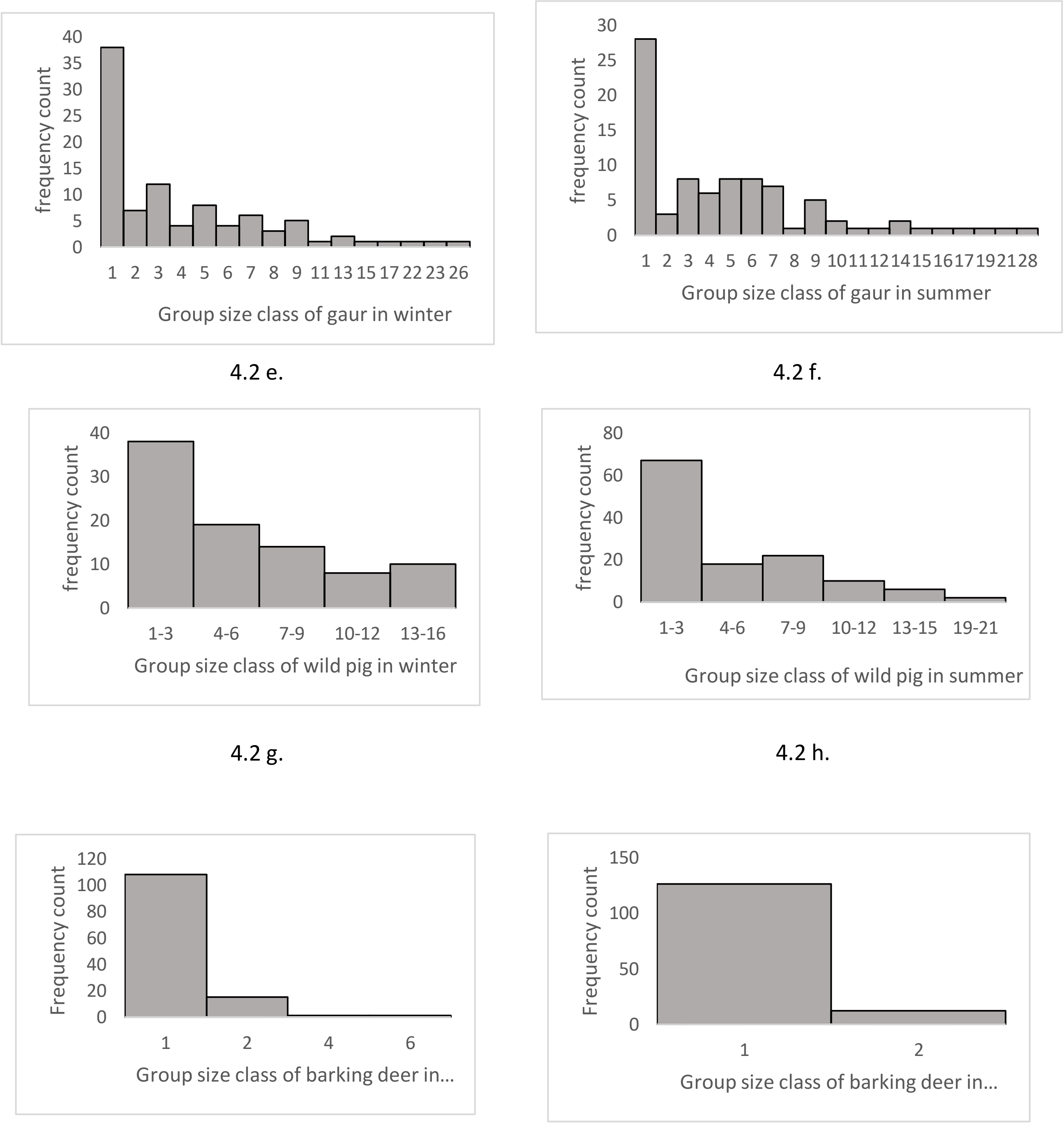
4.2 a.



4.2 b.

4.2 c.

4.2 d.



4.2 e.

4.2 f.

4.2 g.

4.2 h.

4.2 i.

4.2 j.

Figure 4. 2 a-j: Group tendencies of ungulates in Kanha National park; a-b Chital in winter and summer; c-d sambar in winter and summer; e-f Gaur in winter and summer; g-h Wild pig in winter and summer; i-j Barking deer in winter and summer.

3.2 Mean Group Size (MGS) and Typical Group Size (TGS) of ungulates in summer and winter

Among all wild ungulates, chital formed the largest group in both summer and winter. In summer, mean group size (MGS) of chital was 11.47 SE±0.59 and Typical Group Size (TGS) is 22.73 SE±0.72 while in winter, MGS of chital was 10.90 SE±0.58 and TGS of 20.79 SE±0.65. However, Typical Group Sizes of chital were smaller in winter than summer **(Table 4.1)**. The sambar formed smaller group in Kanha (MGS=2.78 SE±0.10 in summer and 2.45 SE±0.08 in winter; TGS=3.64 SE±0.12 in summer and 3.26 SE±0.09 in winter) **(Table 4.1)**. The larger group was also observed for gaur (MGS=5.33 SE±0.55 and 4.41 SE±0.45; TGS= 10.28 SE±0.55 and 9.87 SE±0.91 in summer and winter respectively) and wild pig (MGS=4.81 SE±0.38 in summer and 5.53 SE±0.45 in winter; TGS of 8.61 SE±0.12 in summer and 8.85 SE±0.08 in winter) **(Table 4.1)**. Barking deer is a solitary animal, occasionally they were found in pairs consisting mostly young and mother or an adult male or female. The barking deer was mostly observed solitary, with a mean group size of 1.08 SE=0.02 in summer and 1.16 SE±0.04 and typical group size of 1.16 SE±0.06 in summer and 1.36 SE±0.04 in winter **(Table 4.1)**.

Table 4. 1Typical (TGS) and Mean group sizes (MGS) of ungulates in Kanha National park during summer and winter in Kanha National park.

Species	**Summer**		**Winter**	
	MGS (SE)	**TGS (SE)**	**MGS (SE)**	**TGS (SE)**
Chital (n=692)	11.47 (0.59)	22.73 (0.72)	10.90 (0.58)	20.79 (0.65)
Sambar (n=481)	2.78 (0.10)	3.64 (0.12)	2.45(0.08)	3.26(0.09)
Gaur (n=181)	5.33 (0.55)	10.28 (0.55)	4.41(0.50)	9.87(0.91)
Wild pig (n=214)	4.81 (0.38)	8.61 (0.12)	5.53(0.45)	8.85 (0.08)
Barking deer (n=263)	1.08 (0.02)	1.16 (0.06)	1.16(0.04)	1.36(0.04)

SE=Standard Error

3.3 Group size of ungulates in different habitat types and seasons

1. **Chital:** There was no significant difference in mean group size of chital between summer (8.94; SE±0.46) and winter (8.24; SE±0.47). (Two-way ANOVA, F=1.203; P= 0.275). Although group size of chital significantly varied among the habitats (**Figure 4.3**; Two-way ANOVA, F=7.232; P=0.001). Chital were observed in all habitats, however, open habitats, i.e. grassland had the highest mean group size (23.7; SE±2.99) and lowest in Sal dense forest (7.94; SE±0.61) (Tukey's Posthoc test, p<0.05).
2. **Sambar**: There was no significant difference in mean group size between seasons (summer 2.60, SE ± 0.10) and (winter, 2.33, SE±0.47) (Two -way ANOVA, F=1.38; P= 0.24) and habitats (**Figure 4.3**; Two-way ANOVA, F=1.22 ; P=0.31).
3. **Gaur**: There was no significant variation in the mean group size among the different seasons (Two-way ANOVA, F=1.75; P=0.18) and habitat (**Figure 4.3**; Two-way ANOVA, F=2.64; P= 0.06) in Kanha.
4. **Wild pig**: There was no significant difference in mean group size between habitats (**Figure 4.3**; Two-way ANOVA, F=0.32; P=0.33) and season (Two-way ANOVA, F=0.42; P=0.28).
5. **Barking Deer**: There was no significant difference in mean group size in relation to different habitats (**Figure 4.3**; Two-way ANOVA, F= 1.02; P= 0.31) and they also did not vary seasonally (Two-way ANOVA, F= 0.45; P=0.31). It indicates that group size in barking deer was not influenced by factors such as food availability and density.

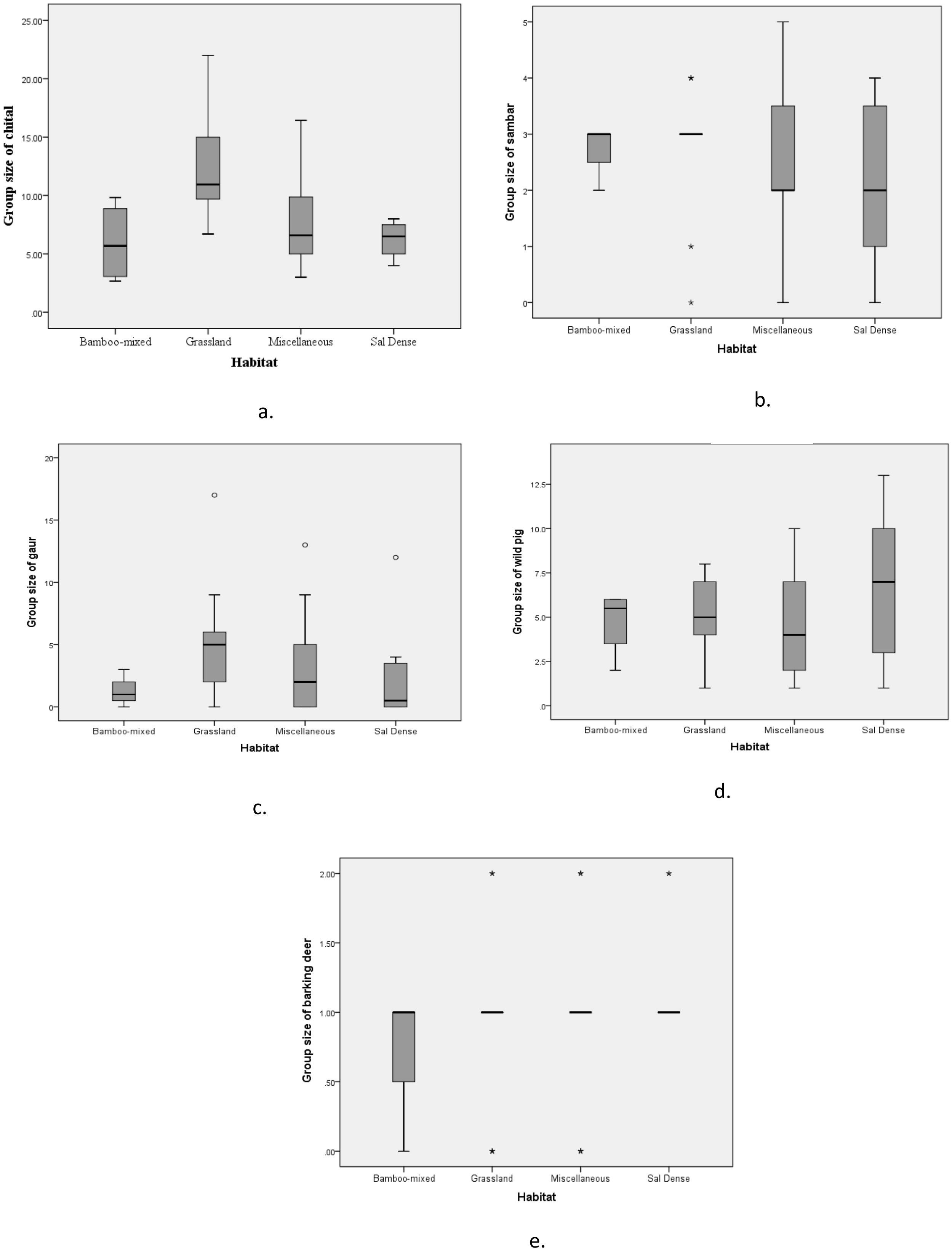
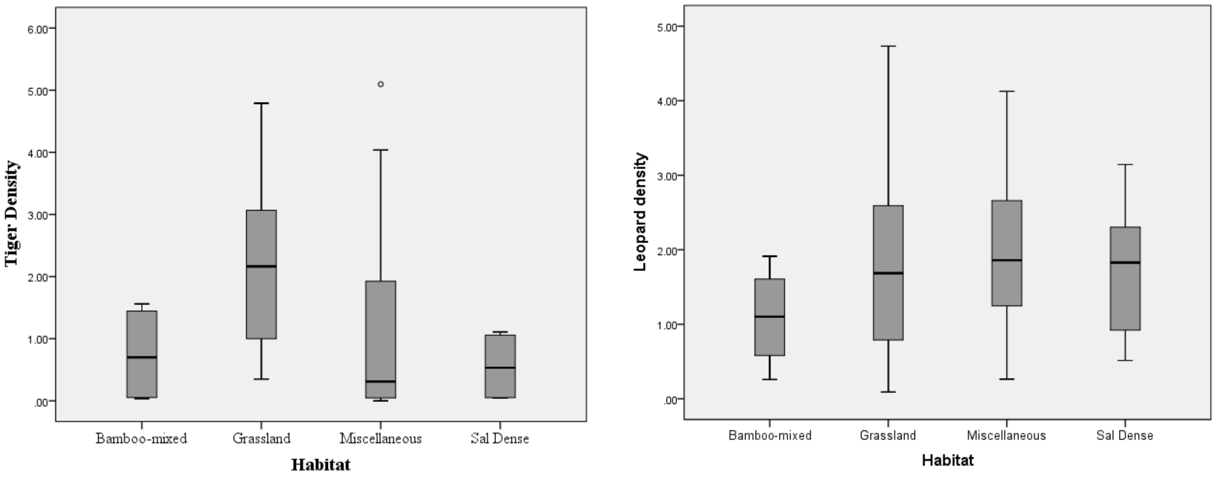


Figure 4. 3 a-e Relationship of group size of ungulates with different habitat types. a. Chital, b. Sambar, c. Gaur, d. Wild pig and e. Barking deer.



a.

b.

Figure 4. 4 a-b Relationship of predator densities with different habitat types a. Tiger and b. Leopard.

3.4. Prey selection by tiger and leopard:

From another study on carnivore ecology in Kanha (Kumar 2020), the researcher collected 180 tiger scats and 133 leopard scats from the study area. The analysis showed that wild ungulates were selected over other prey (90% (percentage of occurrence) of all prey consumed) (Figure 4.5). I have used this information in this chapter to analyze ungulate group sizes.

Chital were the most important species in this respect accounting for 35.3% of the primary diet of tiger and leopard, followed by sambar (16.7%), gaur and wild pig (15%). Other wild ungulates such as chousingha and barking deer together only represent 3% (Figure 4.5). Ivlev's selectivity index (1961) showed that the gaur was negatively selected (E= -0.3) by tigers. In contrast, chital, sambar and wild pig were positively selected (E=0.4, 0.2, 0.8) by tigers, being consumed more often from their estimated availability in the study area (Figure 4.6).

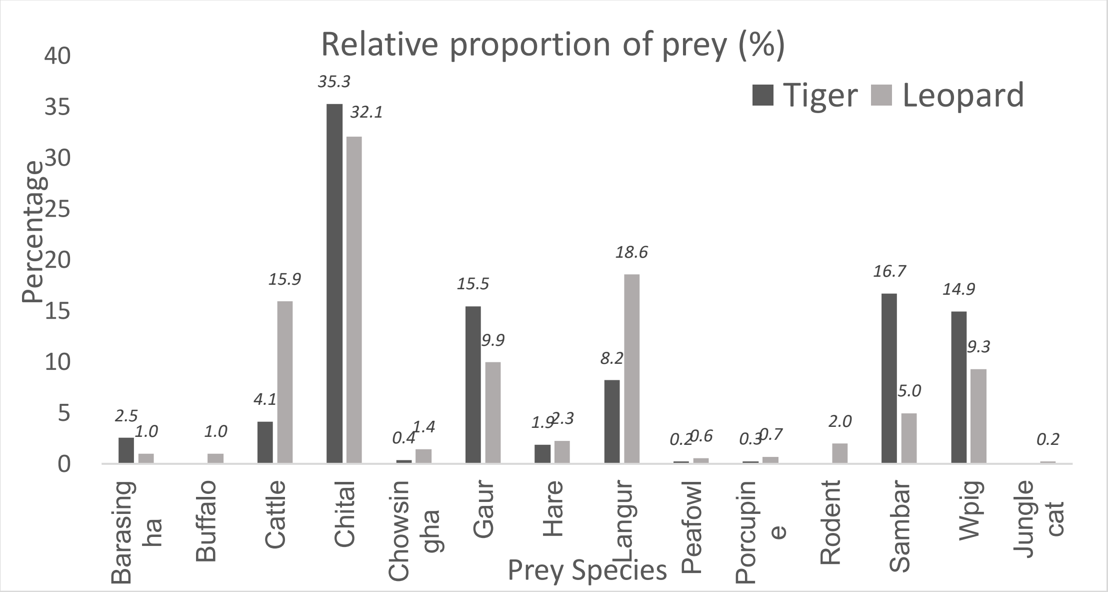


Figure 4. 5 Prey composition in the diet of Tiger and Leopard in Kanha (Source: Kumar 2020).

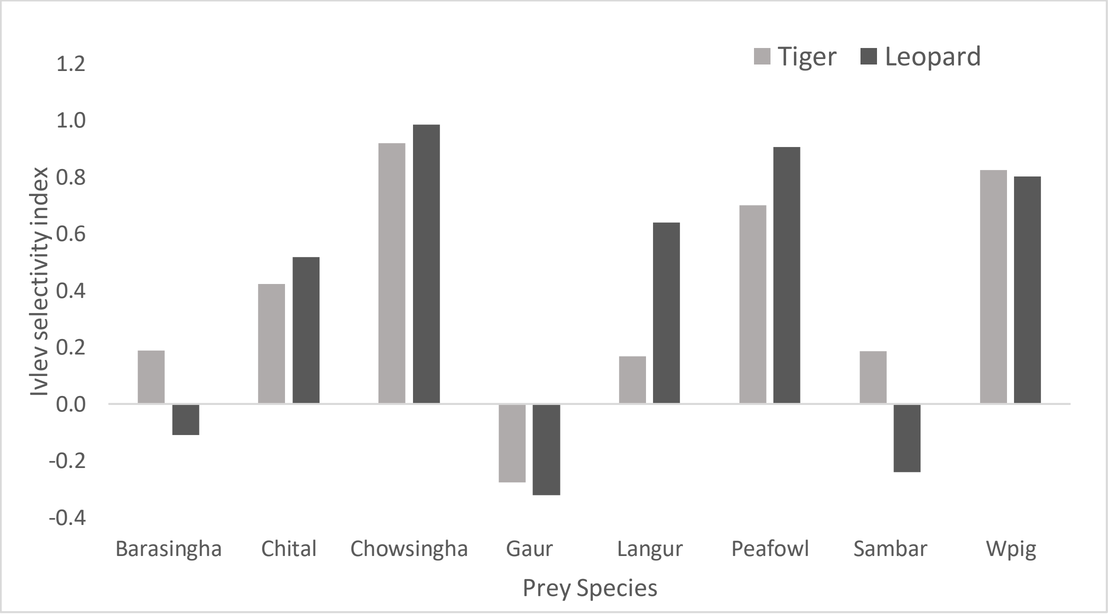
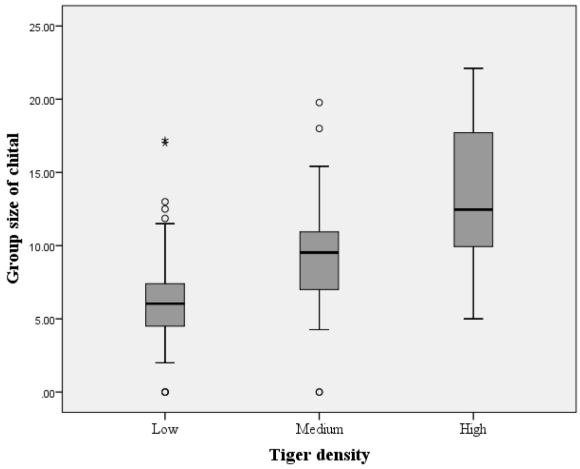


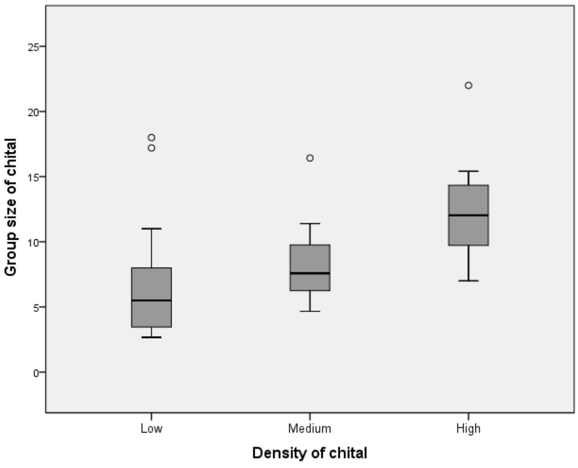
Figure 4. 6 Ivlev selectivity index of prey items in tiger and leopard diet (Source: Kumar 2020).

3.5. Relationship of group size of ungulates (response variable) with predator and ungulate density

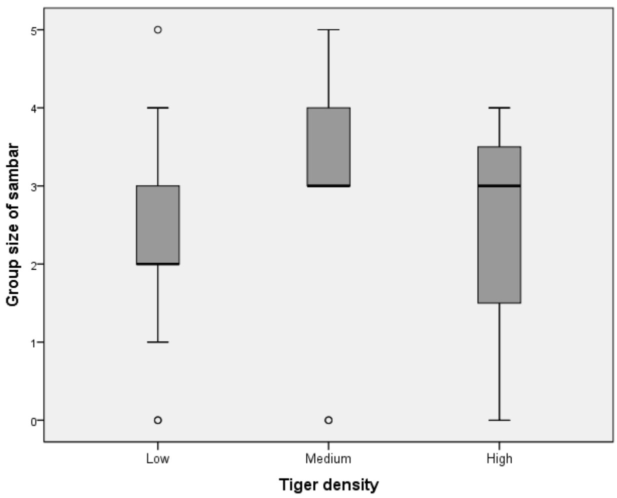
Variation among populations of mean group size of chital was most strongly correlated with its density (**Figure 4.7**; Pearson correlation coefficients; r= 0.40, P=0.00) and tiger density (**Figure 4.7** r=0.41; P=0.00). Large groups tend to increase with population density (Caughley 1964) and consequently, predator density will be dependent on ungulate density. However, Chital group size was not correlated with leopard density (Pearson correlation coefficients, r= 0.00, P=0.99). Group size of sambar was significantly correlated with tiger density (**Figure 4.7**; Pearson correlation coefficient; r=0.35; P=0.00). Group size of gaur was not significantly correlated with tiger density **(Figure 4.7;** r= 0.16, p=0.24) and leopard density (r=0.01, p=0.92), nor was it related to its own population density (**Figure 4.7**; r=2.13, p=0.07).



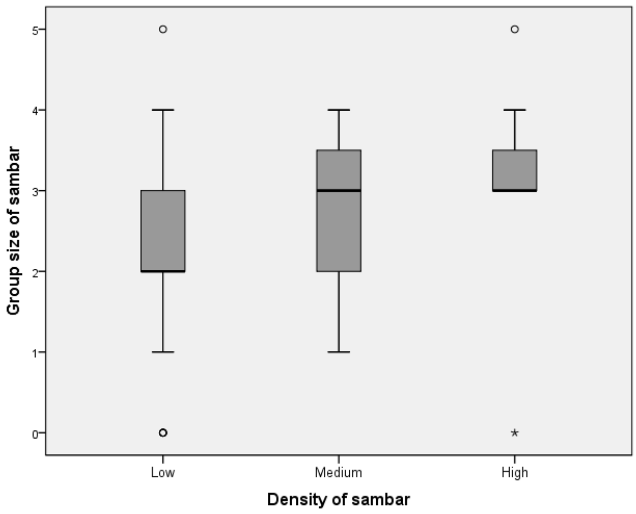
4.7 a.



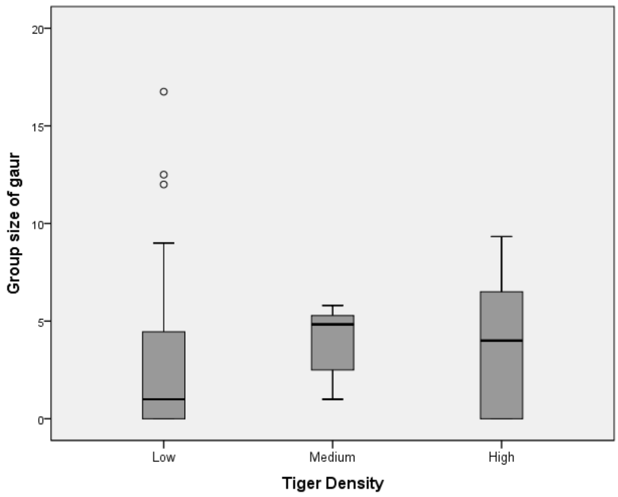
4.7 b.



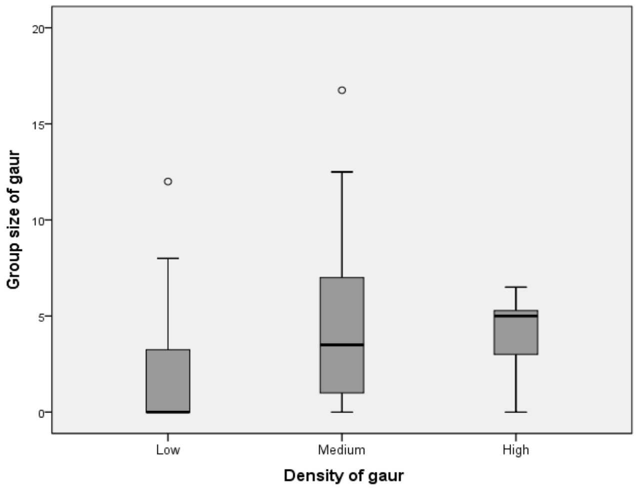
4.7 c.



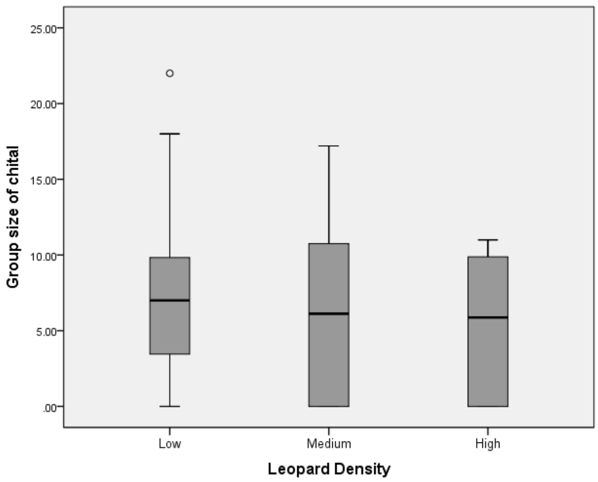
4.7 d.



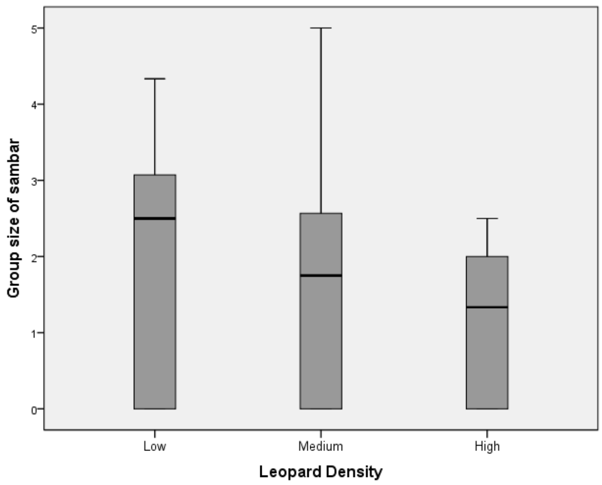
4.7 e.



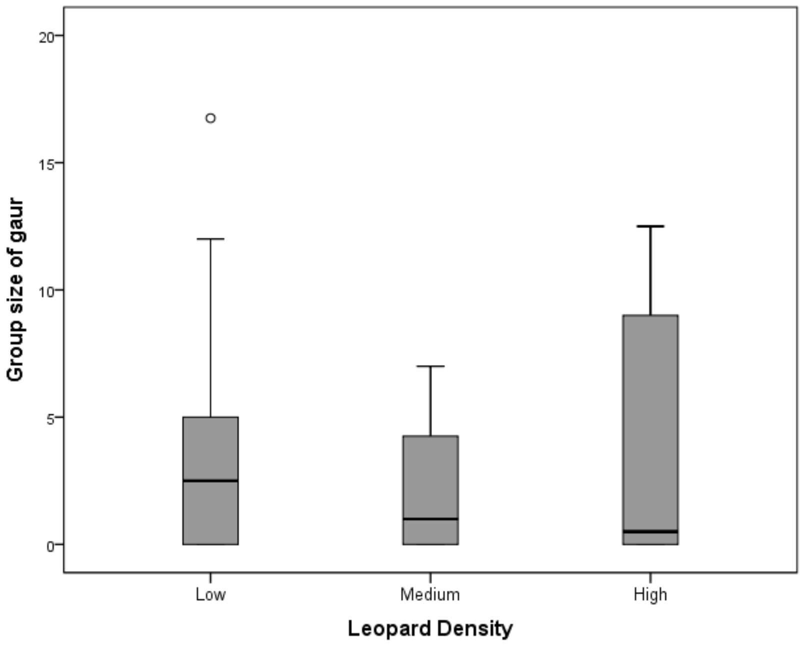
4.7 f.



4.7 g.



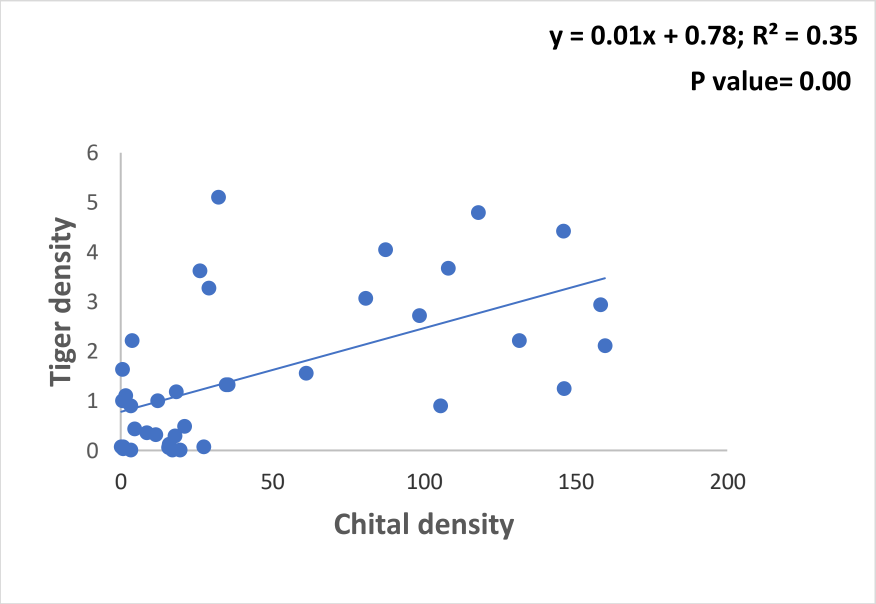
4.7 h.



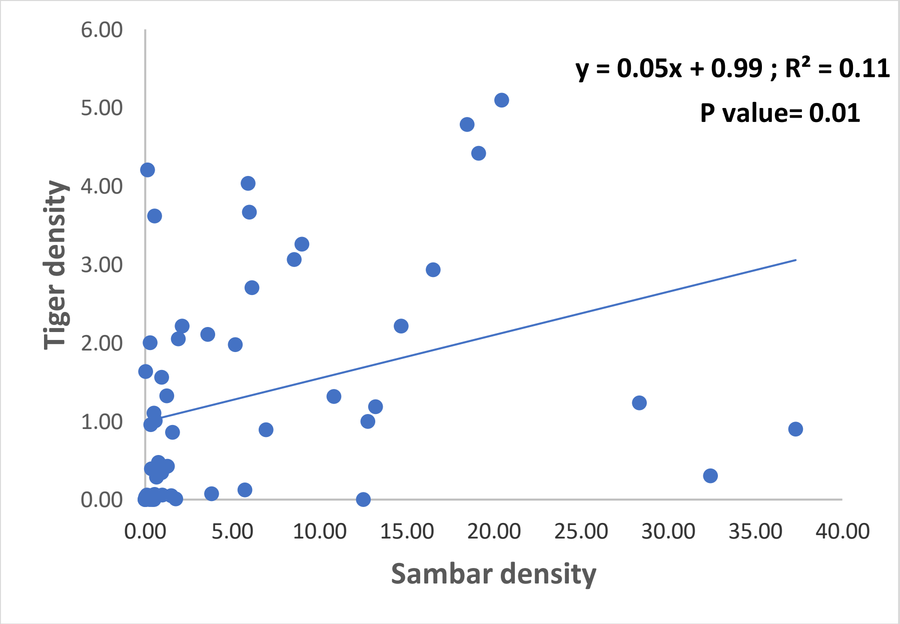
4.7 i.

Figure 4. 7 a-i Relationship of group size of ungulates (response variable) with predator and ungulate density.

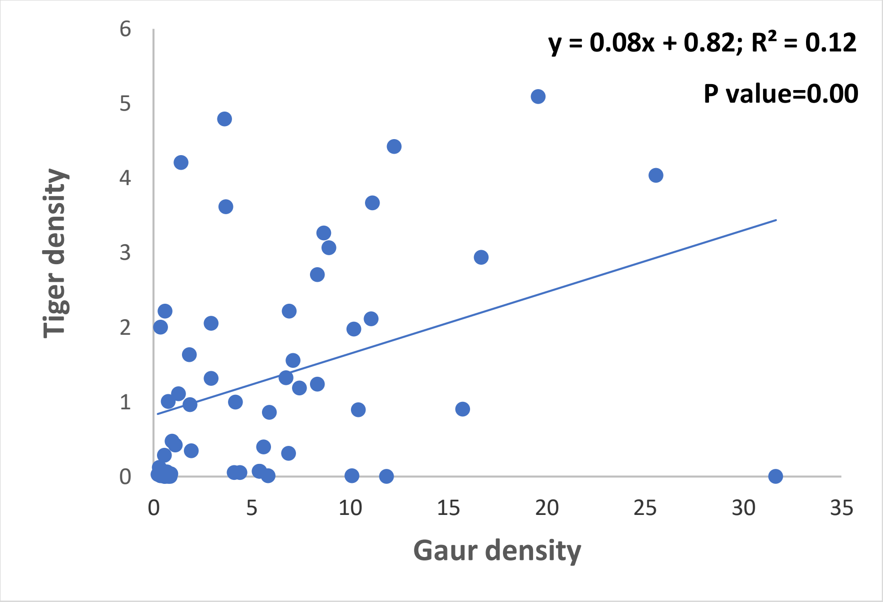
In a linear regression of tiger density and ungulate group size, with ungulate density used as a predictor, density of chital, sambar and gaur explained substantial variation in tiger density **(Figure 4.8;** Chital slope (SE)= 0.01(0.003), P= 0.00, R^2= 0.35; Sambar slope(SE)=0.05(0.02), P=0.01, R^2=0.11; Gaur slope(SE)=0.08(0.02), P=0.00, R^2=0.12). Chital and sambar density explained substantial variation in group size (**Figure 4.9**; Chital slope (SE)= 0.04 (0.01). P=0.00, R^2=0.20; Sambar slope (SE)= 0.06 (0.02), P=0.00, R^2=14), whereas gaur density did not (**Figure 4.9**; slope (SE)= 0.14(0.07), P=0.07, R^2=0.06). After removing the variation explained in group size and tiger density with ungulate density (Figure 5.5) and then regressing the residuals of group size of ungulates against the residuals of tiger density, I found significant relationship of chital(Slope (SE)=0.29(0.15), P=0.05, R^2=0.08) that explained 8% of the variation, and sambar (Slope (SE)=0.26(0.13), P=0.04, R^2=0.07) explained 7% of the variation in group sizes (**Figure 4.10**). However, residuals of tiger density do not influence group size residuals of gaur (Slope (SE)=0.007 (0.001), P=0.57, R^2=0.00; **Figure 4.10**).



4.8 a.

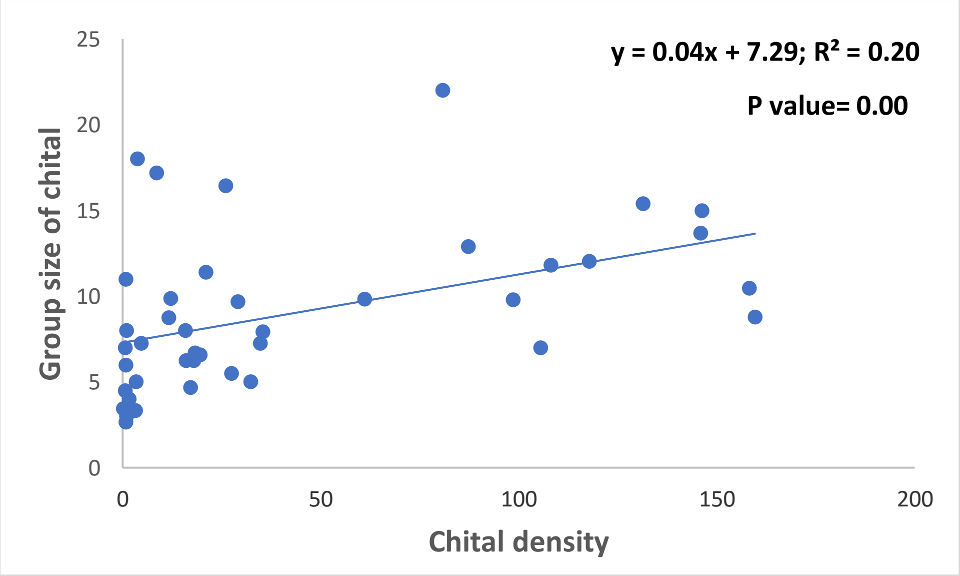


4.8 b.

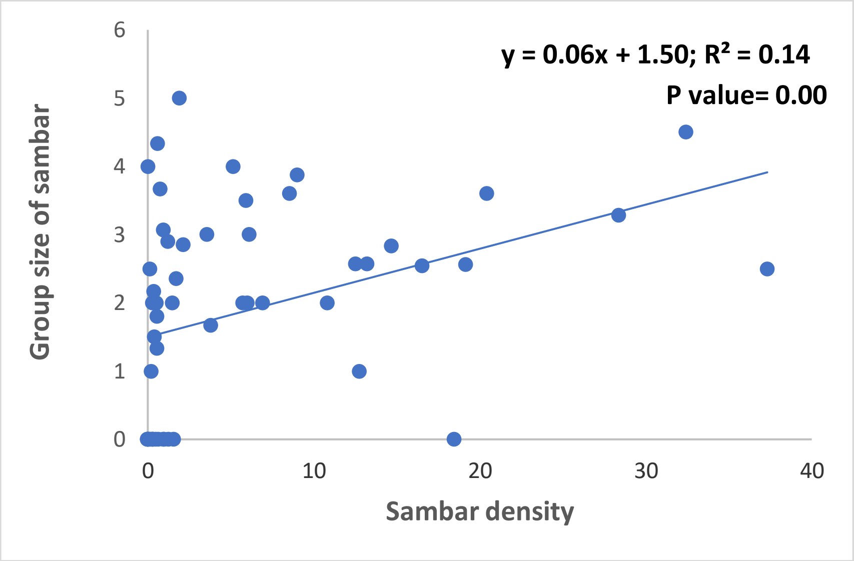


4.8 c.

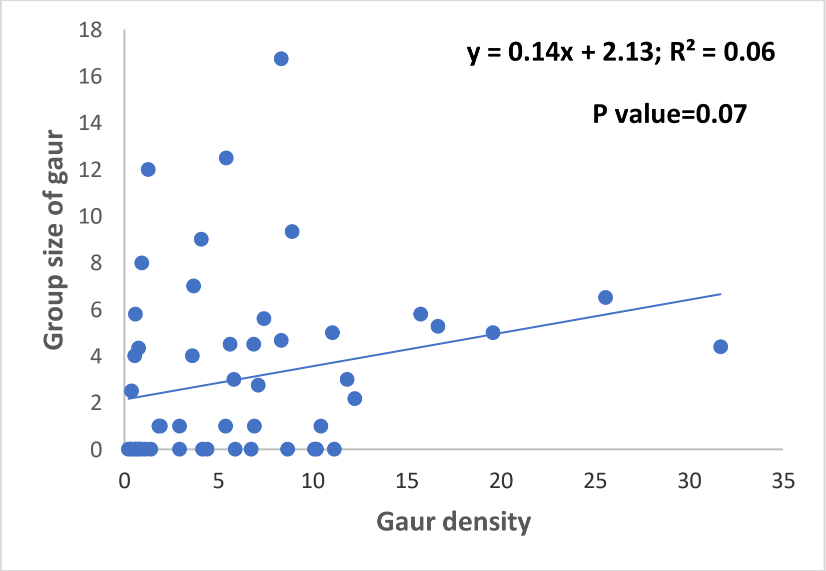
Figure 4. 8 a-c: Relationship between ungulate density and tiger density a. Chital, b. Sambar and c. Gaur.



4.9 a.

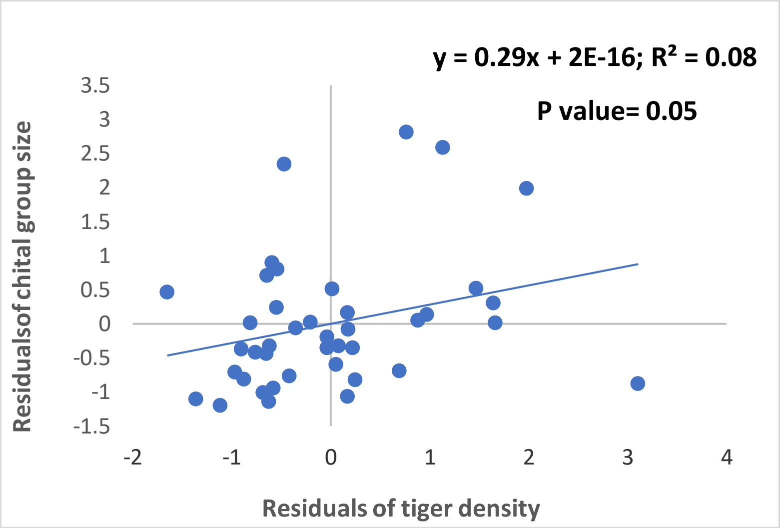


4.9 b.

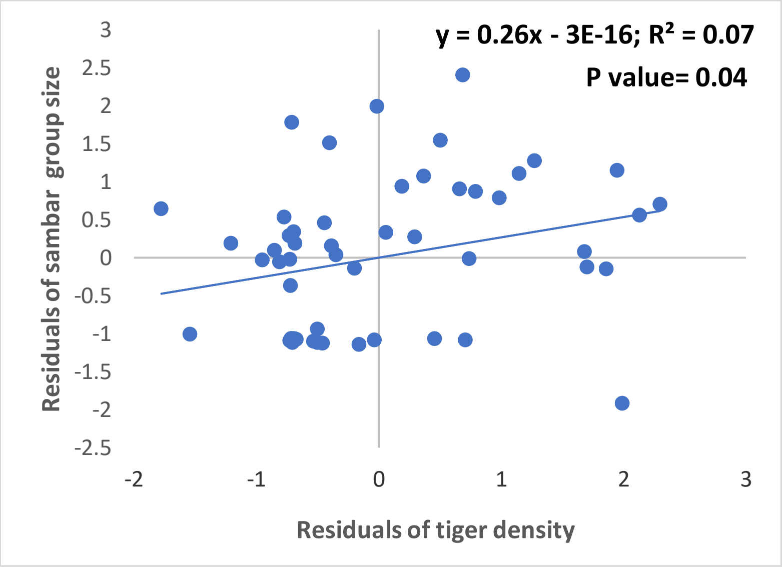


4.9 c.

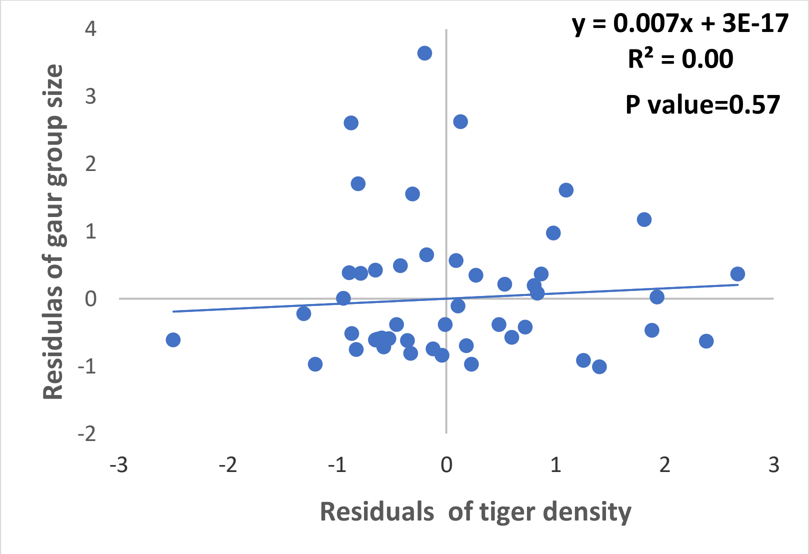
Figure 4. 9 a-c: Relationship between ungulate density and ungulate group size a. Chital, b. Sambar and c. Gaur.


y = 0.29x + 2E-16; R² = 0.08
P value= 0.05
Residualsof chital group size
Residuals of tiger density
3.5
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-1
0
1
2
3
4

4.10 a.


y = 0.26x - 3E-16; R² = 0.07
P value= 0.04
Residuals of sambar group size
Residuals of tiger density
3
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
-2
-2.5
-2
-1
0
1
2
3

4.10 b.



4.10 c.

Figure 4. 10 a-c: Relationship between residuals of tiger density and residuals of ungulate group size a. Chital, b. Sambar and c. Gaur.

4.Discussion

Group living is a widespread biological phenomenon in the animal kingdom. The grouping behaviour of ungulates is mainly attributed to antipredator and forage availability (Krause et al. 2002). Group size is influenced by several factors such as animal density (Caughley 1964), habitat type and predatory movements (Jarman 1974) and seasonal patterns (Rodgers 1977, Raman 1997). A tendency for grouping depends on occupied habitat, environmental conditions and vital cycles in different species (Wilson 1999).

Our results indicate that group size of chital was positively related to habitat type, and groups were largest in the grassland area dominated by vast stretches of open habitats. A similar increase in group size with open habitats have been reported from interspecific (Jarman 1974) and intraspecific comparisons (Hirth 1977). Group formation proposed to reduce predation risk to a higher degree in open habitats than closed habitats (Jarman 1974); grouping in open habitats, improve predator detection and give the advantage of dilution and confusion effects. Conversely, in closed habitats, predation risk is reduced by minimizing the probability of being detected by predators, and so individuals should occur in smaller groups (Jarman 1974).

Results from chital provide strong support for the proposed influence of habitat type on grouping while sambar and gaur did not show any relationship with habitat. Despite the low availability of open grasslands in this landscape, chital showed high density over here (see chapter 2 for details; Awasthi et al. 2016) as well as larger group size in an open habitat of grassland. When food is abundant and distributed evenly in areas of large patches, reduction in competition and larger groups of foraging animals become possible (Jarman 1974). High ungulate density in a particular habitat can be used as an index of high food availability. A positive correlation between population density and group size was suggested for several species (Leuthold and Leuthold 1975). Group size of ungulates increases when density increases because of the higher encounter rate and fusion of groups (as suggested by Caughley 1977). It appears to be the case with chital in the grassland habitat of Kanha. The higher availability of fresh grass sprouts in grassland is likely to have attracted chital in more substantial numbers into this habitat. As chital are predominantly grazers in both summer and winter in Kanha suggesting that forage can constrain group size.

The formation of larger groups in open habitats has also been found in other gregarious ungulates such as gaur, but their group size was not significantly related to the habitats. Large ruminant, requiring a sizeable absolute intake of food, can switch to different habitats to fulfill their daily food intake rate. In contrast, dense habitat contains more browse than grasses, and therefore, browsers are more likely to occur in small groups. Group size of sambar, a browser and a forested species, which mostly live partly solitary and partly gregarious (Geist 1998) occur in small group sizes in forest habitats. This variation in group size is owing to presumably a consequence of food being more dispersed and scattered throughout the habitat (Jarman 1974; Mishra 1982; Johnsingh 1983; Karanth and Sunquist 1992).

Tiger density was also found to be highest in grasslands in comparison to other habitats (Figure 4.4; Kumar 2020). Thus, chital formed larger groups in open habitat within high tiger density area. This habitat hypothesis relies on predation being a crucial selective factor and therefore predicts that group sizes should also vary with predation pressure. Interestingly, tiger density in Kanha was related to a group size of chital and sambar **(Figure 4.10)**; however, they explained less than 10% variation in group sizes.

Grouping of gaurs in habitats is more of a function of resource requirements than a response to higher perceived predation risk from the tiger. In Kanha, gaur is hunted less by tiger or leopard in compare to other prey species such as chital and sambar. (Kumar et al. 2019). Hence, group size variation in gaur does not show an antipredator response. (Figure 4.10). Leopard densities were similar across habitat types and play no role in influencing group size of ungulates which indicates that predation may not be the most important factor currently influencing group size (Brashares and Arcese 2002). Perhaps habitat type modified payoffs to grouping other than those related to predation pressure.

To summarize, the data on ecological correlates of group size variation indicate the overall importance of habitat, forage and predation as selective factors. Additional factors may also explain the variation in group size that is still unaccounted for in this chapter. These factors include the specific dynamics of individual joining and leaving groups (Pullium and Caraco 1984) and the differences in optimal group size. From the results, I highlight that ungulates do respond to carnivore density by forming larger groups, though food plays a major role in group size dynamics. Still, the underlying mechanisms are unclear and need further investigations.

Chapter 5: Resource Partitioning among sympatric ungulates in Kanha Tiger Reserve: space, time and food

1. Introduction

Resource partitioning is a widely studied mechanism for the coexistence of diverse community of sympatric ungulates (Putman and Putman 1996). Survival of sympatric ungulates is possible, either through different species may specialize in distinct resources (Tilman 1982) or temporally and spatially segregate themselves to avoid competition. Schoener 1974 identified food, space and time as essential niche dimensions enabling coexistence. Spatial niche partitioning has been found to be an important factor for sympatric coexistence among a number of ungulate species (McCullough 1981, Smith 1987). Spatial segregation can often result from different body sizes, interspecific differences in the use of habitat and sometimes also reflect the degree of competitive exclusion of one species by another. Temporal segregation has been studied for the coexistence of sympatric ungulate species (Stewart et al. 2002). Different species may be limited by the same resources but differ in terms of when they exploit the resources. (Armstrong and Mcgehea 1976, 1980). Food partitioning also has been extensively studied in niche separation of many ungulate populations (Krausman 1978, Hanley and Hanley 1982).

Processes determining co-occurrence in assemblages of Asian ungulates may depend on the spatial scale at which species associations are analyzed (Darmon et al. 2012). Ungulates are influenced by spatial heterogeneity in their environment at scales ranging from feeding patch to the biome (Du Toit 2003).

At large scales, guild aggregation may result from environmental constraints, such as terrain and distance to water sources, on ungulate distributions (Redfern et al. 2003, Redfern et al. 2006). Within these constraints, ungulate foraging decisions occur at multiple scales, including a selection of home range, habitat or feeding patches, plant species foraged on, and plant parts eaten (Sinclair and Norton-Griffiths 1979, Senft et al. 1987). At the scale of home ranges and feeding patches, ecological separation occurs through habitat preferences and competition (Amarasekare 2003; Tews et al. 2004). Moreover, interspecific competition predominates during the resource lean, dry season (as in case of African Savanna ecosystem) when food is in short supply, and forage of good quality becomes depleted (Arsenault and Owen Smith 2002). Although, larger species have the advantage of tolerating coarser, lower-quality food, and hence, can obtain the bulk of the available forage. Smaller species can survive using the scattered remains of high-quality food. Larger species may also facilitate smaller species by removing coarse material and exposing the high-quality items; thus, facilitation can also explain the close association of two species (Sinclair and Norton-Griffiths 1979). Thus, resource partitioning is achieved by a pattern of different sized ungulates and different temporal activities.

Protected areas of Deccan plateau in India, especially Kanha Tiger Reserve hold high species richness (10 species) of ungulates (Ahrestani et al. 2011) within South-east Asia. Moreover, ungulate biomass in Kanha is estimated as 26,806 kg/km2 (Awasthi et al. 2016). Species considered for resource partitioning study include four ruminants, i.e. two grazers, chital and barasingha, one intermediate feeder gaur, a species whose diet contains a high proportion of browse, sambar, and a nibbler, barking deer as well as one non-ruminant, omnivorous wild pig.

The purpose of our study was to examine patterns of resource use to assess the role of resource partitioning in the coexistence of sympatric ungulates in Kanha. I examine this premise by collecting quantitative data on ungulate densities at the high spatial resolution, temporal activity patterns and seasonal food habits. Resource partitioning between species was expected to be according to the difference in their densities**,** body size and digestive system. Six general hypotheses emerge as follows:

1. There would be an ecological separation between sympatric ungulates (chital, sambar and gaur) at a spatial density level in both summer and winter but would be less pronounced when resources were limited (i.e. in summer) **(Spatial resource partitioning).**
2. There would be temporal segregation between sympatric ungulates in which different ungulates would be active during different parts of the diel cycle if the interspecific overlap in space use is high **(Temporal resource partitioning).**
3. There would be interspecific differences in diets that would maintain low seasonal overlap. Because diet overlap generally increase with a decrease in food abundance (Schwartz and Ellis 1981) **(Food partitioning).**
4. The overlap would be highest during dry summer months (when resources in Central Indian forest would be most limiting, and competition for nutritional food were expected to be accentuated) and lowest in the winter season **(Food partitioning).**

5. Habitat use would be influenced by body size and digestive physiology: small ungulates would be more selective (i.e. have wider niche breadth) than larger ungulates **(Food partitioning).**
6. Facilitation may exist between larger and smaller species (gaur and chital in Kanha) if they co-occur together and when they have same feeding strategies in the summer season. Coarse, semi-dry to dry grass form the bulk of gaur’s diet (85% by volume) in summer season (Schaller 1967), thus permitting regeneration of the annual grass, replenishing and exposing the quality of grass swards for the other ungulate in the guild especially for small-bodied ruminant chital who entirely depend on more nutritious, short and high-quality grasses in the dry season of summer.

2. Materials and Methods

2.1 Spatial resource partitioning

2.1.1 Line transects and field work

I conducted line transects surveys to determine spatially explicit density and space use pattern of sympatric ungulates. Line transects of 2 km were marked within Kanha Tiger Reserve and walked during the early morning (6:00 a.m. to 8:00 a.m.), for three consecutive mornings in summer and winter of 2014. I surveyed the entire reserve with researchers and a team of trained and tested forest department staff who were well versed with fieldcraft and species identification. I trained and tested each observer in the use of laser range finder (Bushnell RX 1000), see-through compass (Suunto KB-20) and GPS (Garmin eTrex 10). In each season, sampling was completed within 30 days. The total transects survey effort comprised 1200 km of the walk along 200 spatial replicates in both seasons (see chapter 2; Figure 2.1). Radial distance, animal bearing and group size were recorded with an encounter of each ungulate species. I estimated the perpendicular distance for each observation to the transect line with the angle and radial distance from the observer to the group for subsequent analysis.

2.1.2. Data analysis: Spatial distribution of ungulate abundance using Density Surface modelling

I determined spatial densities of sympatric ungulates using quantitative data from Density Surface Modelling (DSM) at a high spatial resolution to demonstrate spatial segregation and overlap between species. These spatially explicit models, i.e. Density Surface models (DSM), help to investigate the response of biological populations to different environmental covariates that vary over the study region. A spatially explicit model can explain the between transect variation, which leads to a smaller variance in the estimate of abundance (Miller et al. 2013). Density surface modelling was performed via two stages approach: firstly, by modelling the detection function and later fitting the spatial model (Figure 5.1).

1st stage-modelling the detection function:

Distance sampling allows uncertain detection of animals (Buckland et al. 2001; 2004). A detection function, $g(x)$, is used to model the decrease in detectability with increasing distance, from the observer (Buckland et al. 2001; Miller et al. 2013). The detection function represents the probability of detecting an object given it is at distance x from the transect line. In the first stage, we used the Distance package (Miller et al. 2013) in R (R Development Core Team 2013) to estimate ungulate density and abundance. Three key functions were tested: uniform, half-normal and hazard-rate with the three adjustment terms available (cosine, simple polynomial and hermite polynomial). Detection function choice was based on the Akaike information criterion (AIC, Akaike 1974), aided by visual inspection of the histogram of distance data and goodness-of-fit tests (Burnham et al. 1980). Density surface modelling results are based on the most parsimonious detection function obtained in this first stage.

2nd stage-Density Surface modelling:

The second stage was also performed in R (R Development Core Team 2013) using the package dsm (Miller et al. 2013). Line transects were split into contiguous segments of 250 meter in length and build the buffers from the centre of the 250 m segments using ArcGIS 10.0. Modelling of density was implemented at the 250-meter segment level, totalling 1,776 segments. The count method of Hedley and Buckland (2004) was applied, using the number of animals in each segment as the response variable in the density surface model.

Six observation level spatial covariates were extracted through Arc MAP (version 10.1) from the remotely sensed data such as i) NDVI; ii) Distance to the nearest human settlements iii) EVI (Enhanced Vegetation Index; degree of deciduousness) iv) Elevation v) Ruggedness of terrain, and vi) Moistness of the forest. I used Pearson’s correlation in SPSS (ver. 21) and tested for spatial correlation of all covariates used at the scale the data was analyzed (i.e. 250 m *250 metres).

The number of animals (response variable) for each segment was related to the predictor variables through Generalized Additive Models (GAMs) (Hastie and Tibshirani 1990): a tweedie distribution and a logarithmic link function were used. The choice of the best density surface model was based on the lowest AIC value while accounting for the deviance explained by each model, ecological plausibility and the p-value of each spatial variable.

A prediction grid of 0.0625 sq. Km. (250 m *250 m) was built in ArcMap (version 10.1). The abundance of ungulates in the study area was estimated as the sum of the estimated abundance in each one of the grid cells, relying on the spatial model chosen for inference. Based on the predictions inferred by the density surface model, and taking into account the value of each variable in each grid cell, an abundance map of each ungulate species (except Barasingha) for the entire Kanha Tiger Reserve was drawn in R (R Development Core Team 2013). For Barasingha, I used group size data of different grassland areas of Kanha as DSM analysis was not possible for this species. Variance for the abundance estimates of DSM analysis was obtained through the variance propagation method described by Williams et al. (2011). This approach enables a prompt variance estimate for both the global and sub-areas density estimates. Subsequently, 3D surface plots of three major species; chital, sambar and gaur were plotted against each other in different axes (x, y and z). Surface plots were generated to understand co-occurrence pattern (degree of spatial overlap and segregation) in both summer and winter season using NCSS version 19.0.

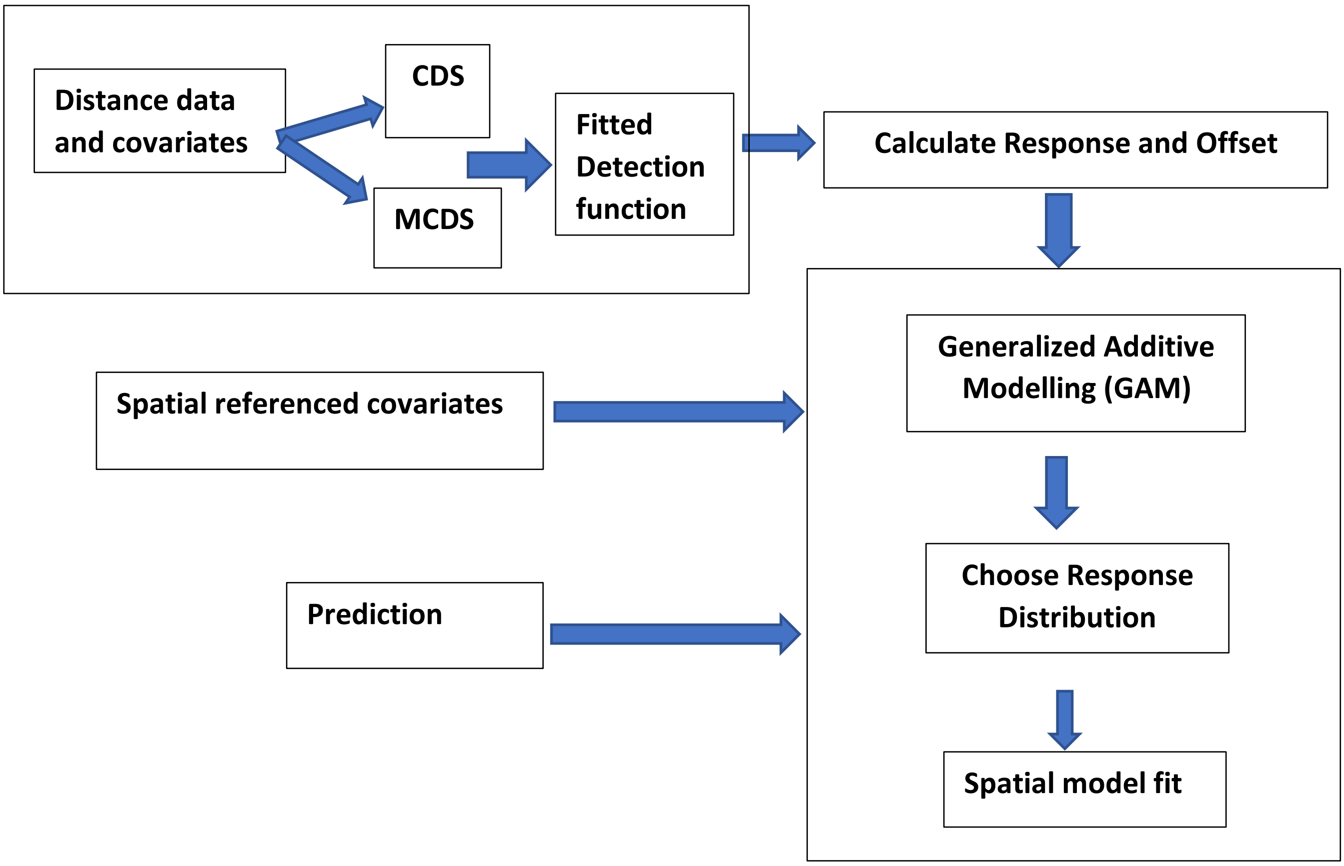


Figure 5. 1 Flow diagram showing the density surface modelling (DSM) following Miller et. al. 2013 (CDS is Conventional Distance Sampling and MCDS is Multiple Covariate Distance Sampling).

2.2 Temporal partitioning

2.2.1 Camera trapping and field work

The camera trap methodology was used to understand temporal partitioning between sympatric ungulates in Kanha Tiger Reserve. Camera traps were placed on the forest roads, animal trails and dry streams so that the sufficient number of animal captures could be obtained primarily in the case of ungulates (Frey et al. 2017). Camera trapping was being done for estimating carnivore populations through Capture Mark Recapture (CMR), but consequently, photo-captures of all other species were also obtained. Herein, I used ungulate photo-captures to compute time-activity patterns of different species.

Extensive coverage of camera traps in the entire Tiger Reserve with a minimum spacing of 0.5 km **(Figure 5.2)** provided useful information on ungulate temporal activity pattern.

2.2.2 Data analysis

Ridout and Linkie (2009) developed a method to fit kernel density functions to the time of observations of animals from photo-capture dates. To assess the temporal activity pattern of ungulates, I used time of photo-capture obtained from camera trap pictures. I kept 30 minutes interval between two consecutive times of photo-capture to make independent capture events. I used overlap package ver. 0.2.4 (Meredith and Ridout 2014) to plot kernel density curve from the time of capture data.

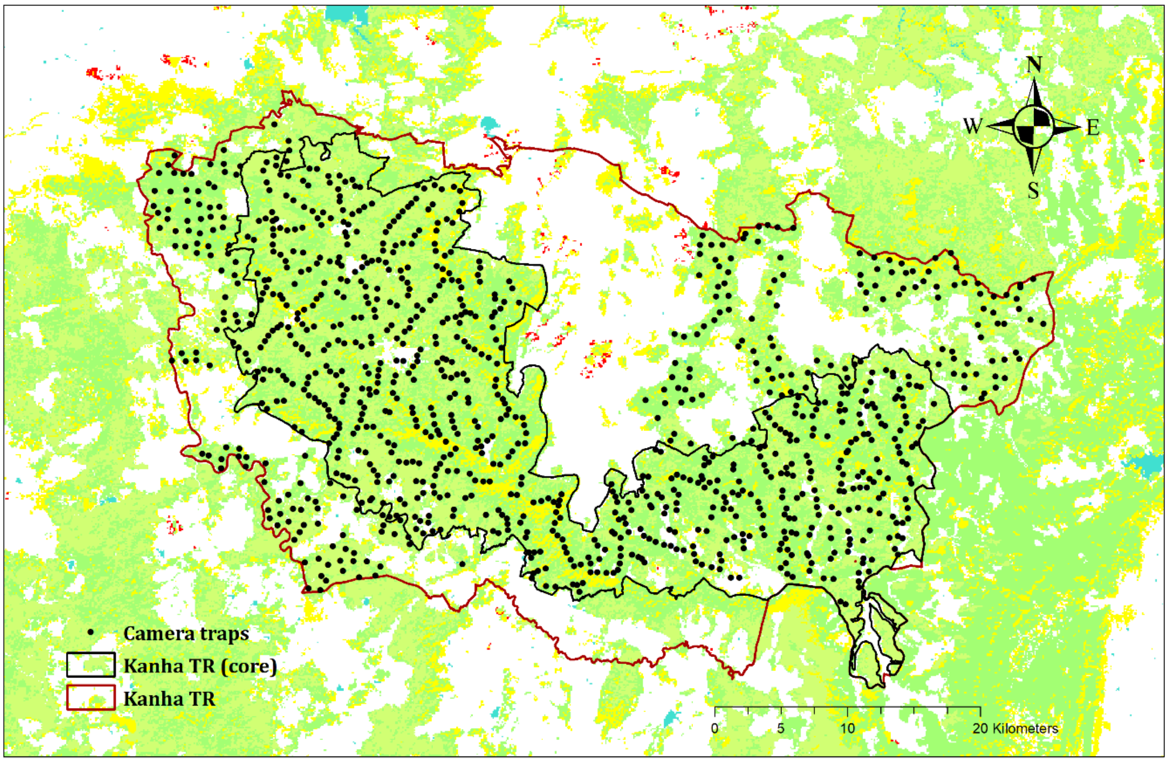


Figure 5. 2 Camera trap locations placed with minimum spacing of 0.5 km throughout the Kanha Tiger Reserve.

2.3 Food Partitioning: field method and data analysis

2.3.1 Activity pattern of ungulates

The scan animal sampling technique (Altmann 1974) was used to investigate the percentage foraging activity and habitat use of chital, sambar and gaur from dawn to dusk. Ungulate herds in the intensive study area were habituated during reconnaissance study to the continuous presence of the observer in the vicinity. Preliminary observations suggested a scan interval of 10-15 minutes to be appropriate for understanding the activity pattern of ungulates. The field observations were carried out with the aid of 32x8 binocular **(Appendix 1).** Observations were recorded from 30 to 50-meter distance, so that focal herd doesn't get disturbed. Ethogram is an inventory of behaviour exhibited by behavior used in ecology (Martin and Bateson 2007). The ethogram behavior states recorded were grazing and browsing along with cud chewing (rumination), standing, lying, moving and the other activities which contributed little (e.g. social interaction, standing alert etc. (Dave 2008, Powell et al. 2013). A minimum of seven scan sampling sessions from dawn to dusk (minimum of 12 hrs.) was carried out on chital, sambar and gaur in summer and winter season. The foraging activities such as grazing' and 'browsing' were merged into broader activities as 'foraging' for seasonal comparisons. The proportion of foraging activity in each habitat was estimated for chital, sambar and gaur in Kanha.

2.3.2. Food habits of ungulates:

Field research design to advance our understanding of foraging ecology is essential for science and wildlife management (Prins & Van 2008). The food habit study was carried out by direct observations, i.e. focal animal sampling (Altmann 1974; See Appendix 1). Direct observations have been widely used for estimating food habits of large herbivores (Jhala 1997). Individual free-ranging animals (2-3 animals in a group) were selected randomly, whenever observed specifically in areas known to be intensively used by ungulates for feeding. Animals were watched through binoculars, or 20x-60x spotting scope as they graze or browse within a radius of 30 m of the observer and the type and the frequency of bites of plant parts and species consumed were recorded in different habitats in different seasons (Appendix 1). Observations were quantified as bite counts (number of bites of a particular food item) (Jhala, 1991 & 1997; Schaller, 1967). Approximately 1000 to 2000 bites were counted seasonally in each habitat types for each animal species, i.e. chital, sambar and gaur. Later, a fixed number of bites (100 bites for chital, sambar and gaur respectively) were simulated by hand plucking the parts of major food species eaten by chital, sambar and gaur. The fresh weight of these simulated bites was taken immediately and then stored in paper bags for the dry weight **(Appendix 1).** The simulated bites were dried at 57^0C in hot air oven to constant weight to determine the dry weight per bite. This exercise was carried out for chital, sambar and gaur in different habitat types known to be used by ungulates during different seasons **(Table 5.1)** through continuous scan sampling for understanding foraging activity patterns.

For food habits study, habitats were defined according to the proportion of foraging activity of chital, sambar and gaur in each of them as estimated from scan animal sampling (Jhala, 1997). The seasonal aggregate of the total number of bites recorded for each food item in each habitat was multiplied by the proportional foraging activity of ungulates in that habitat. It provided the proportional contribution of different food item bites to the ungulates diet for each habitat type. The actual contribution of each food item to the total seasonal diet was derived using the dry weight per bite of each food item, proportional contribution to the total bites observed during direct observations and proportionate habitat use for foraging (**See Table 5.4 & 5.5 for formulation**). The detailed food habits of all three ruminants were computed for summer and winter seasons following Jhala 1997 (**See Table 5.4 a,b,c & 5.5 a,b,c).**

Table 5.1 Comparative account of sampling effort invested in estimating seasonal food items for chital, sambar and gaur in Kanha Tiger Reserve in 2018.

Season	Habitat	Number of individuals			Number of food species			No of bites		
		Chital	Sambar	Gaur	Chital	Sambar	Gaur	Chital	Sambar	Gaur
Winter 2018	Grassland*	9	1	---	21	1	---	4559	58	---
	Sal	10	11	2	10	6	2	971	2100	875
	Bamboo-mixed	21	8	8	9	4	3	2769	1224	2019
	Miscellaneous	15	7	10	18	4	17	1743	803	2988
Summer 2018	Grassland*	16	---	9	11	---	11	2210	---	1726
	Sal	16	6	5	6	5	7	1048	616	351
	Bamboo-mixed	8	12	9	4	4	2	768	1725	1687
	Miscellaneous	11	3	4	9	3	11	570	150	520

***Gaur in winter and sambar in summer were not observed to forage in this habitat.**

2.3.3. Diet niche width and overlap:

The basic approach to understanding the potential of interspecific competition or level of interaction between sympatric species is to evaluate the diet niche breadth (McDonald et al. 2000, Pianka 1986) and niche overlap (Thill & Martin, 1986; Major & Sherburne, 1987). The diet niche breadths of three sympatric species (chital, sambar and gaur) were evaluated using Levin's standardized niche breadth measure (Krebs, 1989). The most common resources measured in order to calculate overlap are food and space. Since food is one of the most critical dimensions of the niche; the analysis of dietary overlap is closely related to the issue of niche specifications among sympatric species (Krebs, 1989).

Several measures of niche overlap have been proposed (Schoener 1970; Hurlbert, 1978; Abrams, 1980; Linton et al. 1981). However, here, we used the

MacArthur and Levins' niche overlap indices (Krebs 1989) which is the simplest measure of niche overlap to interpret in the case of an asymmetrical diet of chital, sambar and gaur and amplitude of resource use overlap pattern between these sympatric species. The seasonal dietary overlap between chital – sambar, chital – gaur and sambar-gaur were computed using the proportion of each food item to total bite count corrected with the proportionate habitat use for the foraging activities. The dietary overlap was also computed for different habitat types in summer and winter seasons to understand the descriptive measure of community organization in different habitats. The dietary overlap was computed for all three possible combinations, i.e. chital-sambar, sambar-chital and sambar-gaur.

3 Results

3.1 Spatial co-occurrence pattern:

Since correlation coefficient values were less than 0.7 (+0.7 and -0.7) between each covariate, there were no issues of collinearity in using any of the covariates together in the model. Hence, six covariates were used in combination for developing ecologically relevant density surface models of ungulates **(Table 5.2).** Chital, sambar and gaur were better explained by elevation and EVI (**Table 5.3, S16**). In contrast, models of wild pig and barking deer using covariates did not perform better than the null model, hence we used the null model (model without covariate) for these two ungulates **(S16). Figure 5.3a-b** shows the smoothed spatial covariates used in the model, being elevation and EVI the most important variable in the analysis as revealed by significant P-values **(Table 5.3).** In accordance with the DSM model (Elevation and EVI for chital, sambar and gaur; and null model for wild pig and barking deer) chosen for inference, the distribution map of ungulates is shown in **Figure 5.4.**

Chital, gaur and sambar occupy high density distribution in western Banjar catchment (Kanha-Kisli-Mukki landscape) compared to eastern Halon catchment (Supkhar-Bhaisanghat landscape) of the National park **(Figure 5.4a-f** and also **see chapter 3 for habitat map** with Banjar and Halon catchments; **Figure 3.1**). At the same time, wild pig and barking deer occur at high densities within the buffer zone in comparison to the core zone of Kanha Tiger Reserve **(Figure 5.4g-j; see chapter 2 for habitat map; Figure 2.1**). Large group size of barasingha was seen in grassland areas with a high density of chital in core zone of Kanha (**Figure 5.4k**). Gaur and sambar co-occur at high densities in areas with low chital densities for both summer and winter season **(Figure 5.5).** However, co-occurrence between sambar and gaur was relatively high in winter **(Figure 5.5).**

Table 5. 2 Correlation matrix depicting degree of correlation between different spatial covariates at (250m *250 meter) scale and sample size (n=36720).

Covariates N=36720	Elevation	EVI	Distance to human settlements	NDVI	Moistness	Ruggedness
Elevation	1	0.32**	0.00	- 0.17**	0.22**	0.51**
EVI	0.32**	1	0.02**	- 0.01**	0.12**	0.39**
Distance to human settlements	0.00	0.02**	1	0.03**	- 0.03**	-0.01**
NDVI	- 0.17**	- 0.01**	0.03**	1	- 0.30**	- 0.10**
Moistness	0.22**	0.12**	- 0.03**	-0.30**	1	0.13**
Ruggedness	0.51**	0.39**	-0.01**	- 0.10**	0.13**	1

****. Correlation is significant at the 0.01 level (2-tailed)**

Table 5.3 Best DSM model among the set of candidate models for ungulates in summer and winter 2014.

Species	Season	Covariates	k'	edf	p-value	significance level	Deviance explained
Chital	Winter	s(x,y)	49	32.54	<2e-16	***	33.90%
		s(elv)	19	3.68	<2e-16	***	
		s(EVI)	19	9.49	<2e-16	***	
	Summer	s(x,y)	49	36.54	<2e-16	***	29.80%
		s(elv)	19	4.28	<2e-16	***	
		s(EVI)	19	3.11	<2e-16	***	
Sambar	Winter	s(x,y)	49	23.04	<2e-16	***	20.30%
		s(elv)	19	4.65	<2e-16	***	
		s(EVI)	19	2.41	<2e-16	***	
	Summer	s(x,y)	49	23.31	<2e-16	***	21.60%
		s(elv)	19	3.21	<2e-16	***	
		s(EVI)	19	1.66	<2e-16	***	
Gaur	Winter	s(x,y)	49	19.12	<2e-16	***	27.80%
		s(elv)	19	1	0.02	*	
		s(EVI)	19	2.31	0.025	*	
	Summer	s(x,y)	49	25.45	<2e-16	***	27.40%
		s(elv)	19	2.01	<2e-16	***	
		s(EVI)	19	1.48	<2e-16	***	

s(x,y) = smooth of geographical locations, s(elv) = smooth of elevation, s(EVI) = smooth of Enhance vegetation index, k' = basis dimension of smooth in the GAM model, edf= Effective degree of freedom. Significance codes (* = 0.001, ** = 0.01 , * =0.05).**

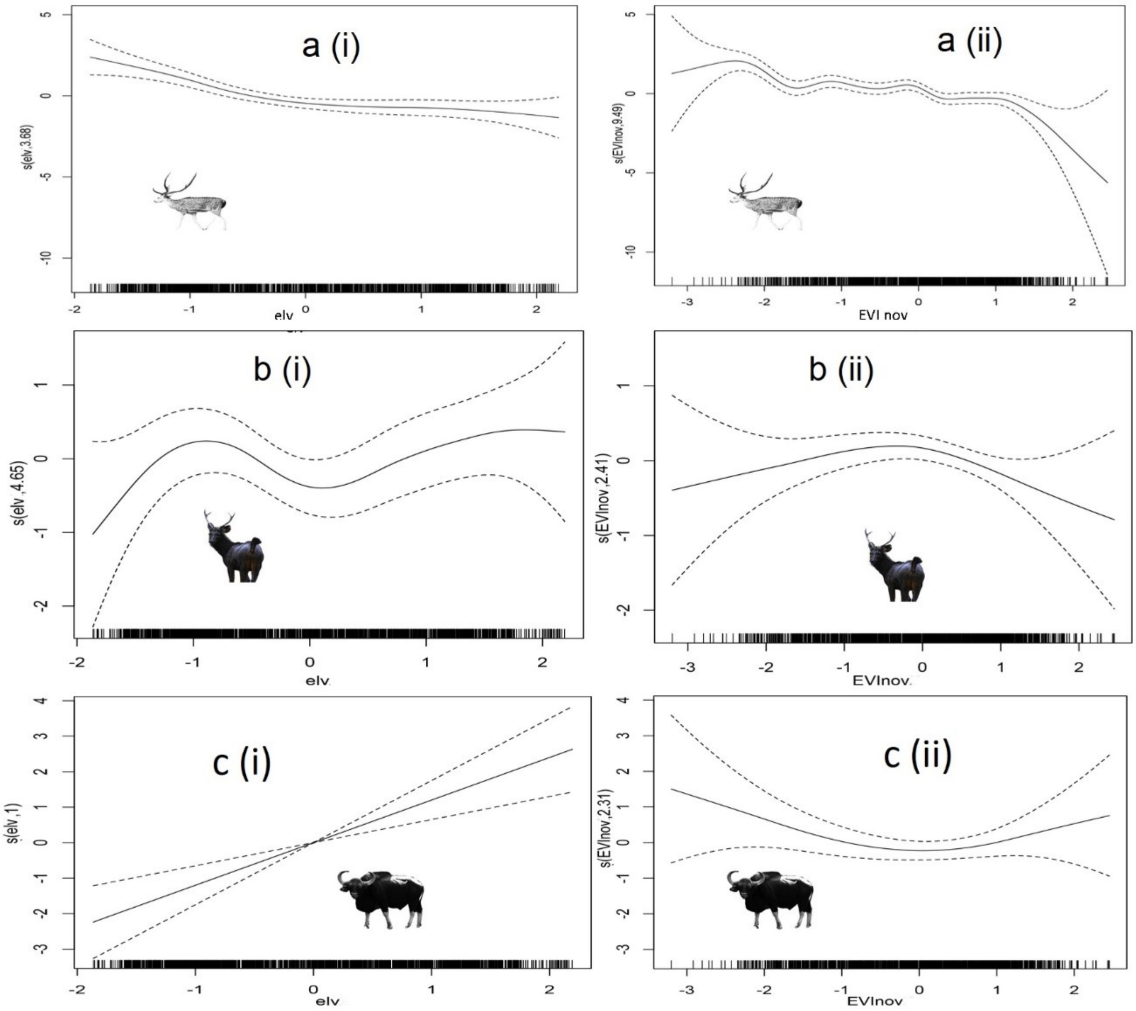


Figure 5. 3a: Shape of the functional forms of smooth spatial covariates with the DSM elevation and EVI (Enhanced Elevation Index) of ungulates in winter 2014.

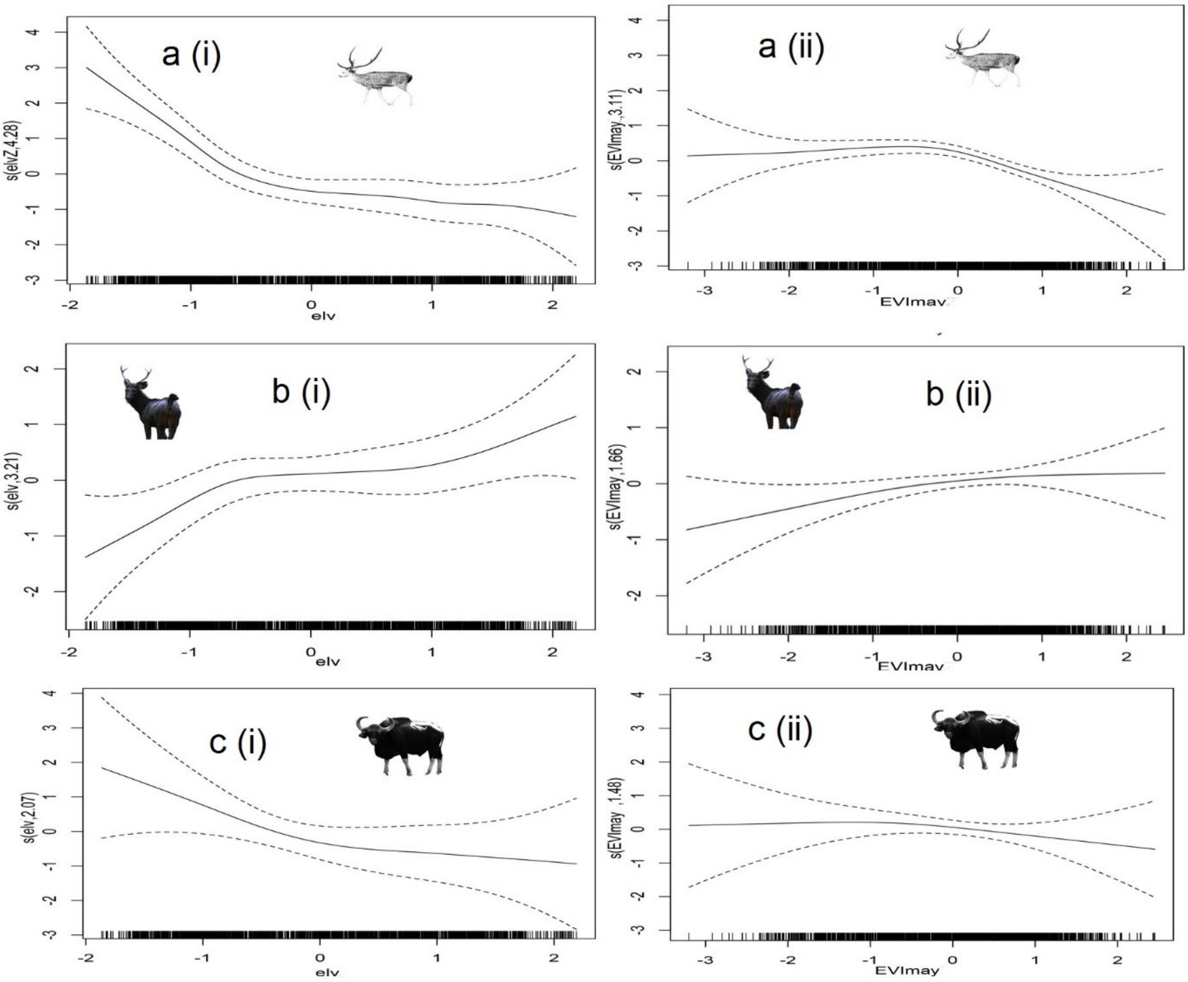
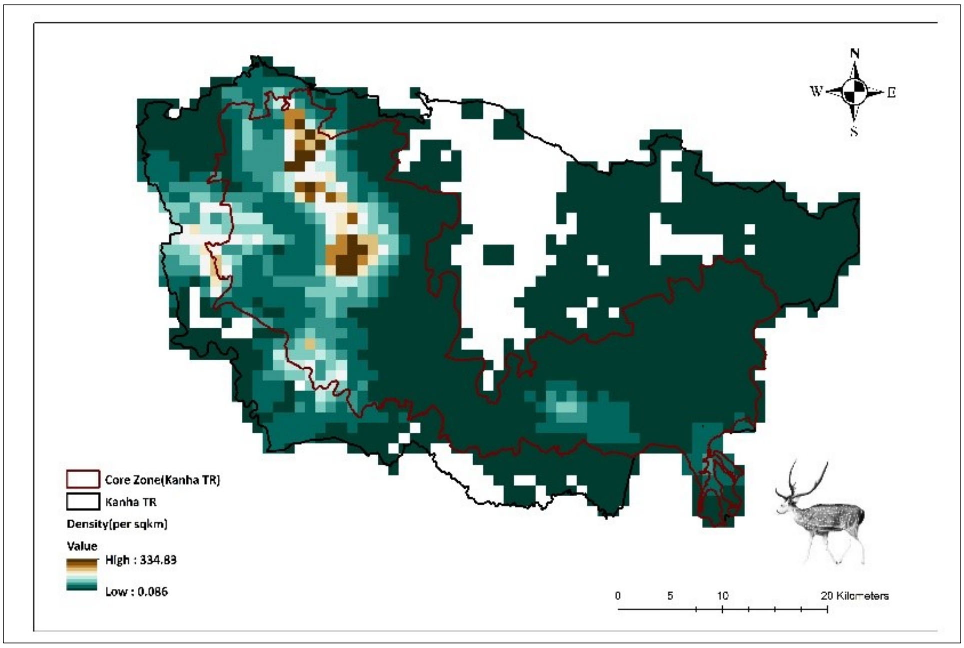


Figure 5.3b Shape of the functional forms of smooth spatial covariates with the DSM elevation and EVI (Enhanced Elevation Index) of ungulates in summer 2014.


N
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Core Zone(Kanha TR)
Kanha TR
Density(per sqkm)
Value
High : 334.83
Low : 0.086
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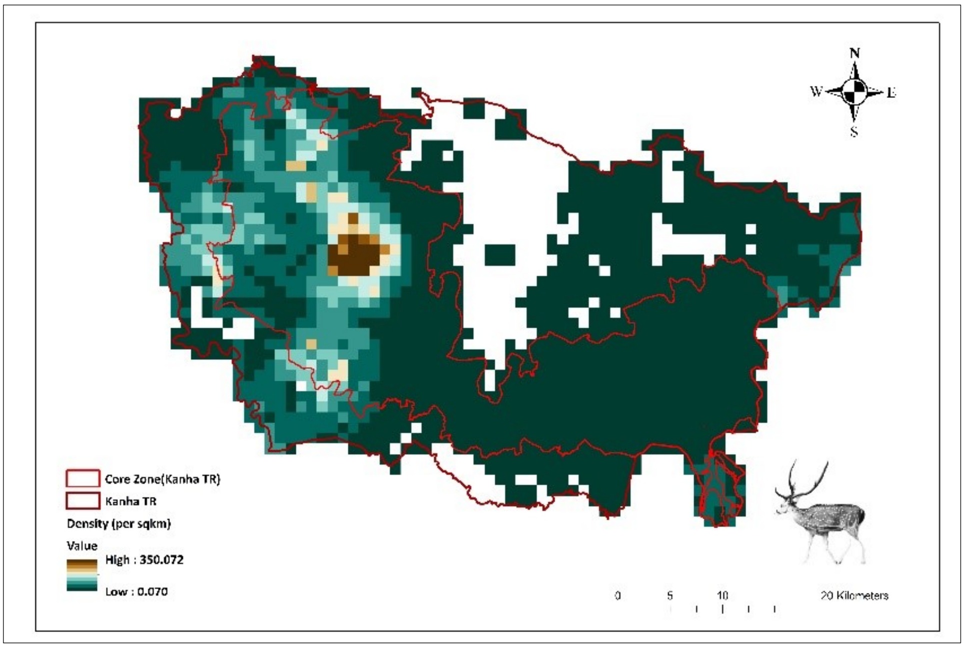
5.4 a.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Kanha TR
Density (per sqkm)
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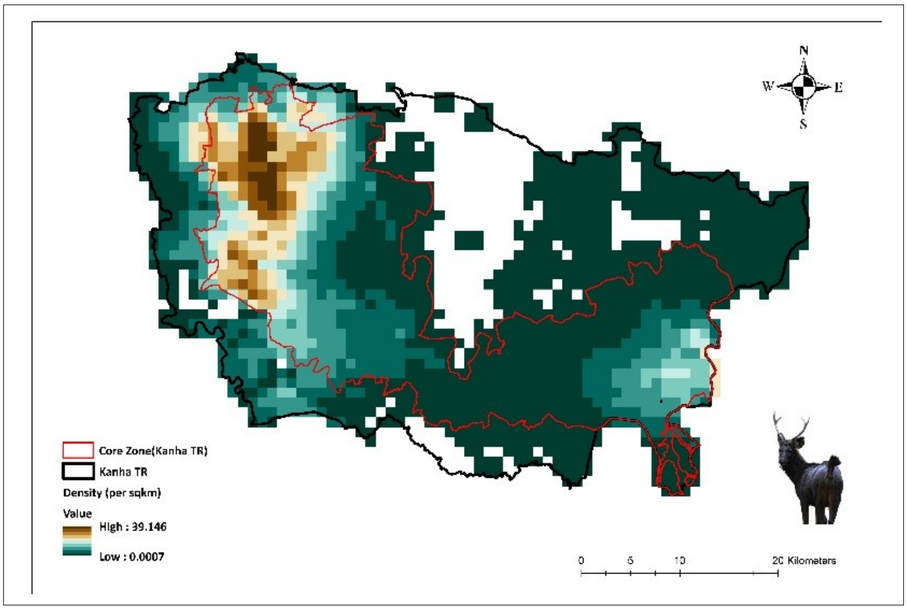
5.4 b.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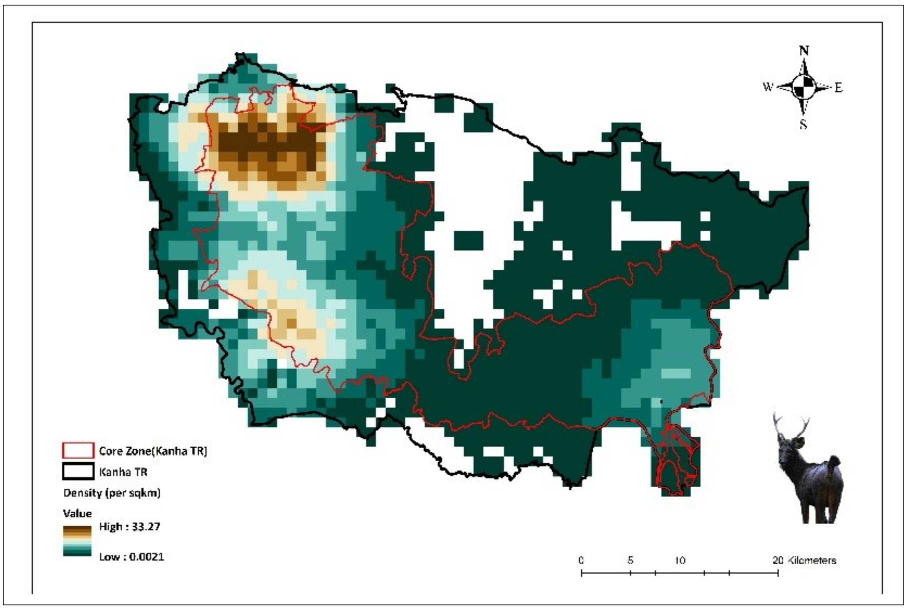
5.4 c.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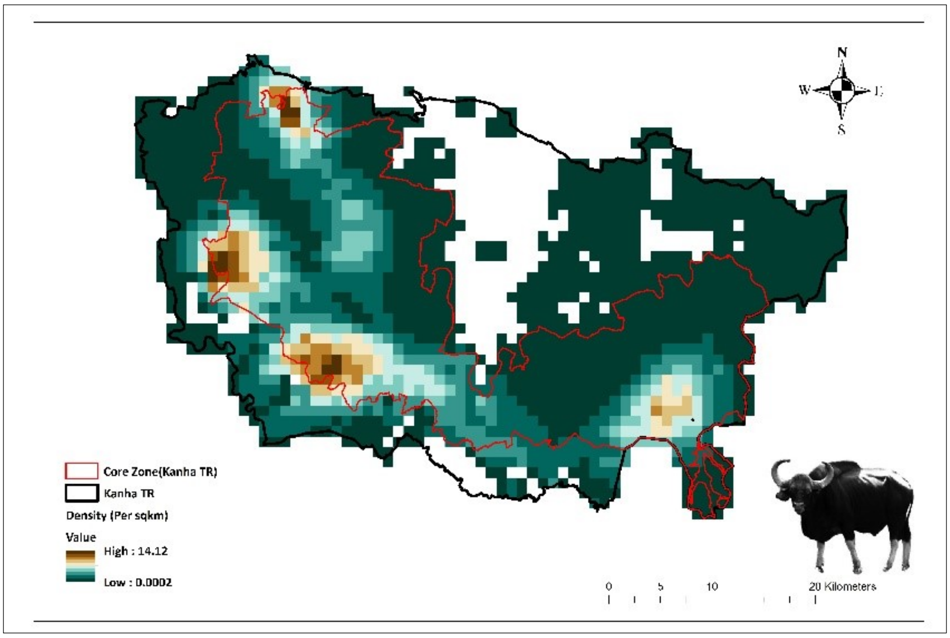
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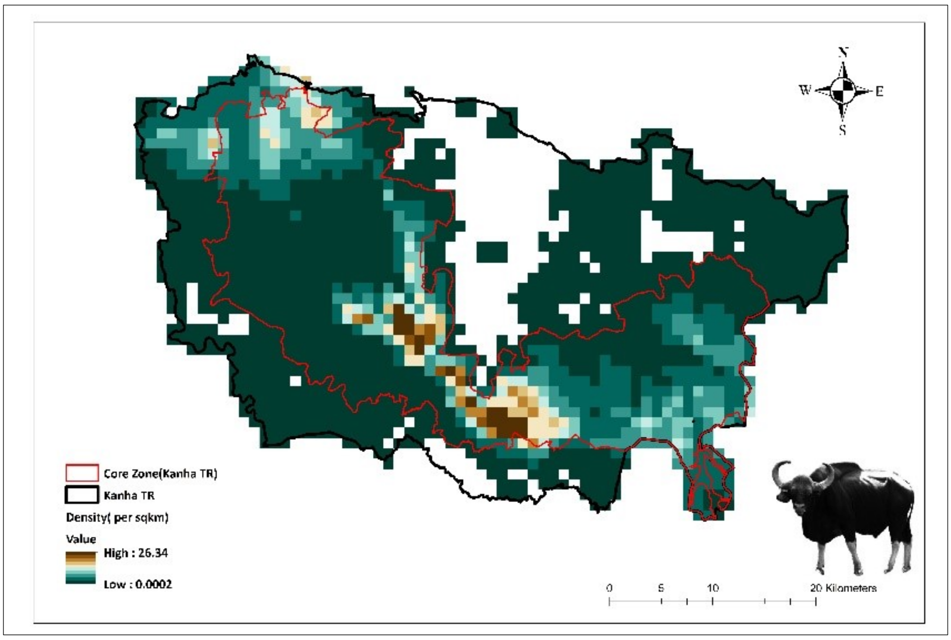
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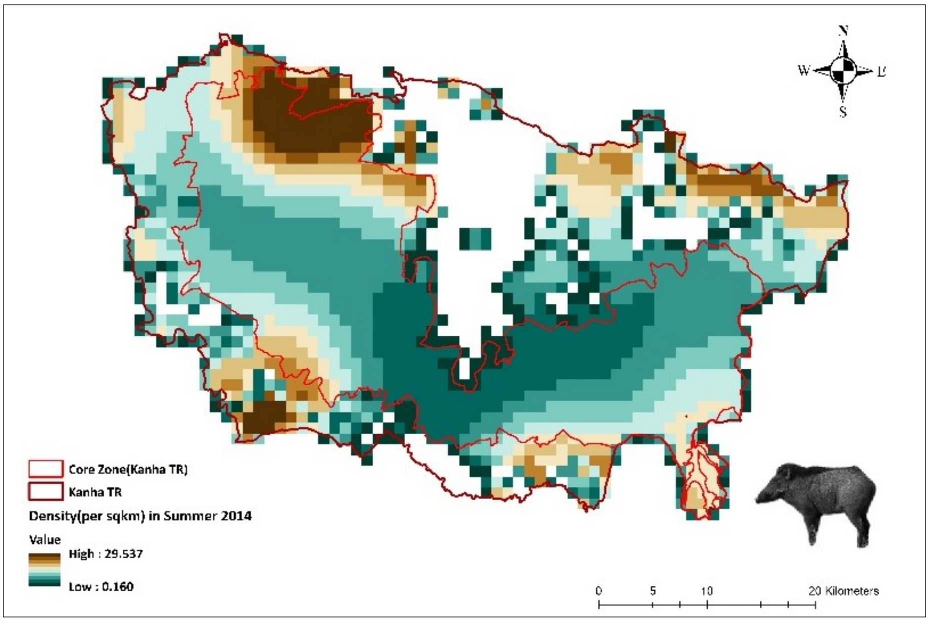
5.4 f.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Density(per sqkm) in Summer 2014
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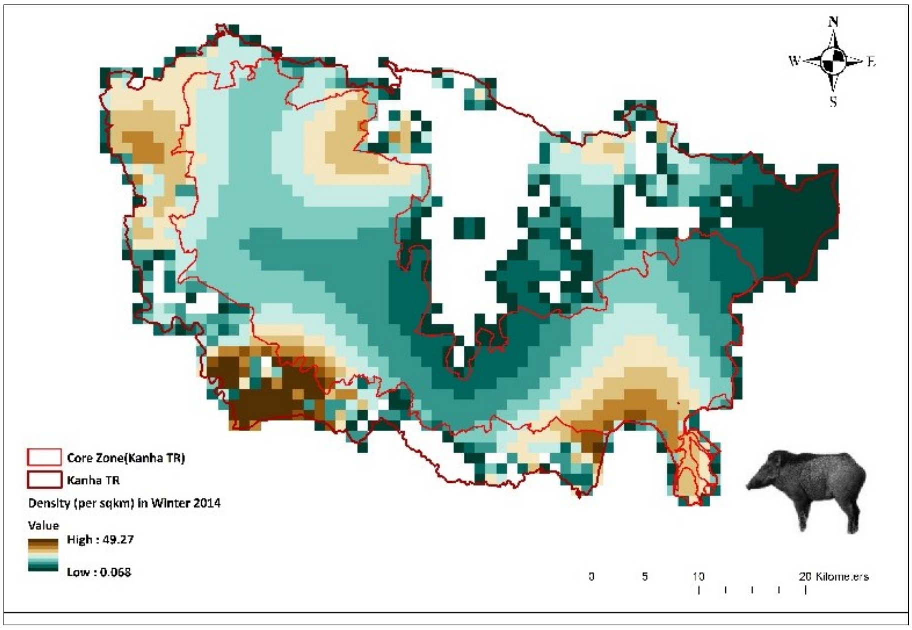
5.4 g.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Density (per sqkm) in Winter 2014
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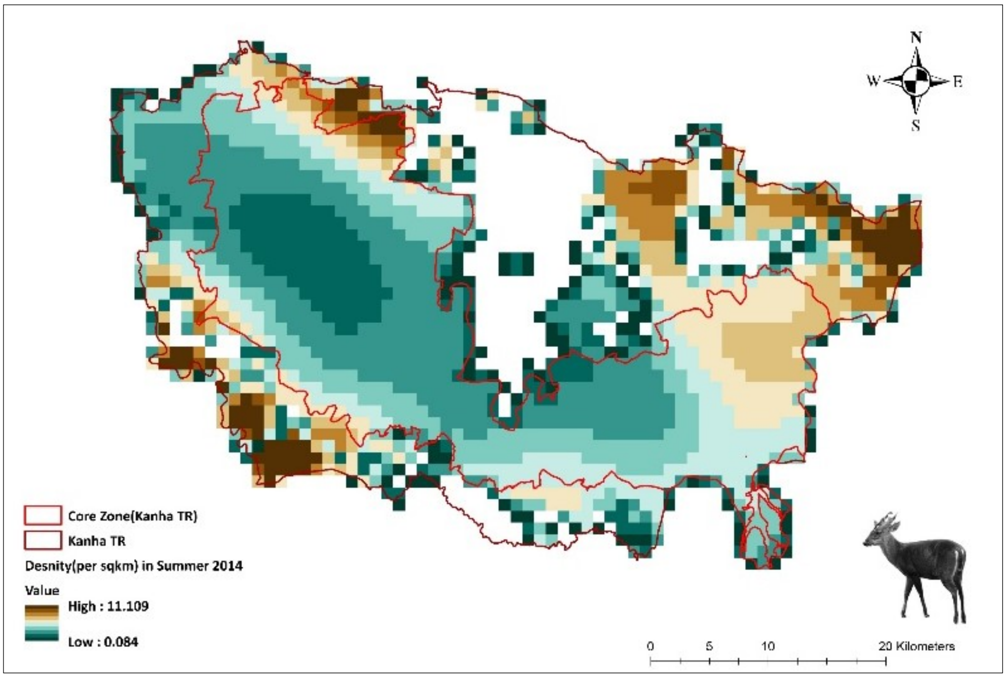
20 Kilometers

5.4 h.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Core Zone(Kanha TR)
Kanha TR
Desnity(per sqkm) in Summer 2014
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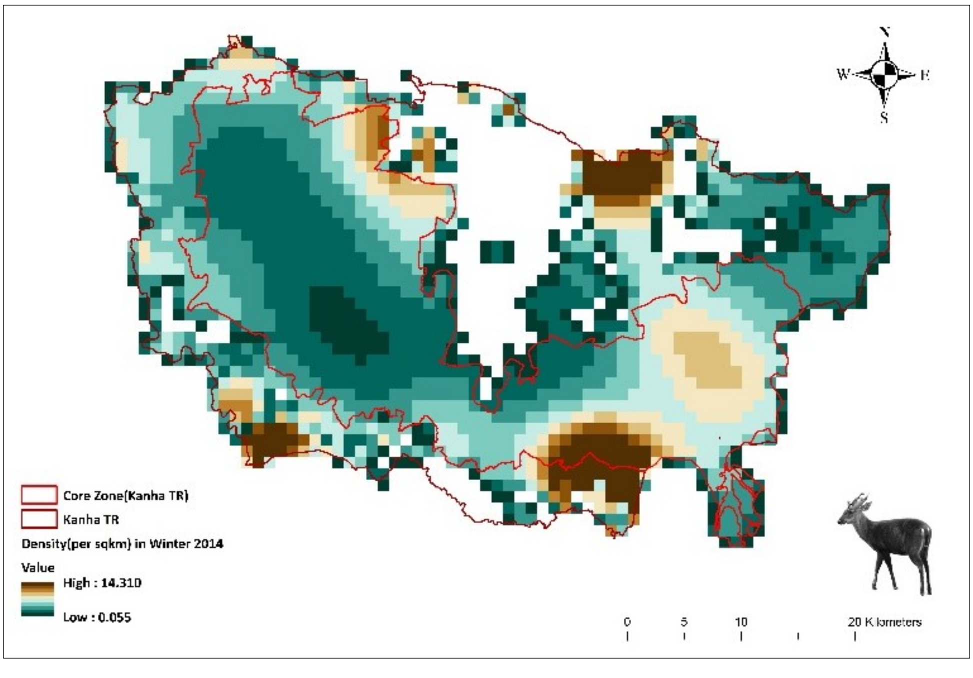
20 Kilometers

5.4 i.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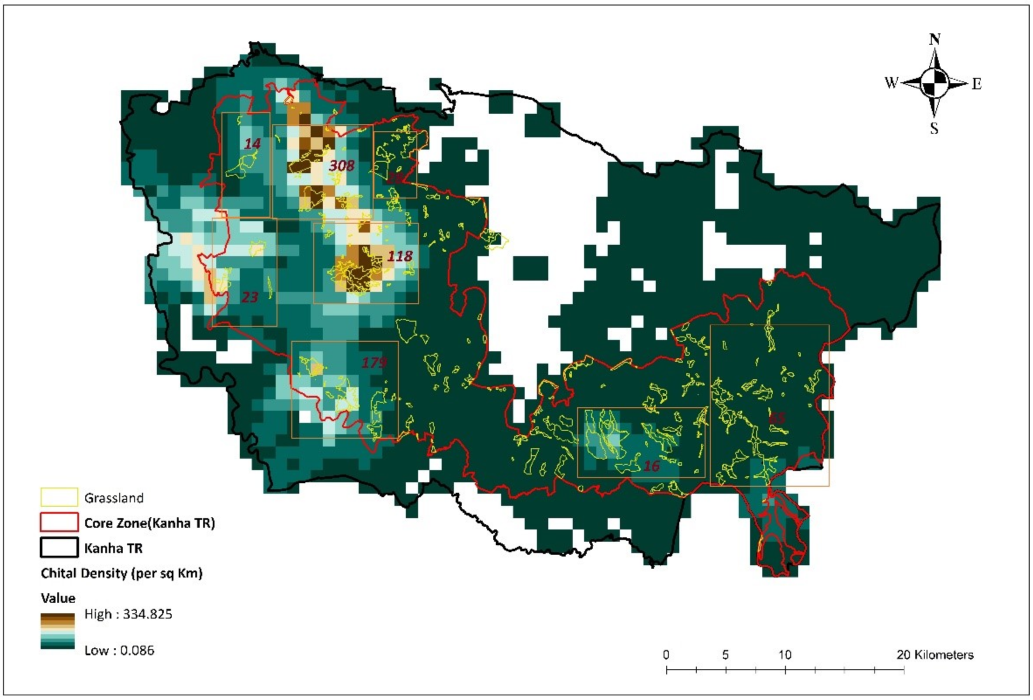
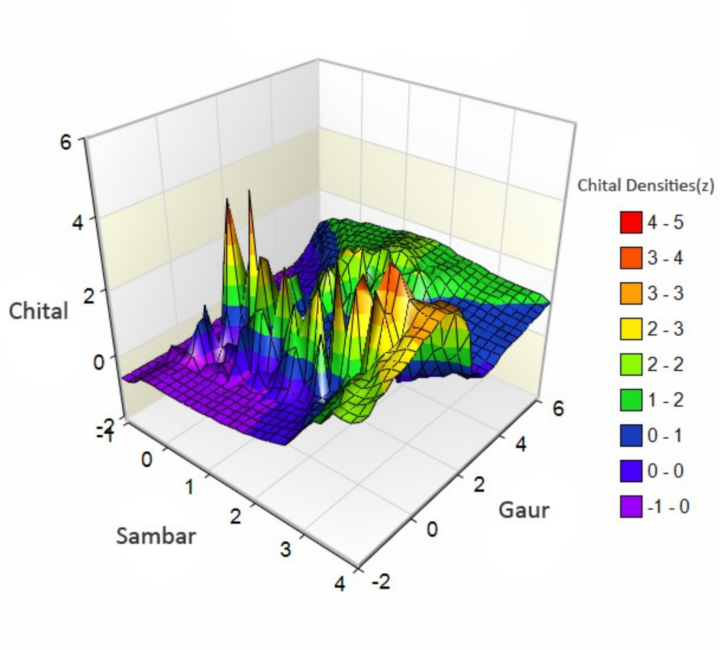
W
E
S
Core Zone(Kanha TR)
Kanha TR
Density(per sqkm) in Winter 2014
Value
High : 14.310
Low : 0.055
0
5
10
20 Kilometers

5.4 j.

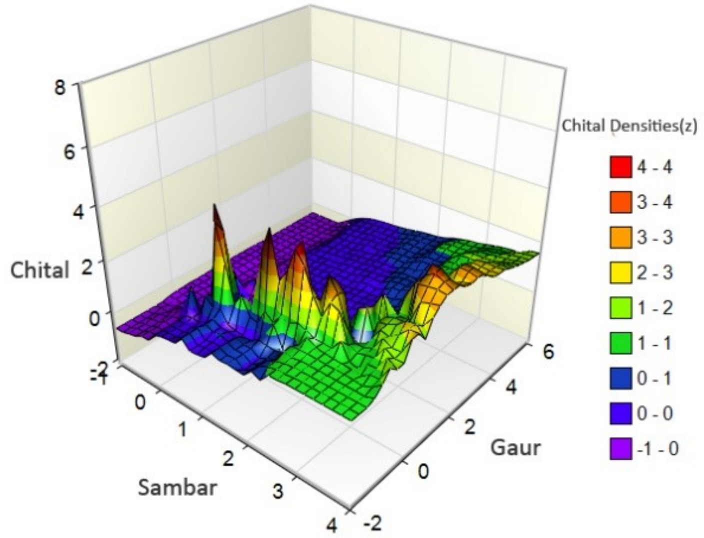


5.4 k.

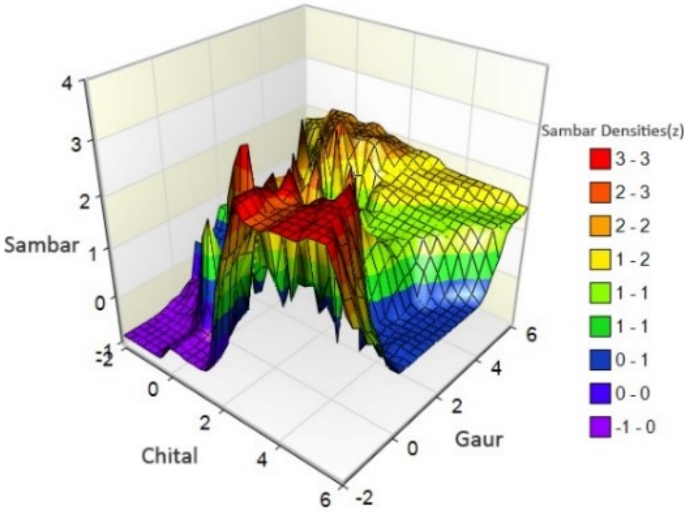
Figure 5. 4 a-k Density surface maps of a) chital summer, b) chital winter, c) sambar summer, d) sambar winter, e) gaur summer, f) gaur winter, g) wild pig summer, h) wild pig winter, i) barking deer summer, j) barking deer winter and k) barasingha group size in grassland polygons (high chital density area) in summer and winter season of 2014 in Kanha Tiger Reserve. Maps for the 2074 km^2 prediction area were constructed according to the corresponding best fit Density Surface models (DSMs).


6
4
2
0
-2
Chital
-1
0
1
2
3
4
Sambar
-2
0
2
4
6
Gaur
Chital Densities(z)
4 - 5
3 - 4
3 - 3
2 - 3
2 - 2
1 - 2
0 - 1
0 - 0
-1 - 0

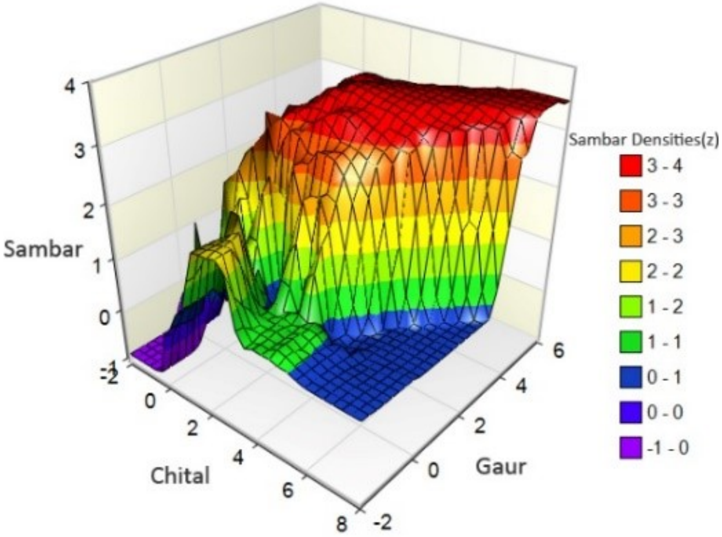
5.5 a.


8
6
4
2
0
-2
Chital
-1
0
1
2
3
4
Sambar
-2
0
2
4
6
Gaur
Chital Densities(z)
4 - 4
3 - 4
3 - 3
2 - 3
1 - 2
1 - 1
0 - 1
0 - 0
-1 - 0

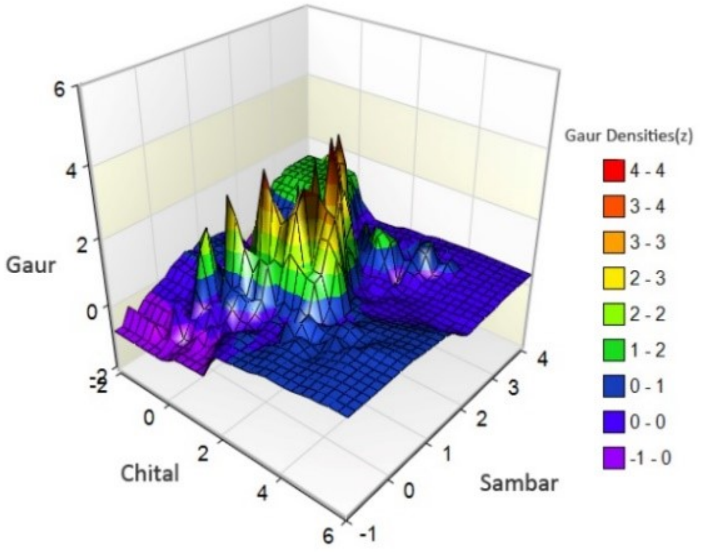
5.5 b.


Sambar
4
3
2
1
0
-1
-2
0
2
4
6
Chital
-2
0
2
4
6
Gaur
Sambar Densities(z)
3 - 3
2 - 3
2 - 2
1 - 2
1 - 1
1 - 1
0 - 1
0 - 0
-1 - 0

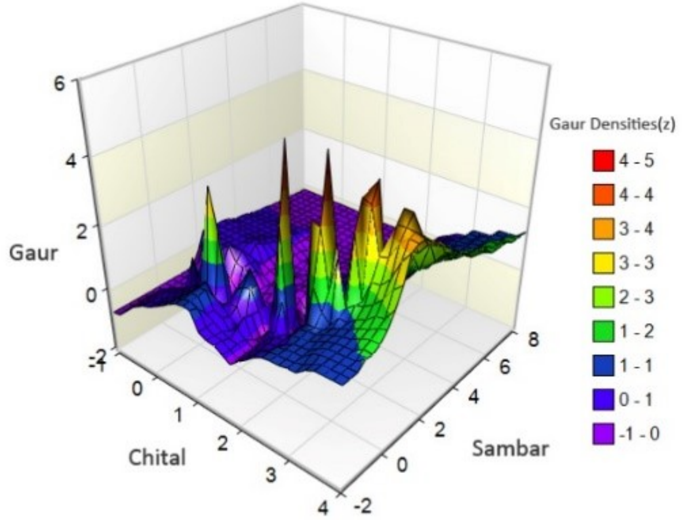
5.5 c.


Sambar
4
3
2
1
0
-1
-2
0
2
4
6
8
Chital
-2
0
2
4
6
Gaur
Sambar Densities(z)
3 - 4
3 - 3
2 - 3
2 - 2
1 - 2
1 - 1
0 - 1
0 - 0
-1 - 0

5.5 d.



5.5 e.



5.5 f.

Figure 5. 5 a-f: Surface plots (3D) showing chital, sambar and gaur co-occurrence pattern in summer and winter season (2014) in Kanha National park. Chital densities against sambar and gaur in summer and winter (a-b); Sambar densities against chital and gaur in summer and winter (c-d) and Gaur densities against chital and sambar in summer and winter (e-f).

3.2 Temporal activity pattern: All ungulates showed bimodal activity patterns; however, some were more pronounced than others **(Figure 5.6).** Gaur and sambar were nocturnal with crepuscular peaks of activity. While chital, barasingha, barking deer and wild pigs were more diurnal again with crepuscular peaks. Chital had equi-modal activity peaks after sunrise and before sunset **(Figure 5.6).**

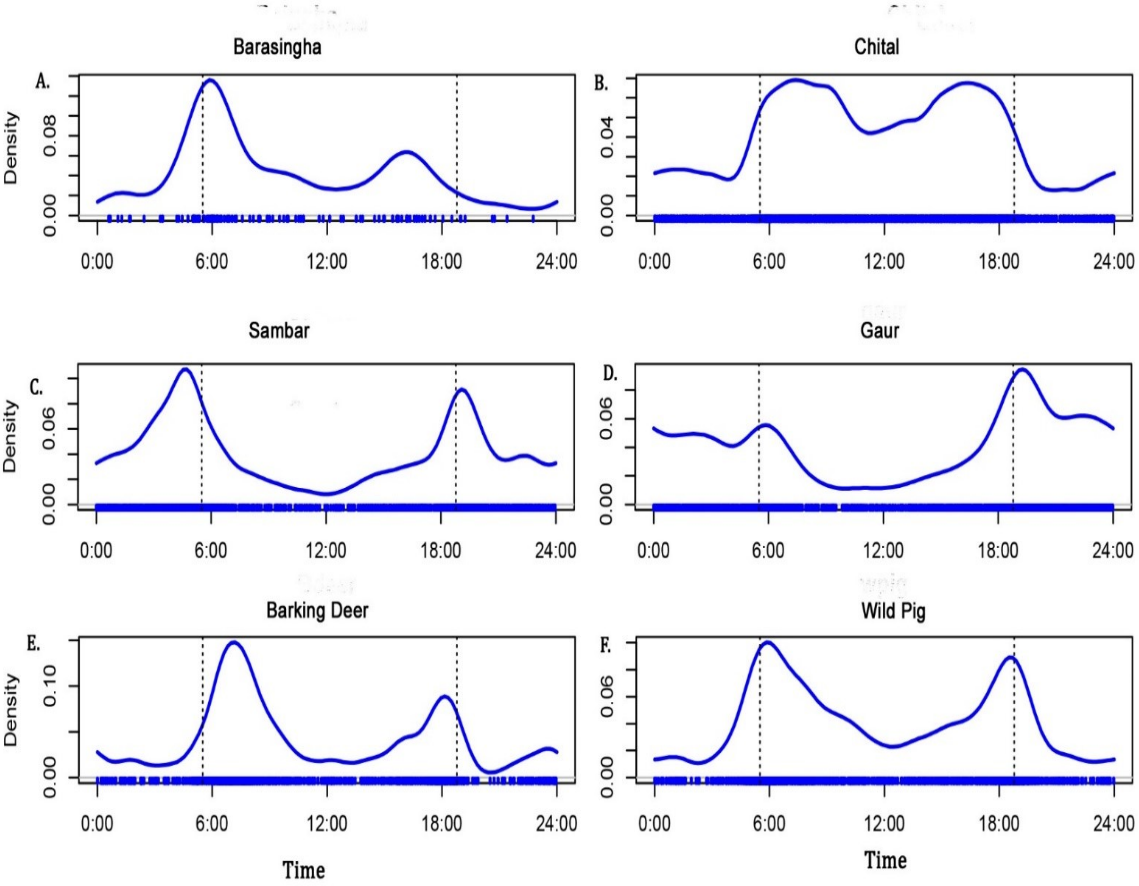


Figure 5. 6 Temporal activity pattern of ungulates in Kanha National Park in 2014.

3.3 Food Partitioning:

3.3.1. Food habits of chital, sambar and gaur in summer and winter season of Kanha National Park

Chital, sambar and gaur ate a total of 62 different food items including various species of grasses, forbs, dicotyledonous herbs, leaves and fruits of the tree in each season throughout in the year 2018 **(Appendix 3).** Chital were seen feeding on 50 plant species while sambar and gaur fed on 14 and 36 plant species, respectively **(Appendix 3).** The comparative account of the sampling effort invested in estimating seasonal food habits of chital, sambar and gaur for the different habitat type is given in **Table 5.1.**

a. **Winter:**

Chital was observed to forage chiefly on grasses compared to browse items. Desmotachya species and Chloris species contributed predominantly to the winter diet of chital, whereas sambar and gaur diets were composed mainly of browse during the same season. Chital in Kanha National Park relied primarily on the grasslands for obtaining food while sambar forage more in bamboo-mixed and miscellaneous habitat and gaur forage exclusively in the miscellaneous forest **(Figure 5.8).** It is well reflected in food habitat study too. The maximum number of food items (21) obtained by chital was from grassland compared to sal forest (10), bamboo-mixed (9) and miscellaneous habitat (18). The maximum dry biomass contribution to chital diet was from grassland **(Table 5.4a; Figure 5.7, 5.8).**

Similarly, like chital, the number of food items were obtained almost equally by sambar from different habitats, i.e. sal (6), bamboo-mixed (4) and miscellaneous habitat (4). In contrast, for gaur, maximum food items were obtained from miscellaneous habitat (17). The maximum dry biomass of sambar diets was from bamboo-mixed habitat while for gaur is from miscellaneous habitat **(Table 5.4 b, c; Figure 5.7, 5.8).** The sal forest contributes little to total biomass consumption by any of these animals. Gaur and sambar totally avoided grassland in the winter season. Among all consumed food items by chital, whole plant of Desmotachya bipinnata (47.70%) followed by grass leaves of Chloris barbata contributed 7.99% to the dry biomass of winter diet. Dendrocalamus strictus was the major food item of sambar and gaur, contributing 53.37% and 50.23% to the winter diets of sambar and gaur, respectively. Hence, during winter, chital was observed to be a grazer more than a browser while sambar and gaur were browsers **(Table 5.4 a, b, c; Figure 5.7).**

Table 5. 4 a Computation of chital food habits in winter season (2018) of Kanha Tiger Reserve.

Food item (species)	Grassland (A)	Sal (B)	Bamboo-mixed (C)	Miscellaneous (D)	% bite in diet (E)	Dry wt per bite (F)	Dry wt in 100 bites (G)	% dry wt in diet (H)
Desmotachya	19.62	0.34	0.51	0.39	20.86	3.97	82.76	47.70
Chloris	1.77	5.47	2.42	1.54	11.20	1.24	13.86	7.99
Dendrocalamus	0.00	0.57	9.71	1.01	11.29	0.89	10.08	5.81
Madhuca	1.24	0.44	0.63	1.29	3.61	2.63	9.49	5.47
Terminalia	1.65	0.00	1.71	0.61	3.97	2.28	9.07	5.22
Diaspyros	0.35	0.13	0.00	0.86	1.34	6.27	8.40	4.84
Bothrichlora	4.52	0.00	0.37	0.00	4.88	1.39	6.79	3.91
Themeda	0.00	0.78	0.28	0.27	1.33	4.51	5.98	3.45
Heteropogon	1.23	0.00	0.00	2.23	3.45	1.53	5.28	3.04
Others (< 3%)	30.57	3.14	1.44	2.92	38.06	22.10	21.81	12.57

A = Percentage of bites of a food item in the grassland multiplied by proportional grazing activity in grassland for that season.
B= Percentage of bites of a food item in the sal habitat multiplied by proportional grazing activity in sal habitat for that season.
C= Percentage of bites of a food item in the bamboo-mixed habitat multiplied by proportional grazing activity in bamboo-mixed for that season.
D= Percentage of bites of a food item in the miscellaneous habitat multiplied by proportional grazing activity in miscellaneous for that season.
E= the sum of A+B+C (percentage of bites in the actual diet).
F= dry weight of single bite of that particular food item
G= contribution by dry weight of food items in 100 bites (E X F = G)
H= percentage contribution in dry weight to the actual diet [$G(\sum G)^{-1}$] X 100

Table 5.4 b Computation of sambar food habits in winter season (2018) of Kanha Tiger Reserve.

Food item	Grassland (A)	Sal (B)	Bamboo-mixed (C)	Miscellaneous (D)	% bite in diet (E)	Dry wt per bite (F)	Dry wt in 100 bites (G)	% dry wt in diet (H)
Dendrocalamus	0.00	0.22	53.65	5.24	60.96	2.50	152.41	53.37
Lantana	0.00	6.06	0.00	19.45	26.31	3.50	92.08	32.25
Mallotus	0.00	0.73	0.00	4.67	5.57	3.70	20.61	7.22
Chloris spp.	0.00	0.00	2.37	0.00	2.44	3.98	9.73	3.41
Others (>3%)	0.00	0.65	2.78	1.14	4.71	9.63	10.73	3.76

A = Percentage of bites of a food item in the grassland multiplied by proportional grazing activity in grassland for that season.

B= Percentage of bites of a food item in the sal habitat multiplied by proportional grazing activity in sal habitat for that season.

C= Percentage of bites of a food item in the bamboo-mixed habitat multiplied by proportional grazing activity in bamboo-mixed for that season.

D= Percentage of bites of a food item in the miscellaneous habitat multiplied by proportional grazing activity in miscellaneous for that season.

E= the sum of A+B+C (percentage of bites in the actual diet).

F= dry weight of single bite of that particular food item

G= contribution by dry weight of food items in 100 bites (E X F = G)

H= percentage contribution in dry weight to the actual diet [$G(\sum G)^{-1}$] X 100

Table 5.4c Computation of gaur food habits in winter season (2018) of Kanha Tiger Reserve.

Food item	Grassland (A)	Sal (B)	Bamboo-mixed (C)	Miscellaneous (D)	% bite in diet (E)	Dry wt per bite (F)	Dry wt in 100 bites (G)	% dry wt in diet (H)
Dendrocalamus	0.00	0.00	6.23	16.43	22.66	16.43	372.27	50.23
Phoenix	0.00	0.00	0.00	9.12	9.12	9.12	83.15	11.22
Lantana	0.00	4.46	0.00	5.89	10.35	5.89	60.94	8.22
Zizyphus	0.00	0.00	0.00	6.49	6.49	6.49	42.12	5.68
Mallotus	0.00	0.65	0.00	5.31	5.96	5.31	31.66	4.27
Bauhinia spp	0.00	0.00	0.00	4.93	4.93	4.93	24.30	3.28
Grewia	0.00	0.00	0.00	4.82	4.82	4.82	23.23	3.13
Desmotachya	0.00	0.00	0.00	4.55	4.55	4.55	20.68	2.79
Others (<3%)	0.00	0.00	0.75	30.78	31.52	28.81	82.75	11.17

A= Percentage of bites of a food item in the grassland multiplied by proportional grazing activity in grassland for that season.
B= Percentage of bites of a food item in the sal habitat multiplied by proportional grazing activity in sal habitat for that season.
C= Percentage of bites of a food item in the bamboo-mixed habitat multiplied by proportional grazing activity in bamboo-mixed for that season.
D= Percentage of bites of a food item in the miscellaneous habitat multiplied by proportional grazing activity in miscellaneous for that season.
E= the sum of A+B+C (percentage of bites in the actual diet).
F= dry weight of single bite of that particular food item
G= contribution by dry weight of food items in 100 bites (E X F = G)
H= percentage contribution in dry weight to the actual diet [$G(\sum G)^{-1}$] X 100.

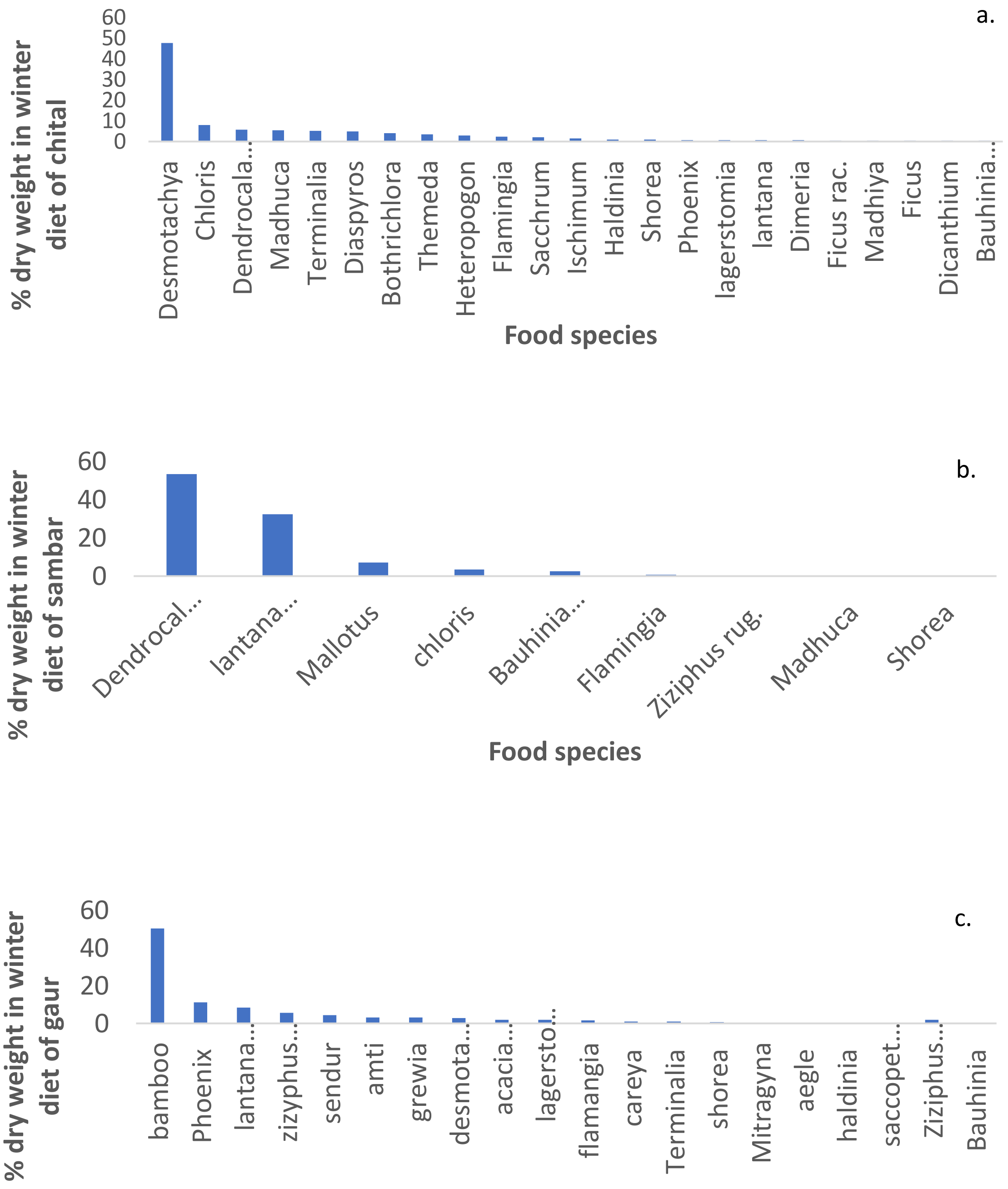
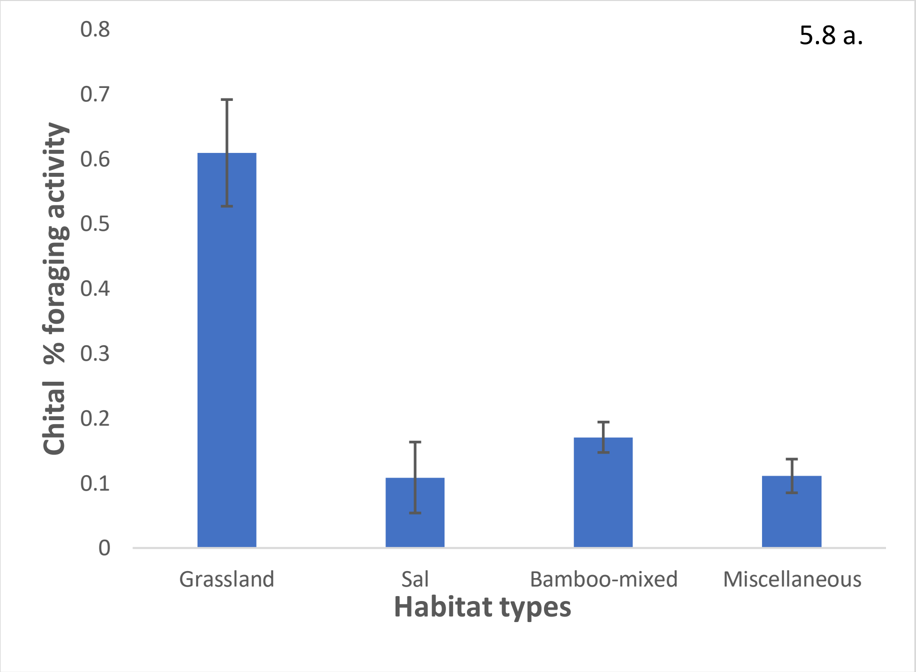
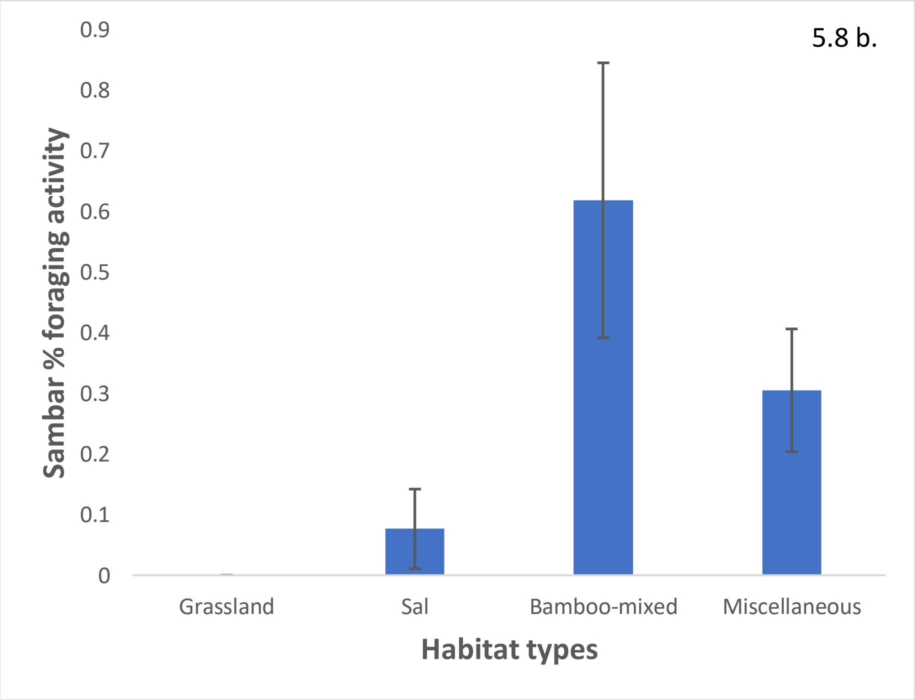


Figure 5. 7 a-c: Percentage dry biomass contribution of major food species to winter diet of ungulates in Kanha National Park.


5.8 a.
Chital % foraging activity
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Grassland
Sal
Bamboo-mixed
Miscellaneous
Habitat types


5.8 b.
Sambar % foraging activity
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Grassland
Sal
Bamboo-mixed
Miscellaneous
Habitat types

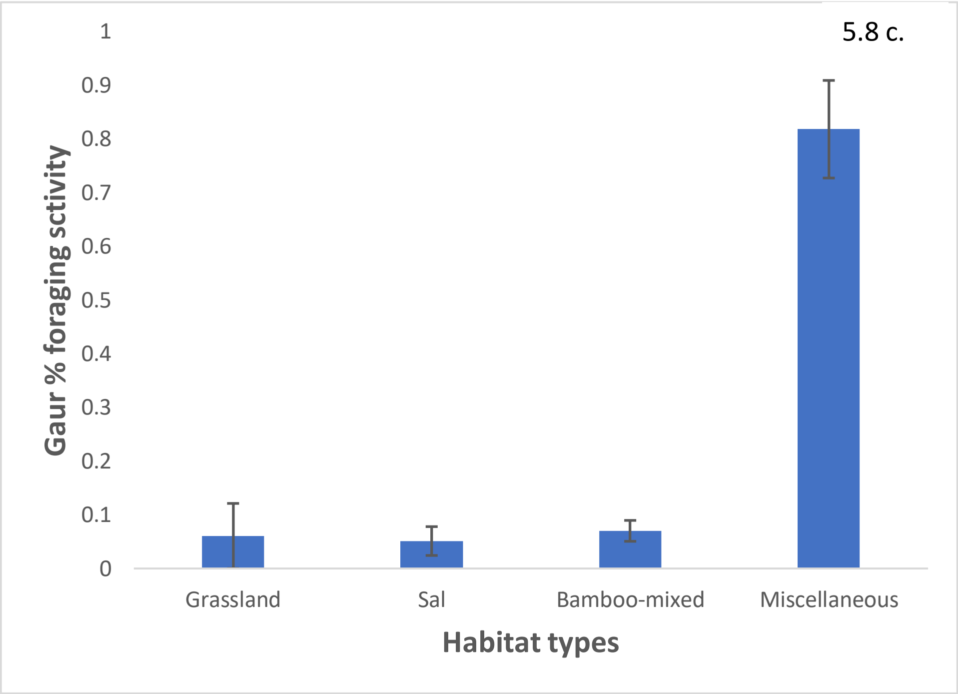


Figure 5. 8 a-c: Proportionate foraging activity of ungulates in different habitats in winter season.

b. Summer:

During summer, chital and gaur diet was largely constituted by mixed of grass and browse items, therefore were observed to be an intermediate feeder and sambar, a browser. However, chital were observed foraging maximum in the grassland habitat during summer similarly as winter season **(Figure 5.10).** The maximum number of food items obtained by chital and gaur was almost equally from habitats such as grassland (11 and 11) and miscellaneous forest (9 and 11). The maximum number of food items of sambar were obtained from almost equally from different habitats except for grassland. Chital diet was equally composed of grass and browse items, i.e. they fed largely on the grass leaves of Chloris barbata (18.08% of the total dry biomass composition of summer diet), leaves of Ischimum indicum (8.62%) along with tree leaves of Shorea robusta (7.12%) and fruits of Ficus racemosa (8.60 %). Sambar diets (dry biomass consumption) were largely contributed by leaves of Dendrocalamus strictus (45.77%) and Shorea robusta (26.73%) as they forage maximum on bamboo-mixed habitat while diets of gaur were mixed of grass and browse in summer, i.e. Dendrocalamus strictus (29.04%) Chloris barbata (10.48%), Imperata cylindrica (8.95%) and leaves of Mallotus phillipinnes (5.04%) **(Table 5.5 a, b, c; Figure 5.9)**. In summer, gaur foraging activity was relatively equal in all habitat types **(Figure 5.10).**

Table 5. 5 a Computation of chital food habits in summer season (2018) of Kanha Tiger Reserve.

Food Items (species)	Grassland (A)	Sal (B)	Bamboo-mixed (C)	Miscellaneous (D)	% Bite in diet (E)	Dry wt per bite (F)	Dry wt in 100 bites (G)	% Dry wt in diet (H)
Chloris	1.67	0.00	0.00	0.43	2.11	2.23	4.71	18.08
Ischimum	2.63	0.00	0.00	0.00	2.63	0.85	2.24	8.62
Ficus rac.	0.00	0.00	2.47	1.09	3.55	0.63	2.24	8.60
Shorea (leaves)	0.00	2.49	2.78	0.98	6.25	0.30	1.85	7.12
Dimeria	11.66	0.00	0.00	0.00	11.66	0.14	1.64	6.32
Pavetta	0.00	0.25	0.00	0.27	0.52	2.50	1.30	5.01
Desmotachya	10.19	0.00	0.00	0.00	10.19	0.13	1.29	4.94
Dicanthium	14.95	0.00	0.00	0.00	14.95	0.07	1.11	4.25
Syzygium	0.00	0.00	1.55	0.00	1.55	0.65	1.01	3.88
Penicitum	4.72	0.00	0.00	0.00	4.72	0.21	0.99	3.79
Dendrocalamus	0.00	0.00	4.78	0.67	5.45	0.17	0.95	3.66
Shorea (flowers)	0.00	9.75	0.00	0.00	9.75	0.10	0.95	3.65
Gardenia	0.00	0.00	0.00	0.11	0.11	8.10	0.88	3.38
Basin	6.58	0.00	0.00	0.00	6.58	0.13	0.84	3.22
Haldinia	0.00	0.25	0.00	0.00	0.25	3.15	0.79	3.03
Others (< 3%)	13.36	0.38	3.34	2.64	19.72	2.80	3.24	12.45

A = Percentage of bites of a food item in the grassland multiplied by proportional grazing activity in grassland for that season.
B= Percentage of bites of a food item in the sal habitat multiplied by proportional grazing activity in sal habitat for that season.
C= Percentage of bites of a food item in the bamboo-mixed habitat multiplied by proportional grazing activity in bamboo-mixed for that season.
D= Percentage of bites of a food item in the miscellaneous habitat multiplied by proportional grazing activity in miscellaneous for that season.
E= the sum of A+B+C (percentage of bites in the actual diet).
F= dry weight of single bite of that particular food item
G= contribution by dry weight of food items in 100 bites (E X F = G)
H= percentage contribution in dry weight to the actual diet [$G(\sum G)^{-1}$] X 100

Table 5.5b Computation of sambar food habits in summer season (2018) of Kanha Tiger Reserve.

Food items (species)	**Grassland (A)**	**Sal (B)**	**Bamboo-mixed (C)**	**Miscellaneous (D)**	**% bite in diet (E)**	**Dry wt per bite (F)**	**Dry wt in 100 bites (G)**	**% dry wt in diet (H)**
Dendrocalamus leaves	0.00	0.03	0.56	0.09	69.60	0.34	23.38	45.77
Shorea leaves	0.00	0.02	0.02	0.06	10.32	1.32	13.65	26.73
Pavetta	0.00	0.00	0.00	0.10	10.29	0.77	7.89	15.45
Flamingia	0.00	0.00	0.02	0.00	2.30	1.26	2.91	5.69
Bauhinia	0.00	0.00	0.04	0.00	3.77	0.56	2.11	4.14
Others (>3%)	0.00	0.04	0.00	0.00	3.71	1.50	1.13	2.21

A = Percentage of bites of a food item in the grassland multiplied by proportional grazing activity in grassland for that season.

B= Percentage of bites of a food item in the sal habitat multiplied by proportional grazing activity in sal habitat for that season.

C= Percentage of bites of a food item in the bamboo-mixed habitat multiplied by proportional grazing activity in bamboo-mixed for that season.

D= Percentage of bites of a food item in the miscellaneous habitat multiplied by proportional grazing activity in miscellaneous for that season.

E= the sum of A+B+C (percentage of bites in the actual diet).

F= dry weight of single bite of that particular food item

G= contribution by dry weight of food items in 100 bites (E X F = G)

H= percentage contribution in dry weight to the actual diet [$G(\sum G)^{-1}$] X 100

Table 5.5c Computation of gaur food habits in summer season (2018) of Kanha Tiger Reserve.

Food item	Grassland (A)	Sal (B)	Bamboo-mixed (C)	Miscellaneous (D)	% bite in diet (E)	Dry wt per bite (F)	Dry wt in 100 bites (G)	% dry wt in diet (H)
Dendrocalamus leaves	0.00	1.36	25.91	0.71	27.98	0.68	19.03	29.04
Chloris	0.43	0.00	0.00	0.94	1.37	5.00	6.86	10.48
Imperata	6.41	6.00	0.00	2.59	15.00	0.39	5.86	8.95
Mallotus	0.00	0.00	0.71	3.53	4.24	0.78	3.30	5.04
Shorea leaves (dry)	0.00	3.00	0.00	0.00	3.00	1.07	3.22	4.92
Flamangia	0.00	3.49	0.00	0.24	3.73	0.80	2.97	4.54
Desmotachya	5.37	0.00	0.00	11.78	17.15	0.17	2.95	4.50
Madhuca leaves	0.00	1.20	0.00	0.00	1.20	2.45	2.95	4.50
Shorea leaves	0.00	0.00	0.00	1.88	1.88	1.48	2.78	4.24
Diaspyros	0.00	0.00	0.00	0.47	0.47	5.50	2.59	3.95
Syzigium	0.00	0.00	0.00	0.94	0.94	2.60	2.45	3.74
Others (>3%)	17.51	4.09	0.00	1.41	23.02	12.23	10.55	16.10

A= Percentage of bites of a food item in the grassland multiplied by proportional grazing activity in grassland for that season.
B= Percentage of bites of a food item in the sal habitat multiplied by proportional grazing activity in sal habitat for that season.
C= Percentage of bites of a food item in the bamboo-mixed habitat multiplied by proportional grazing activity in bamboo-mixed for that season.
D= Percentage of bites of a food item in the miscellaneous habitat multiplied by proportional grazing activity in miscellaneous for that season.
E= the sum of A+B+C (percentage of bites in the actual diet).
F= dry weight of single bite of that particular food item
G= contribution by dry weight of food items in 100 bites (E X F = G)
H= percentage contribution in dry weight to the actual diet [$G(\sum G)^{-1}$] X 100

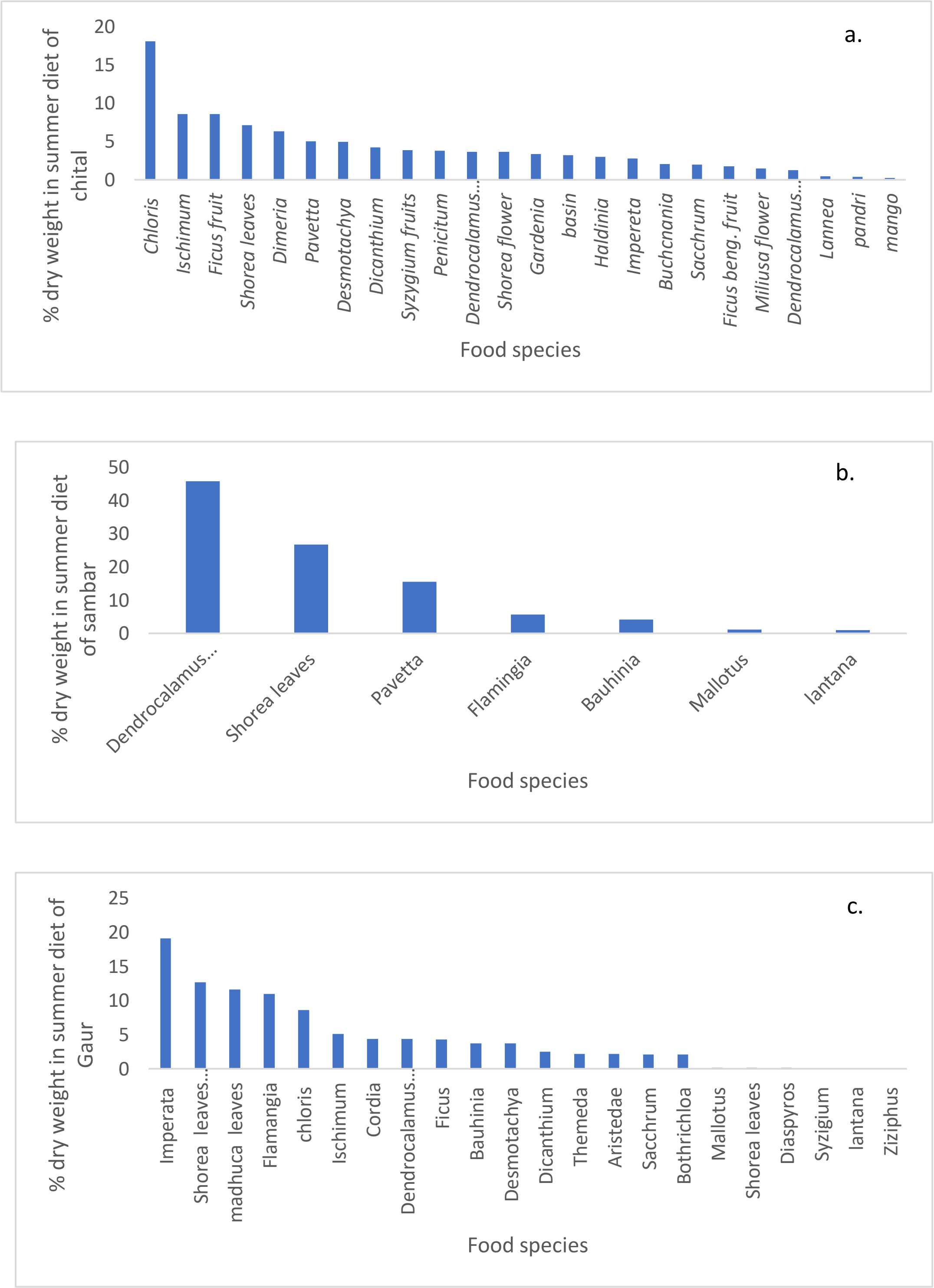
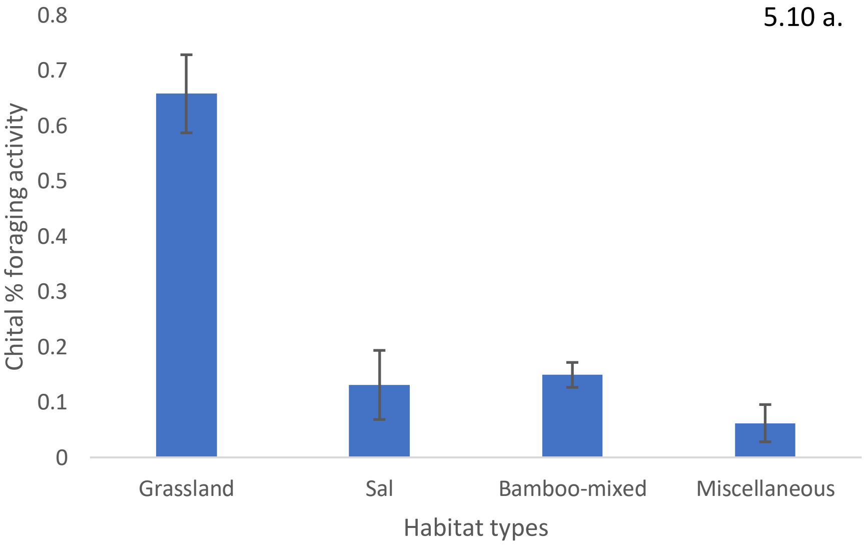
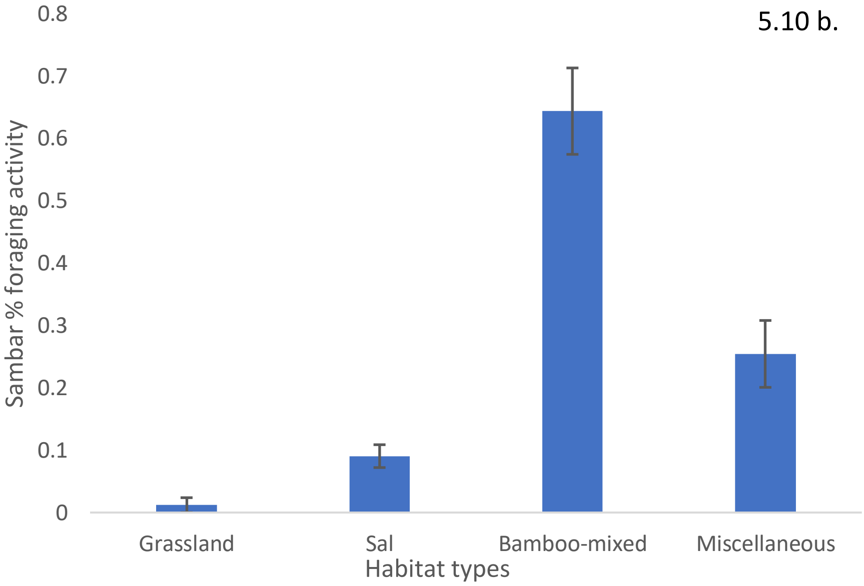


Figure 5. 9 Percentage dry biomass contribution of major food species to summer diet of ungulates in Kanha National Park



5.10 a.

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Chital % foraging activity
Grassland
Sal
Bamboo-mixed
Miscellaneous
Habitat types



5.10 b.

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Sambar % foraging activity
Grassland
Sal
Bamboo-mixed
Miscellaneous
Habitat types

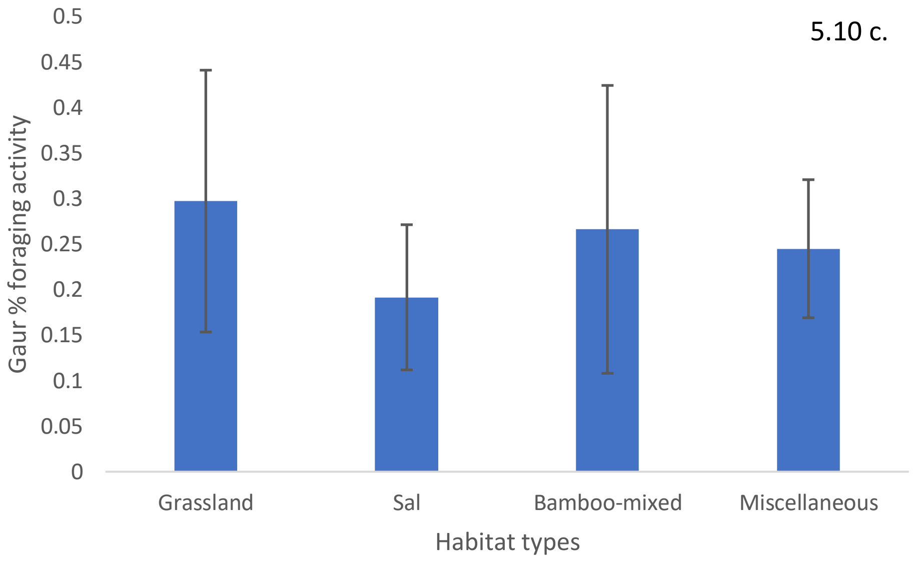


Figure 5. 10 a-c: Proportionate foraging activity of ungulates in different habitats in summer season.

3.3.2. Overall annual diet composition of chital, sambar and gaur

The overall annual diet of chital was largely composed of various grasses as grazing contributed more than 50% of the dry biomass of the major food items (which contributed more than 3% to the seasonal bite counts). In contrast, an annual diet of sambar and gaur were chiefly composed of browse items as different browse contributed 99% and 75% of the dry biomass of major food items of sambar and gaur, respectively. Chital food items mainly included leaves of Dendrocalamus strictus (26.31% of total dry biomass of chital diet), two annual grasses viz Desmotachya bipinnata (15.35%) and Chloris barbata (13.03%). Sambar and gaur chiefly included leaves of Dendrocalamus strictus (49.57% for sambar and 27.51% for gaur) to their annual diet while leaves of Shorea robusta contributed 13.38% for sambar and 6.75 % for gaur **(Table 5.6).**

Table 5. 6 Percentage contribution of major food items (>3% bite counts) to annual diet compositions of chital, sambar and gaur in Kanha Tiger Reserve in 2018.

Food items (species)	Chital	Sambar	Gaur
Dendrocalamus strictus	26.31	49.57	27.51
Shorea robusta	4.0	13.38	6.75
Desmotachya bipinnata	15.35	-	3.31
Flamangia macrophylla	-	3.27	6.24
Lantana camara	-	16.64	3.0
Mallotus phillipines	-	4.18	4.0
Chloris barbata	13.03	-	-
Ischimum indicum	5.04	-	-
Dimeria arnothopoda	3.43	-	-
Sacchrum spontaneum	1.42	-	-
Bauhinia spp	-	3.29	-
Haldinia cordifolia	2.03	-	0.19
Dicanthium coricosum	2.31	-	-
Ziziphus spp	-	-	3.0
Others (<3%)	37.70	9.78	46.75

'-'. represent plant not eaten by ungulates annually.

3.3.3. Niche breadth and Niche overlap of chital, sambar and gaur in Kanha

The diet niche breadth of sambar and gaur were relatively narrower than chital in both summer and winter **(Figure 5.11).** Chital and gaur diet niche breadth was largest during summer and narrower during winter whereas sambar diet niche breadth was relatively equal during both the season. Chital had a broader niche breadth compared to sambar and gaur, and hence chital was a more generalized feeder.

Dietary overlap between chital and gaur (46%) was maximum in summer while dietary overlap was maximum for sambar and gaur (76%) in the winter season. Whereas dietary overlap between chital and sambar was comparatively smaller **(Figure 5.12).**

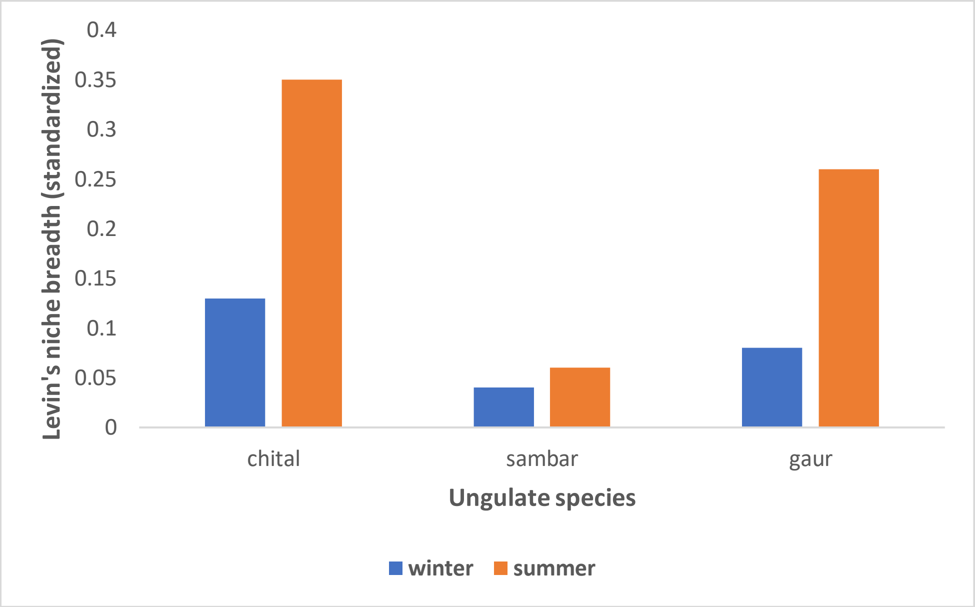


Figure 5. 11 Seasonal diet niche breadth of chital , sambar and gaur in Kanha National Park.

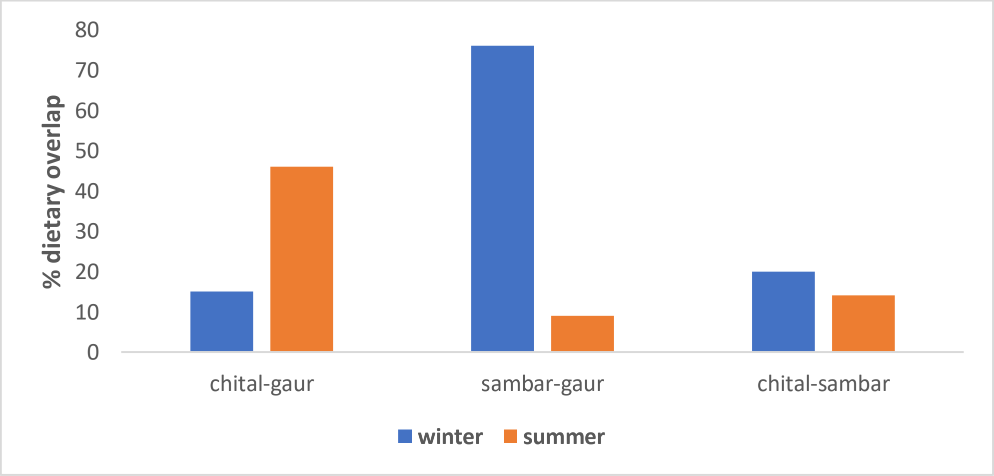


Figure 5. 12 Seasonal percentage dietary overlap among chital, sambar and gaur in Kanha National Park.

3.3.4. Habitat wise seasonal dietary overlap

During winter, maximum dietary overlap in all three combinations, i.e. chital and gaur, chital and sambar as well as sambar and gaur was observed only in the bamboo-mixed and miscellaneous forest. However, sambar and gaur overlap was highest in bamboo-mixed (94%) and miscellaneous forest (76%) in comparison to the other two combinations. During summer, which is believed to be a crucial period for resource competition between sympatric ungulates, only chital and gaur showed higher overlap in grassland (55%) and miscellaneous forest (31%) in comparison to other combinations. Maximum dietary overlap in chital and gaur had shifted from the bamboo-mixed and miscellaneous forest during winter to grassland habitat during summer **(Figure 5.13 & 5.14).**

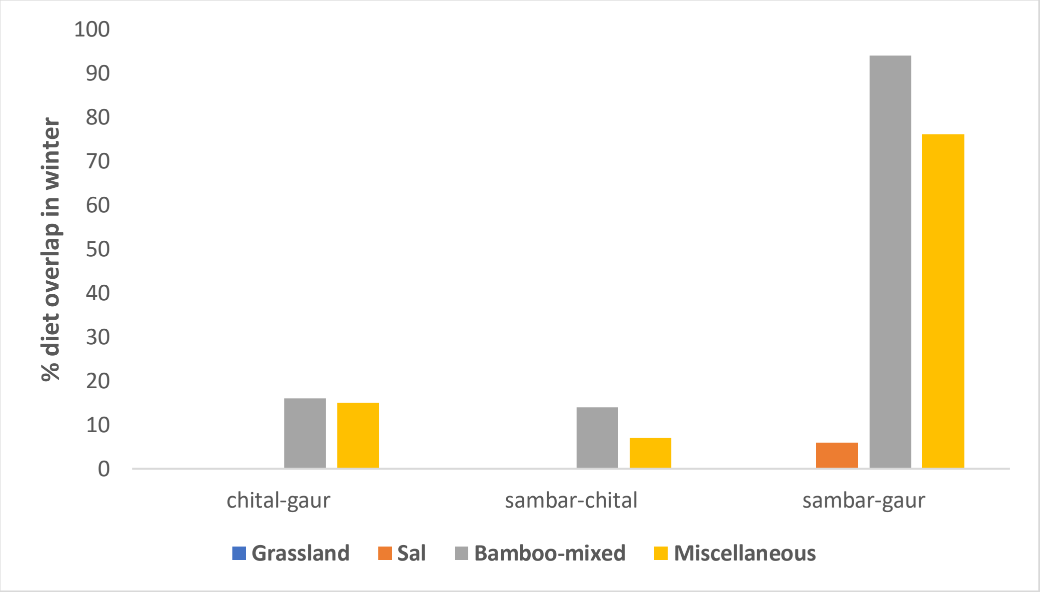


Figure 5. 13 Habitat wise diet niche overlap among chital, sambar and gaur during winter in 2018-19 in Kanha

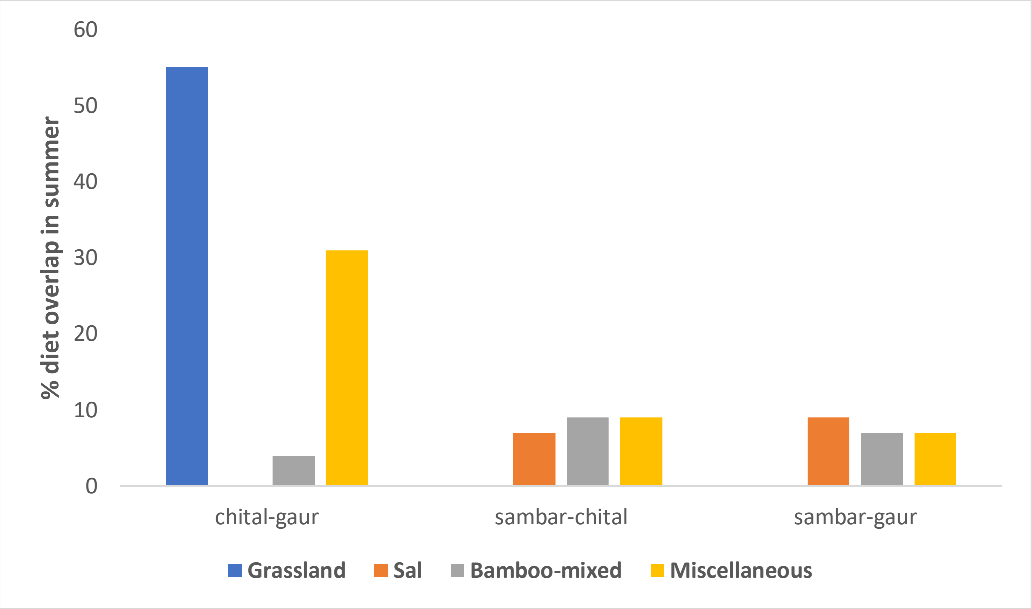


Figure 5. 14 Habitat wise diet niche overlap among chital, sambar and gaur during summer in 2018-19 in Kanha

4. Discussion

There are several potential mechanisms whereby species of similar ecologies may coexist within the same community (Putman and Putman 1996). Coexistence may involve shifts on some axes of either geographical or ecological space (where animals are located spatially), on temporal axes (when animals use their habitat) and on resource axes (which resources individuals use, i.e. food) (Namgail 2001, Kronfeld schor and Dayan 2003). The pattern of resource partitioning varied in different seasons. It can be explained by species-specific differences in mouth morphology, feeding style (selective vs non-selective) and digestive systems (Voeten and Prins 1999). Many of the ungulate species within any given assembly have very similar feeding styles and foraging habit, grouped into the proper functional guild of grazer, browser or intermediate feeders (Hoffmann 1973, 1985).

4.1. Spatial and temporal habitat use

Density surface modelling with GAMs employs model-based inference for abundance and density estimation. With DSM, abundance is related to spatial covariates, and the distribution of the species was visually depicted. The inferred relationship between spatial covariates and population density provide insights on meaningful ecological information to wildlife managers and ecologists. DSM allowed us to assess population ecological requirements through the predicted species distribution. Chital had higher densities in low elevation and less forested areas in both seasons throughout the year. Sambar densities were higher in forested habitat with moderate elevation areas, generally rugged terrains between valleys and plateaus. Gaur densities were higher in high elevation areas, mostly found in flat-topped plateaus in winter but densities in summer were primarily found in valleys. Gaur densities were higher in forested areas in winter; however, in summer, they are distributed in all habitats.

Chital, sambar and gaur are species whose ranges in the Kanha overlap extensively, contradicted our a priori predictions that spatial segregation would occur between sympatric ungulates in both summer and winter. Gaur and sambar co-occur at high densities in areas where chital utilization is low. Although the increased spatial overlap between sambar and gaur may have increased the potential for interference competition, the species maintained a high degree of spatial segregation through differences in the seasonal use of habitat.

A degree of temporal separation occurs between chital with sambar and gaur. Since both sambar and gaur exhibit nocturnal activity, hence, there was a high temporal overlap between them. While chital and other ungulates were diurnal. Diurnal and nocturnal habits of ungulates were based on their use of habitat and terrain for feeding and other different movement activities.

4.2 Foraging habitat use

Feeding strategies are the medium through which species are ecologically separated (Schoener 1971). The species differ in their selectivity for foraging habitats in different seasons of Kanha. Chital and sambar were almost always selective, especially for grassland and bamboo-mixed habitat respectively in both the season, as nearly the half of the population of chital and sambar occupied just one habitat type. By contrast, gaur showed high selectivity for only miscellaneous habitat in the winter season, while associating randomly with different habitats in the summer season. Gaur avoids grasslands preferred by chital in winter, which in turn avoid dry savanna areas used by gaur on plateaus. Gaur may be restricted to their ultimate winter season habitat by the quantity of available fodder as much as by quality. The overlap is higher in summer season in compare to winter, when all three ungulates use habitats low on the valleys to fulfill their water and food requirements. Gaur showed preferences for different regions in different seasons. Gaur appears to follow local cyclic migration from the plateau to valleys synchronized with seasonal vegetation pattern, foraging in dry plateaus during winter and foraging in moist deciduous and riverine areas of valleys during summer.

4.3 Food habits

The overall feeding strategy depends upon animals switching habitats, plant species and plant parts in an attempt to delay an inevitable seasonal decline in the food quality (Sinclair and Norton Griffiths 1979). Chital chose for feeding not only the plant community but also the plant species and the plant parts. In the winter season, chital preferred more grass than browse species. Furthermore, feeding observations of chital in summer season showed that browse from shrubs and trees was eaten more frequently in the dry season of summer when there is less rainfall observed, even though grass remained the principal dietary constituent in both the seasons. Based on several studies of their diet, they are known to be mixed feeders (Hofmann 1985; Jamal 1994; Dave 2008; Ahrestani et al. 2012), taking a varying proportion of grass and browse although grass provides the bulk of their diet in all seasons (Schaller 1967). Chital in Kanha is predominantly grazers, although they increase the proportion of browse in their diet during summer.

Because of their high-quality forage requirements, the smallest of the ruminant species, chital would be affected the most by decreasing nutrient quality of grasses in the summer season. Fruits, flowers, leaves and seeds mainly of trees form a minor, highly seasonal part of the chital’s diet. They are eaten as soon as they become available with their high protein and sugar content, they form valuable food source at a season when the quality and availability of other foods are falling. Finest muzzled species (chital), preferred to eat perennial grass species (especially Chloris barbata) when usually green, short and leafy while the species which grow into tall and tough plants (Desmotachya, Imperata and Themeda spp) were preferred only when they are short and have new shoot growth produced by the onset of the first flush of rains. By avoiding thick grass stems, chital avoided the most fibrous, the lowest quality fraction of the plant.

Gaur strategy involves dispersion to many vegetation communities in the summer season, but retreat in the winter season to only single habitat, in which they subsist on sufficient variety of browse species and large unbroken tracts of forest. Gaur is so large and has a large rumen; they rely on bacterial production of protein and energy by digestion of cellulose obtained from low-quality bulk forage. Moreover, large roughage feeder like gaur have large bite size and broad muzzle (Ahrestani 2018), for whom high-quality forage is less of necessity, are incapable of distinguishing between plant parts. In contrast, sambar consumed the highest proportion of browse among all the species throughout the year, and bamboo leaves (Dendrocalamus strictus) is the dominant food species eaten by them in both the season along with some particular browse species.

In all three species (chital, sambar and gaur), the type and species of plants they eat are not distinct, chital share browse component of their annual diet such as Dendrocalamus strictus with other two. Many of the grass eaten such as Chloris barbata are preferred by all the three species. However, gaur also eats some species when mature such as Aristedae setacea which are avoided by chital. These three species could be characterized as eating bunches of grass and browse unselectively (gaur); stripping leaves of medium height bamboo grass (sambar) and picking green leaves and new stems from short grasses or bushes or taking fruit, seeds and flowers of trees (chital).

4.4 Niche diet breadth and overlap

Chital increased the proportion of browse in their diet as summer season changed to the winter; sambar showed preferences for browse throughout the year and gaur were found to be mixed feeders. Among these three ruminants, sambar showed consistently narrow diet niche breadth in both the seasons, clearly preferred only bamboo-mixed habitat in both the season while gaur and chital exhibit quite flexible and wider diet niche breadth especially in the summer season where they subsist on a wide variety of grass and browse species. However, gaur had the narrower diet niche breadth than chital, i.e. food consisted fewer food items and probably being selective during winter while chital had relatively wider niche breadth during winter which shows how two generalist feeders with different feeding styles and body sizes behave when resources are abundant. Gaur being relatively large-bodied animal exhibit “ time minimizing” foraging strategy, which suggests that they drew their food from few forage species which were abundant to maximize the bulk intake in a short time and small-bodied chital shows “energy maximizing” foraging strategy, obtain food from a wide variety of nutrient-rich food items whenever available.

High observed overlap might imply competition, but only if the shared dietary resources are limited (De Boer and Prins 1990). Overlap in the pattern of resource use need not necessarily tends to cause harm. Interaction between species could be mutualistic or at least of no disadvantage to one partner while positively beneficial to others (Putman and Putman 1996). The results obtained confirm the above principle. During winter in Kanha, food resources are abundant and diverse. Hence, less overlap was observed between chital and gaur, however, during summer, the most unfavorable season of the year for the availability of nutritious green forage when in the searing heat, food in general, is dry and scarce and of low nutritional value, dietary overlap increases between chital and gaur.

In contrast, gaur and sambar show high overlap in winter than summer. It is presumed that with no shortage of resources in the shared habitats they are foraging together, permitting both species to coexist in harmony, experience no effect of competition with each other, until spare capacity has taken up. Moreover, large herbivores like gaur are unselective foragers within feeding stations (Gordon and Prins 2008), with a diet composed only of miscellaneous forest and bamboo-mixed habitat forages in highest abundance, foods clearly and commonly show extensive overlap. Dietary overlap was minimal between chital and sambar in both summer and winter, which suggest differential foraging styles and evolutionary history of both the species.

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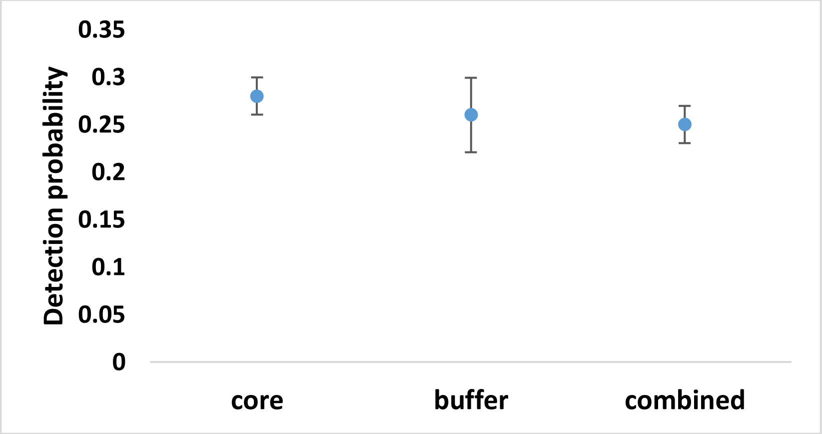
Supplementary Information

S1: Detection probabilities of (a) chital (b) barking deer in core, buffer and combined analysis in DISTANCE 6.2. Error bars represent 95% confidence intervals.

(a)



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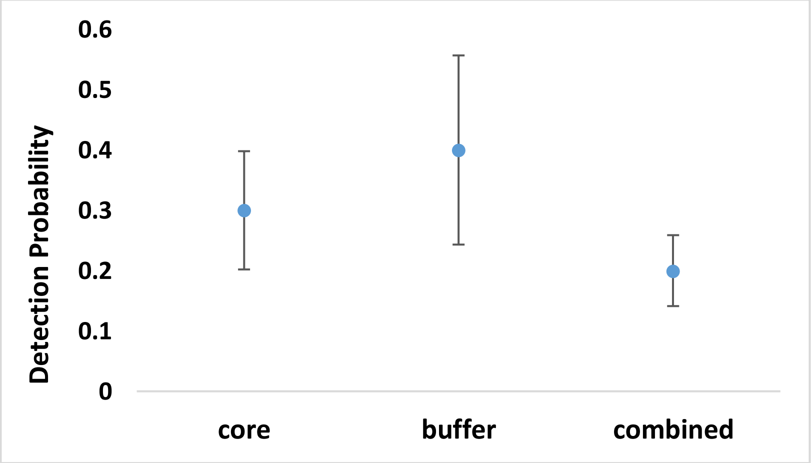
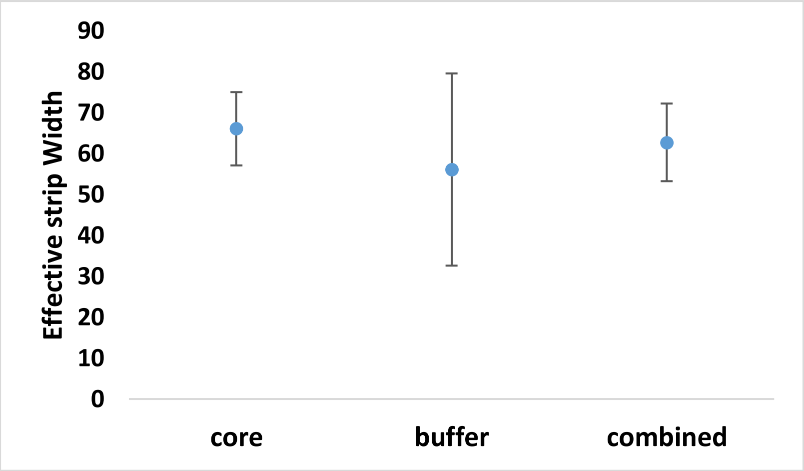


S2: Effective strip width of (a) chital and (b) barking deer in core, buffer, and combined analysis in DISTANCE 6.2. Error bars represent 95% confidence intervals.

(a)



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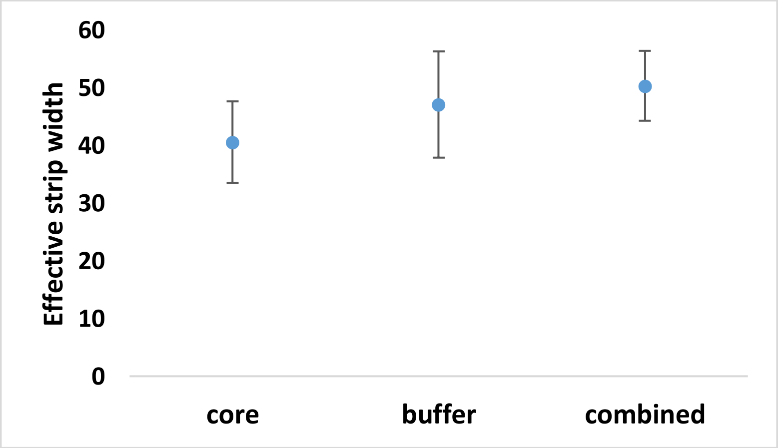
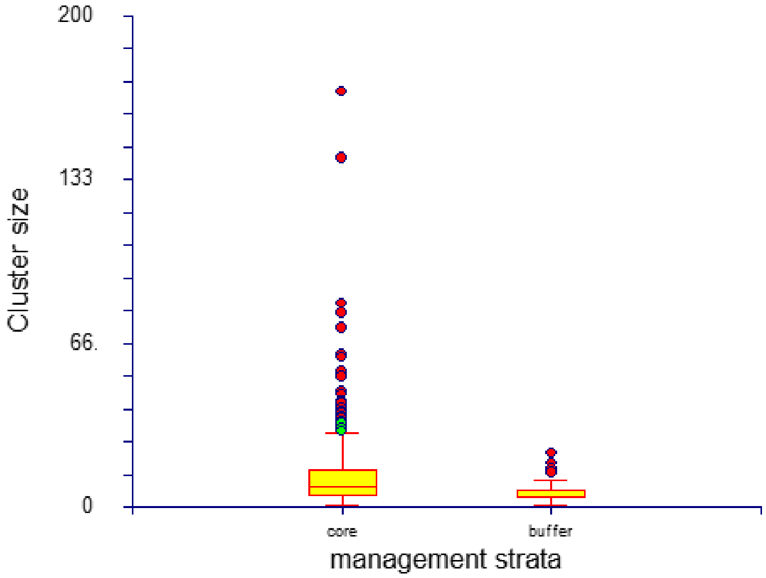


S3: Cluster size of a) chital b) sambar c) gaur d) wild pig in core and buffer zones of Kanha Tiger Reserve.

a)



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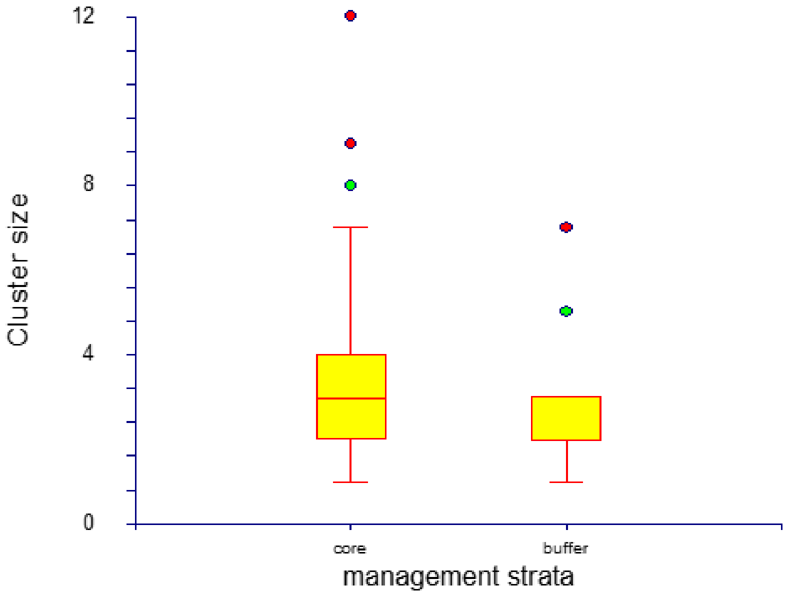
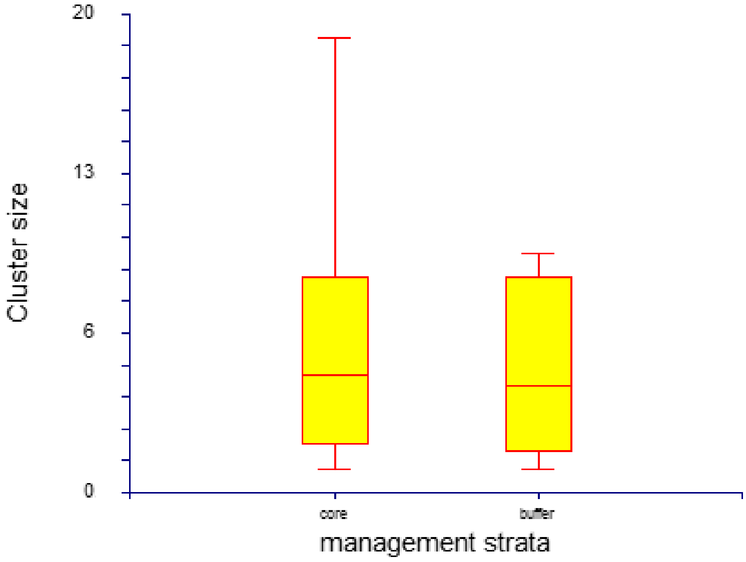
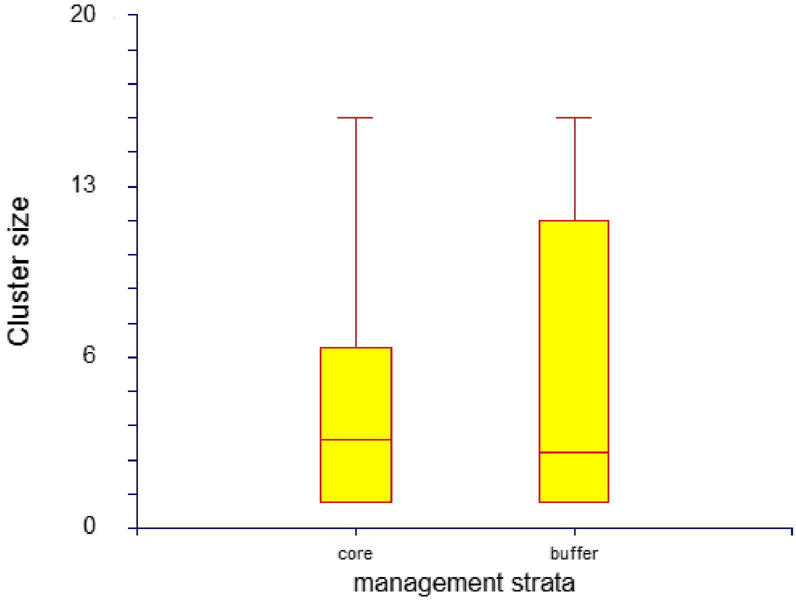


c)


20
13
6
0
Cluster size
core
buffer
management strata

d)


20
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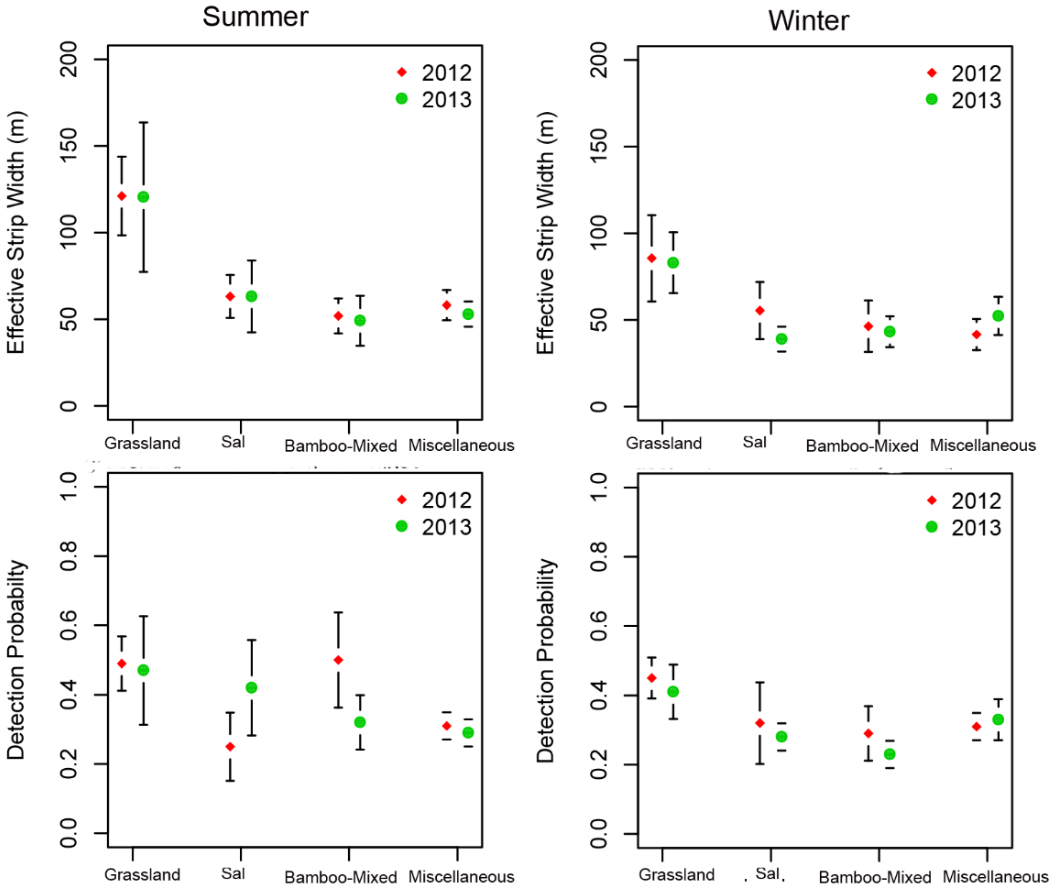
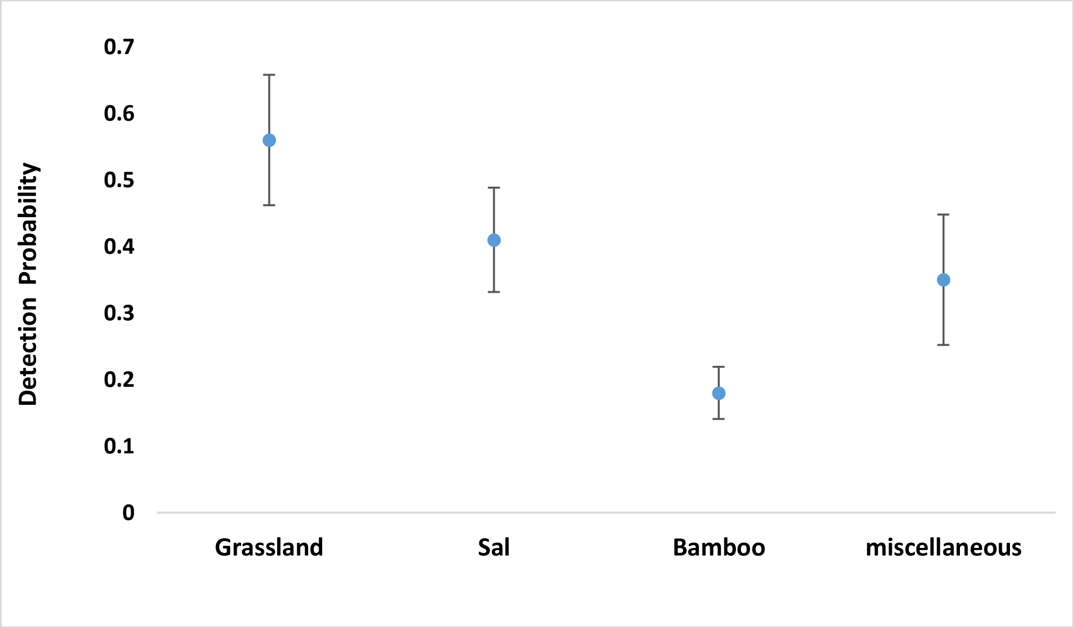
Cluster size
core
buffer
management strata

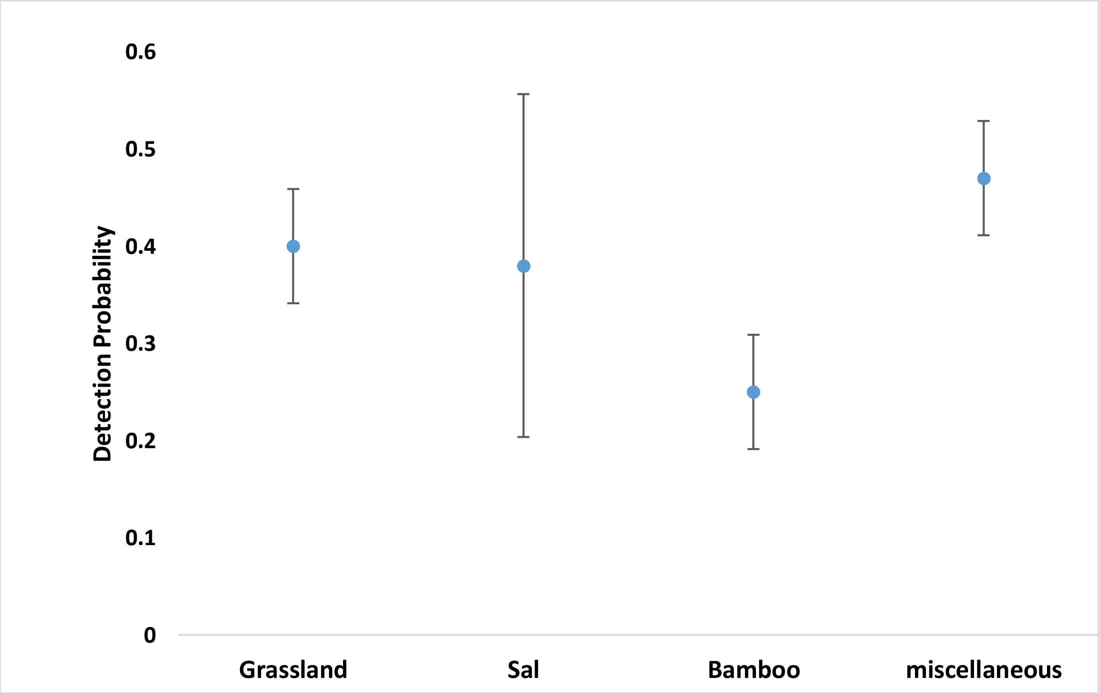
S4: Effective strip width and detection probabilities of chital for summer and winter for year 2013 and 2014 in different habitat types of KTR. Error bars represent 95% confidence intervals



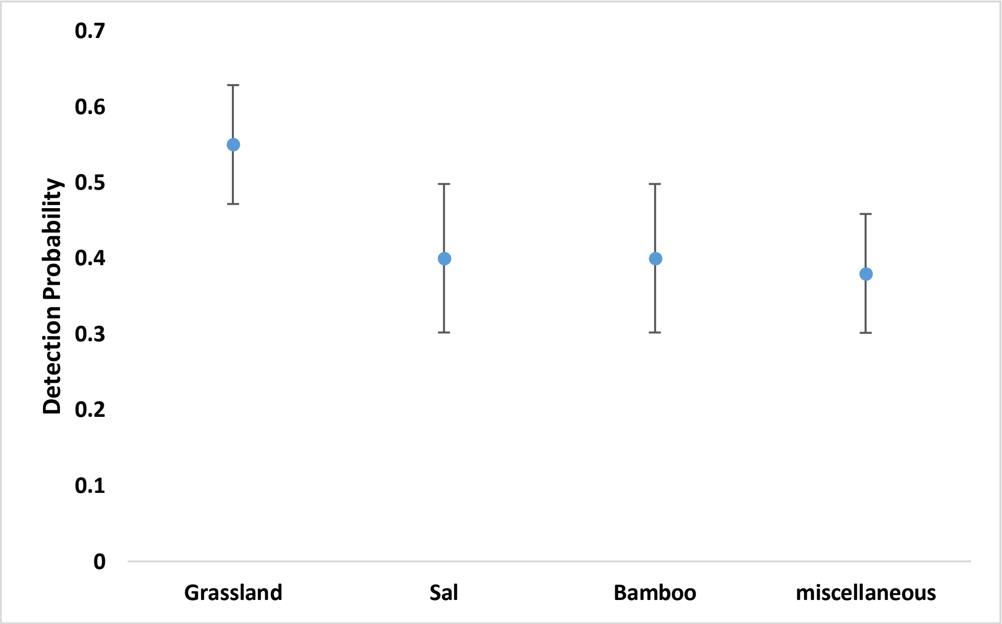
S5: Detection probabilities of chital a) summer b) winter; sambar c) summer d) winter; gaur e) summer f) winter; wild pig g) summer h) winter in different habitat types in KTR. Error bar represent confidence intervals.



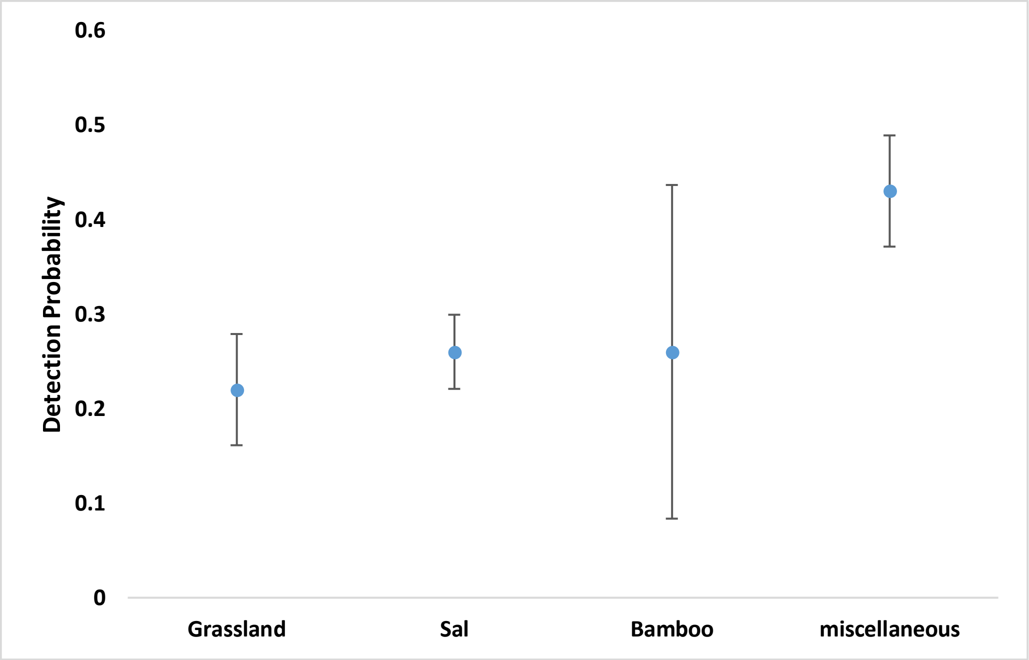
a.



b.


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Detection Probability
Grassland
Sal
Bamboo
miscellaneous

c.


0.6
0.5
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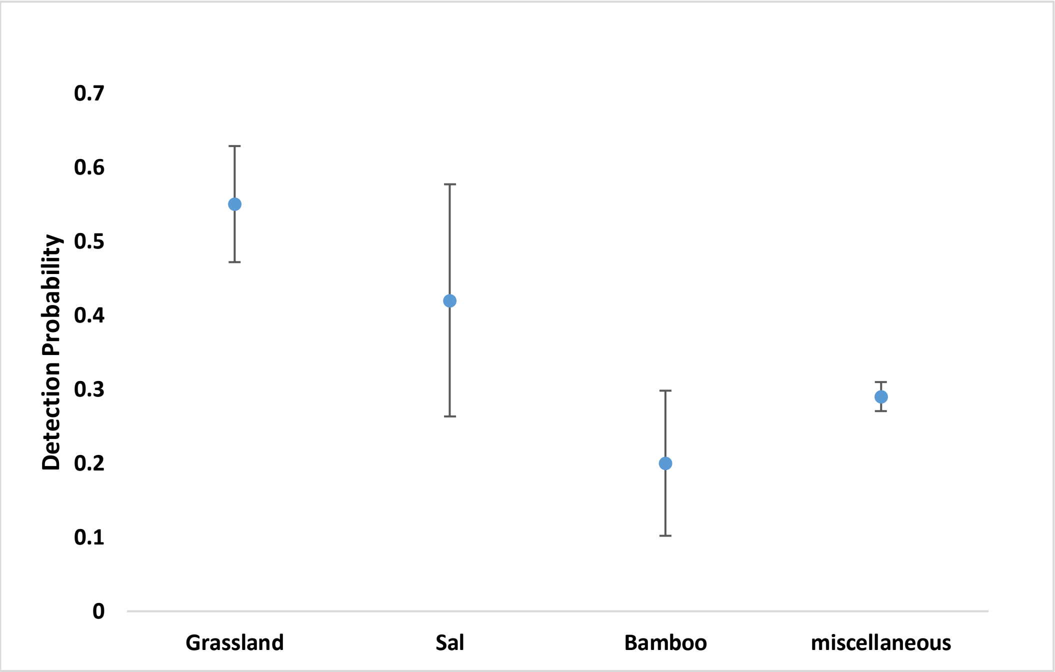
0.3
0.2
0.1
0
Detection Probability
Grassland
Sal
Bamboo
miscellaneous

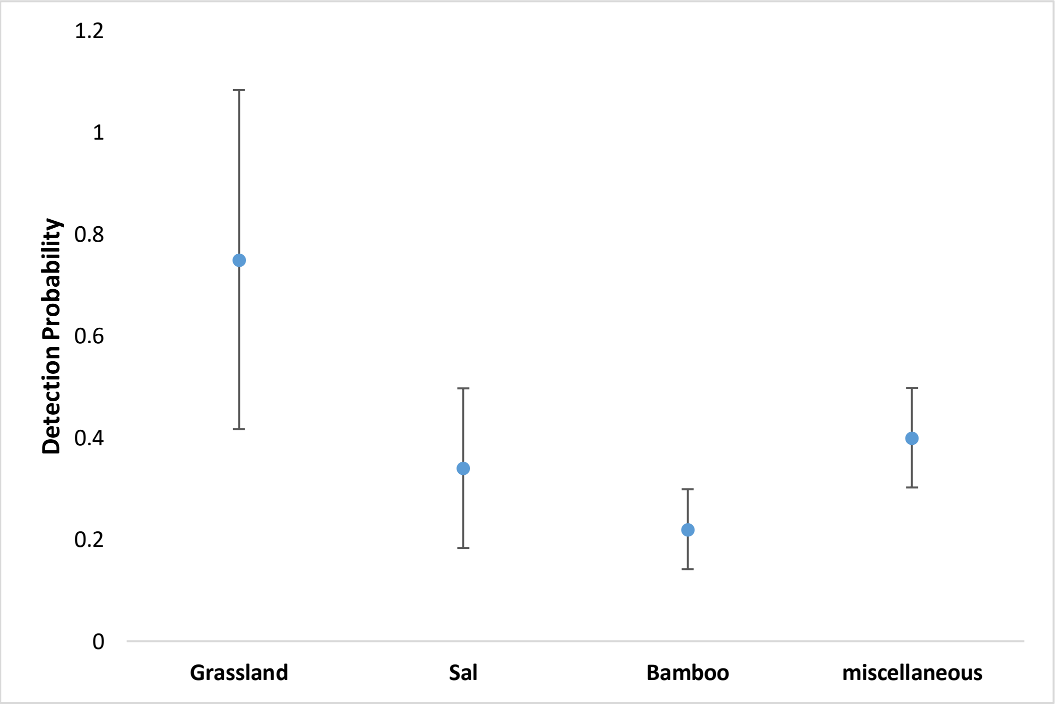
d.

f.



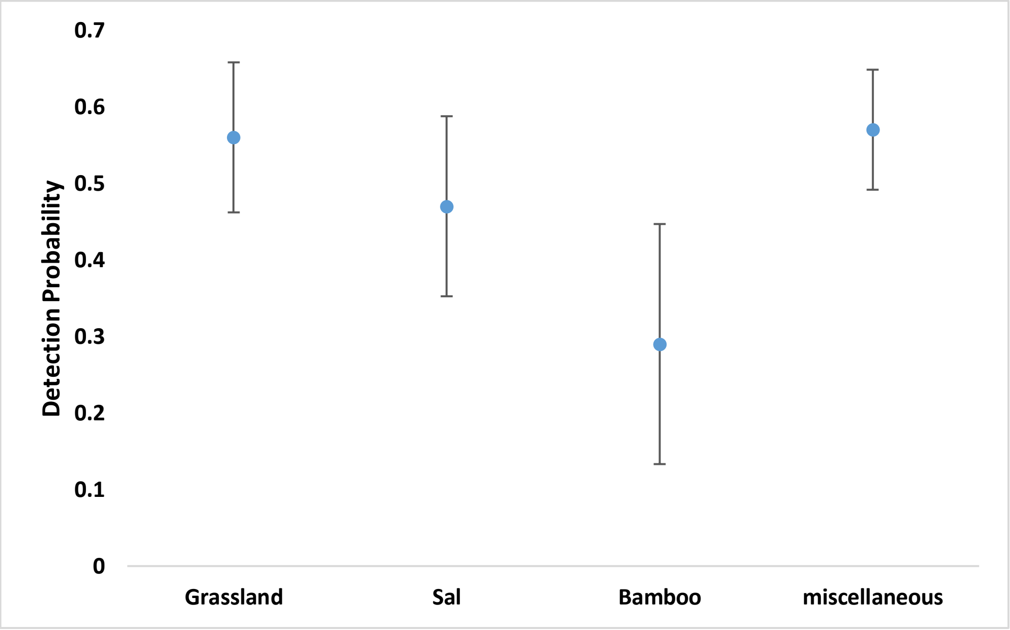
Detection Probability
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Grassland
Sal
Bamboo
miscellaneous

e.



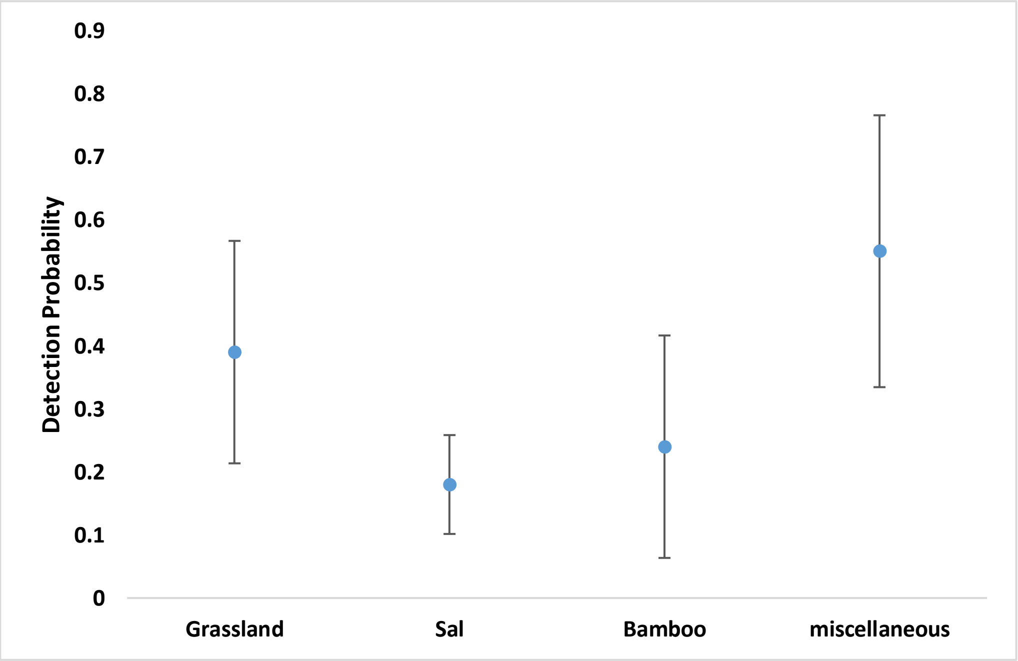
Detection Probability
1.2
1
0.8
0.6
0.4
0.2
0
Grassland
Sal
Bamboo
miscellaneous

f.


0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Detection Probability
Grassland
Sal
Bamboo
miscellaneous

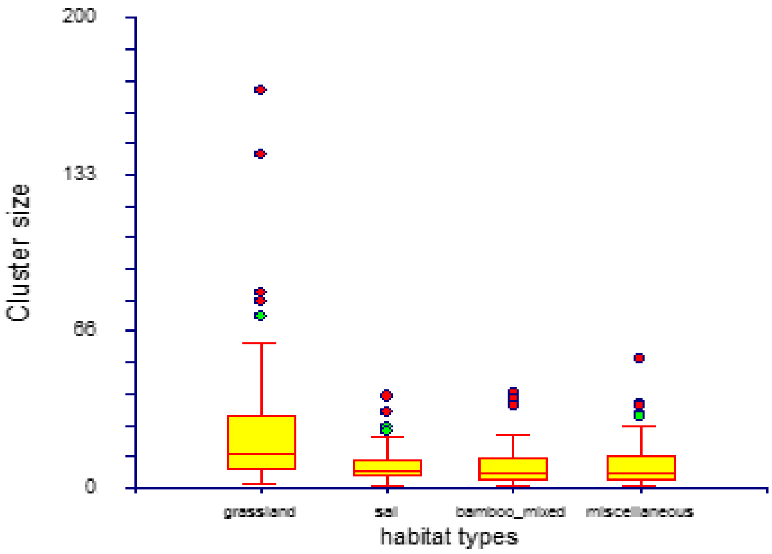
g.

.

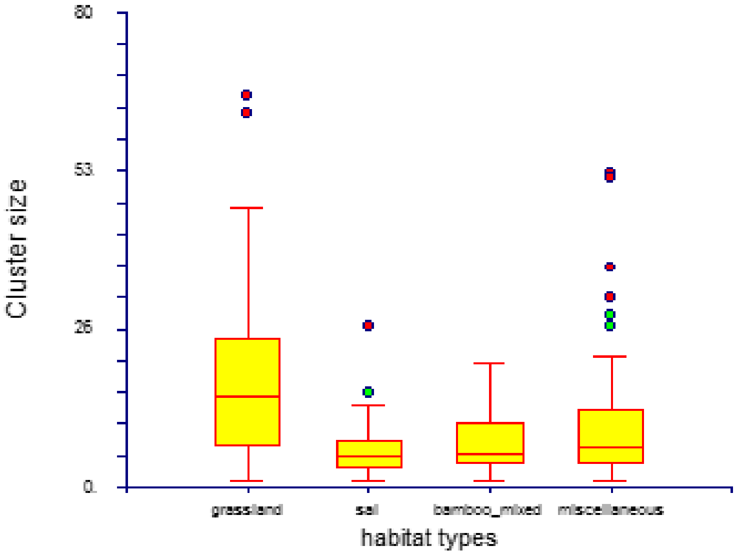

0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Detection Probability
Grassland
Sal
Bamboo
miscellaneous

h.

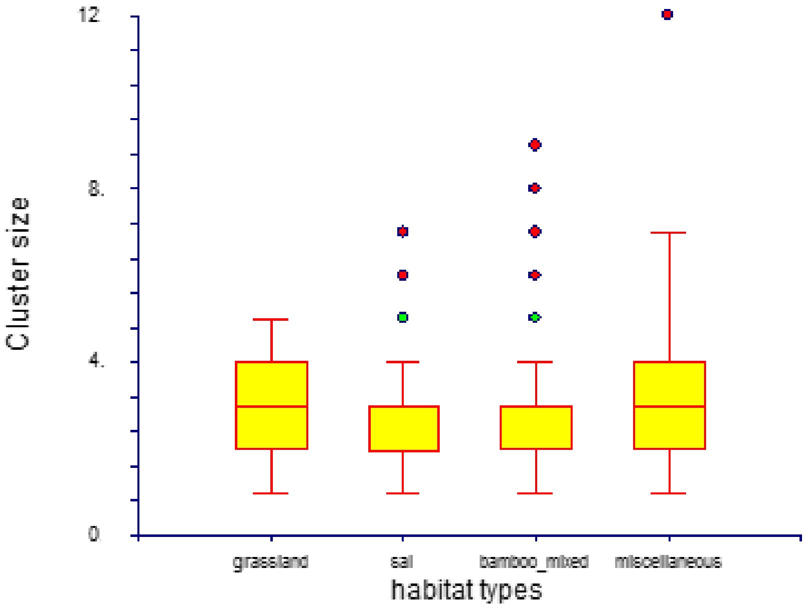
S6: Cluster size of chital a) summer b) winter; sambar c) summer d) winter; gaur e) summer f) winter in different habitat types in Kanha Tiger Reserve.



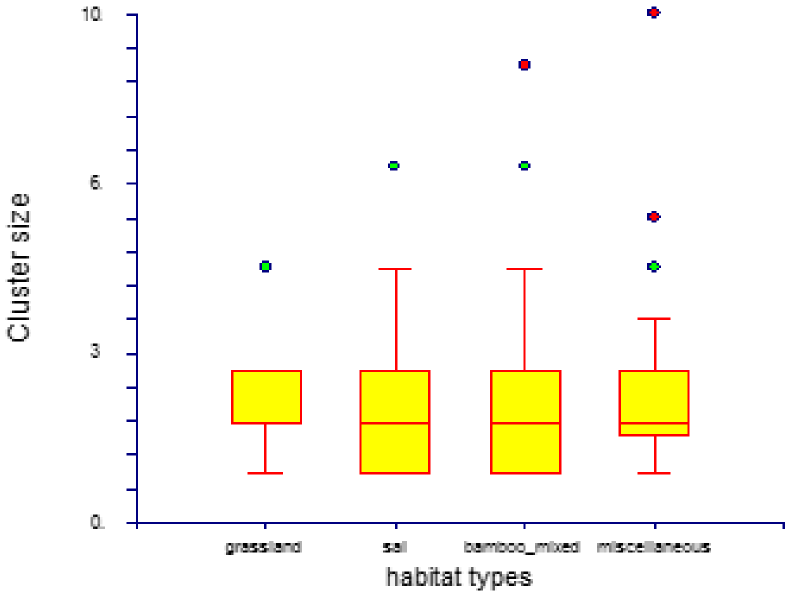
a.



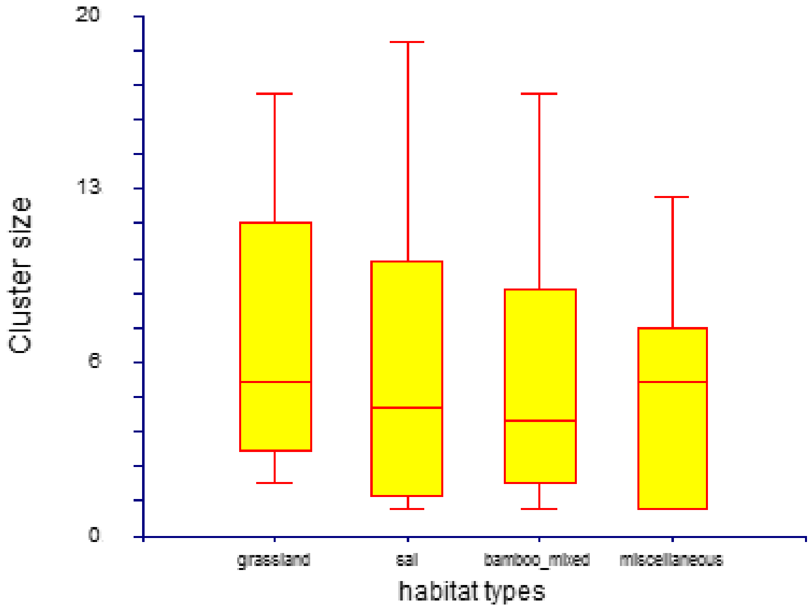
b.


12
8.
4.
0
Cluster size
grassland
sal
bamboo_mixed
miscellaneous
habitat types

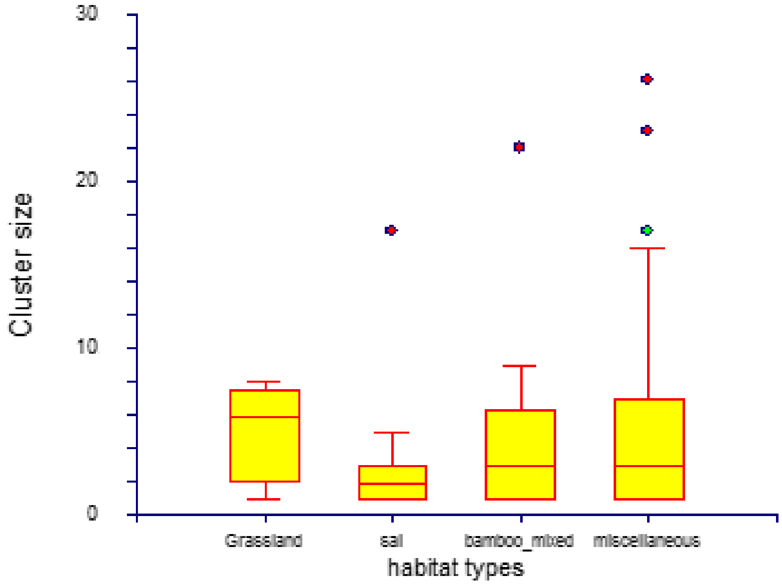
c.


10.
6.
3
0.
Cluster size
grassland
sal
bamboo_mixed
miscellaneous
habitat types

d.

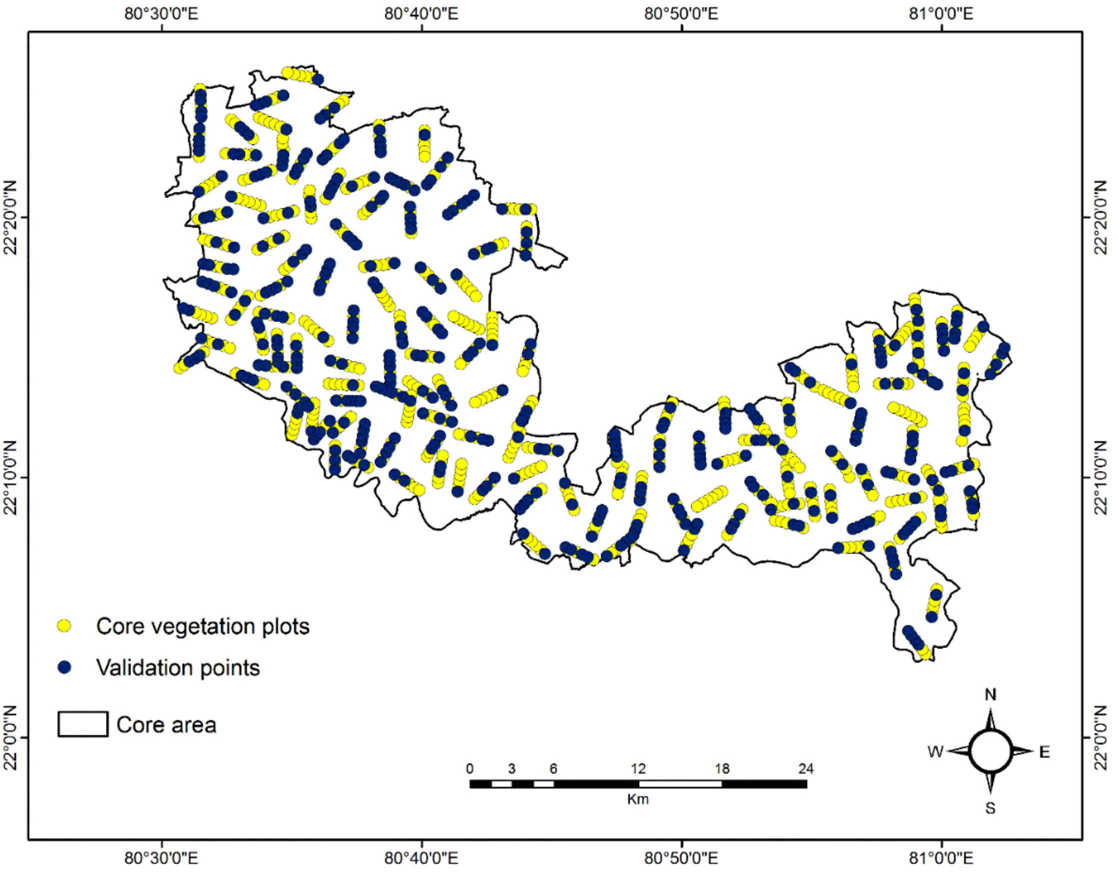

20
13
6
0
Cluster size
grassland
sal
bamboo_mixed
miscellaneous
habitat types

e.


30
20
10
0
Cluster size
Grassland
sal
bamboo_mixed
miscellaneous
habitat types

f.

S7: Location of 900 vegetation plots of which 450 were used as validation points within the core area of Kanha Tiger Reserve.



S8: Seasonal biomass contribution of ungulates in Kanha Tiger Reserve. Biomass was calculated for each season and habitat by multiplying density of each ungulate with their average weight (3/4 of adult female) following Schaller (1972)

Ungulate species	Average weight (kg 3/4th of Adult Female)	summer-biomass contribution (in proportion)	winter-biomass contribution (in proportion)	average biomass (in proportion)
Chital	47	0.31	0.35	0.33
Sambar	136	0.17	0.19	0.18
Wpig	27	0.02	0.03	0.03
Gaur	561	0.44	0.34	0.39
Barking deer	18	0.00	0.01	0.01
Barasingha	109	0.06	0.08	0.07

S9: Seasonal biomass of ungulates in different habitat types of Kanha Tiger Reserve. (Grassland and bamboo habitat together contributes 58.46% of ungulate biomass)

Habitat Type	summer biomass	percentage (%)	winter biomass	percentage (%)	average biomass	percent biomass
Grassland	9637	32	8447	35	9042.16	33.73
Sal	7882	26	3146	13	5513.99	20.57
Bamboo-mixed	8198	28	5062	21	6630.19	24.73
Miscellaneous	4046	14	7194	30	5620.22	20.97
total	29764	100	23849	100	26806.55	100

S10: Habitat selection by ungulates in summer in Kanha Tiger Reserve. When the expected proportion lies outside the simultaneous bonferroni confidence limits then that habitat type is either preferred or not preferred (+ is preferred; - is not prefered and 0 is neutral) at the 0.05 level of significance.

Species	Habitat	Observed Proportion(P_i)	Expected proportion (P_o)	Chi-square (X^2) & *P* value	Bonferroni 95% CI	Selection
Chital	Grassland	0.296	0.092	X^2= 18159.81 *P= 0.0001*	0.290, 0.302	+
	Sal forest	0.189	0.287		0.183, 0.194	-
	Bamboo-Mixed	0.240	0.193		0.234, 0.246	+
	Miscellaneous	0.274	0.427		0.267, 0.280	-
Sambar	Grassland	0.036	0.092	X^2= 2262.71 *P= 0.0001*	0.031, 0.041	-
	Sal forest	0.286	0.287		0.273, 0.297	0
	Bamboo-Mixed	0.383	0.193		0.369, 0.395	+
	Miscellaneous	0.295	0.427		0.283, 0.307	-
Gaur	Grassland	0.061	0.092	X^2= 1135.20 *P= 0.0001*	0.053, 0.069	-
	Sal forest	0.477	0.286		0.460, 0.494	+
	Bamboo-Mixed	0.201	0.193		0.188, 0.215	0
	Miscellaneous	0.258	0.427		0.244, 0.273	-
Wild Pig	Grassland	0.042	0.092	X^2= 719.05 *P= 0.0001*	0.036, 0.049	-
	Sal forest	0.239	0.287		0.226, 0.253	-
	Bamboo-Mixed	0.317	0.193		0.302, 0.331	+
	Miscellaneous	0.400	0.427		0.384, 0.415	-
Barking Deer	Grassland	0	0.092	X^2= 724.26 *P= 0.0001*	0, 0	-
	Sal forest	0.262	0.287		0.238, 0.287	0
	Bamboo-Mixed	0.404	0.193		0.377, 0.431	+
	Miscellaneous	0.332	0.427		0.306, 0.358	-

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S11: Habitat selection by ungulates in winter in Kanha Tiger Reserve. When the expected proportion lies outside the simultaneous bonferroni confidence limits then that habitat type is either preferred or not preferred (+ is preferred; - is not prefered and 0 is neutral) at the 0.05 level of significance.

Species	**Habitat**	**Observed Proportion (P_i)**	**Expected proportion (P_o)**	**Chi-square (X^2) & *P* value**	**Bonferroni 95% CI**	**Selection**
Chital	Grassland	0.306	0.092	X^2= 17494.66 *P= 0.0001*	0.299, 0.312	+
	Sal forest	0.159	0.287		0.153, 0.163	-
	Bamboo-Mixed	0.216	0.193		0.209, 0.221	+
	Miscellaneous	0.319	0.427		0.312, 0.326	-
Sambar	Grassland	0.033	0.092	X^2= 181 *P= 0.0001*	0.027, 0.037	-
	Sal forest	0.247	0.287		0.235, 0.258	-
	Bamboo-Mixed	0.279	0.193		0.266, 0.291	+
	Miscellaneous	0.442	0.427		0.428, 0.455	0
Gaur	Grassland	0.038	0.092	X^2= 1846.39 *P= 0.0001*	0.031, 0.045	-
	Sal forest	0.116	0.286		0.104, 0.128	-
	Bamboo-Mixed	0.100	0.193		0.089, 0.112	-
	Miscellaneous	0.744	0.427		0.728, 0.760	+
Wild Pig	Grassland	0.055	0.092	X^2= 347.84 *P= 0.0001*	0.048, 0.061	-
	Sal forest	0.256	0.287		0.243, 0.269	-
	Bamboo-Mixed	0.268	0.193		0.255, 0.281	+
	Miscellaneous	0.421	0.427		0.406, 0.435	0
Barking Deer	Grassland	0.000	0.092	X^2= 844.92 *P= 0.0001*	0, 0	-
	Sal forest	0.217	0.287		0.201, 0.232	-
	Bamboo-Mixed	0.079	0.193		0.068, 0.089	-
	Miscellaneous	0.704	0.427		0.687, 0.721	+

S12: Carrying capacity of tigers using Hayward et al (2007) derived from ungulate density and biomass

Species (1)	Density (SE range) #/km^2 (2)	3/4th Weight of Adult female (kg) (3)	Biomass(kg) /km^2 (SE range) (4) = (2) x (3)
Chital	33 (28.53 – 37.47)	30	990 (855.9 – 1124.1)
Sambar	8.51 (7.4 – 9.62)	100	851 (740 – 962)
Wild Pig	5.48 (4.52 – 6.44)	30	164.4 (135.6 – 193.2)
Gaur	4.11 (3.31 – 4.91	300	1233 (993 – 1473)

1. Total prey biomass (kg) /km^2 = 3238.4 (2724.5 – 3752.3)
2. $\log_{10}$ of prey biomass = $\log_{10}$ (3238.4) = 3.51
3. Substituting the value of x in Equation (i)

y = 2.158 + 0.377x ………………………………. (i)

here,

$y = -2.158 + 0.377 * (3.51)$

$y = -8.3473$

4. Predicted Tiger Density = antilog of y = $10^{-8.3473}$ = 0.146/km^2 = 14.6/100 km^2
5. Similarly using the SE range of Prey Biomass, the range is (13.7 – 15.4) /100 km^2
6. Therefore, the carrying capacity of Kanha tiger reserve is about 14.6 tigers per 100 km^2 within the range of (13.7 – 15.4) /100 km^2

S13: Comparison of ungulate densities in dry and moist deciduous forest of central India. Sources for the density estimates are: (Bandhavgarh, Panna, Pench, Satpuda, Melghat and Nagarhole from Jhala et al. 2020 (Project Tiger Report), Simlipal (Palei et al. 2016).

Species	Bandhavgarh	Panna	Pench	Satpuda	Melghat	Simlipal	Nagarhole
Chital	39.38	11.32	40.2	3.3	0.24	2.82	24.13
Sambar	3.59	4.8	3.68	5.71	2.06	6.65	4.77
Gaur	0	0	0.26	4.9	1.23	0	1.86
Wild pig	7.95	5.89	3.57	8.53	3.37	4.81	3.46
Barking deer	0.44	0	0	1.96	1.73	3.82	4.93

S14: Literature review regarding studies on sex ratio (Male: Female) of ungulates in different national Park of India.

Sex ratio	**Citations**	**Chital**	**Gaur**	**Sambar**
Kanha National Park	Unpublished present study	1:1.21	1:4	1:1.49
Kanha National Park	Schaller 1967	1: 1.42	1:2.63	1:3.44
Nagarhole	Karanth and Sunquist 1992	1:1.38	--	--
Karnali Bardia	Dinerstein 1980	1:1.88	---	---
Bandipur	Johnsingh 1983	1:1.51	---	----
Sariska	Sankar 1994	1:2.21	1: 2.5	---
Pench	Acharya 2007/Sankar et al 2001	1:2	1:1.6	---
Mudumalai	Ramesh 2010	1:1.63	1:2.38	
Ranthambore	Bagchi et al 2008	---	---	1:1.20
Gir	Khan et al 1966/ Dave 2008	1:2.04	---	1:2

S15: Literature review regarding studies on Adult female: Fawn ratio of ungulates in different national Park of India.

Adult female: fawn ratio	**Citations**	**Chital**	**Gaur**	**Sambar**
Kanha National Park (present study)	Unpublished 2019	1:6	1:4	1:4
Kanha National Park	Schaller 1967	1:2	1:2	1:3
Bandipur	Johnsingh 1983	1:2.04	---	1:2.43
Sariska	Sankar 1994	1:4.54	---	1:3.70
Pench	Acharya 2007/Sankar et al 2001	1:3.70	1:4.16	1:3
Mudumalai	Ramesh 2010	1:6	---	1:3.84
Gir	Dave 2008	1:2.43	---	1:2.56

S16: Comparison between AIC value of each DSM model with comparison of estimated degree of freedom of each variable in summer and winter season

Species	Model	Edf (winter)	AIC value (winter)	Edf (summer)	AIC value (summer)
Chital	s(x,y)+s(elevation)+s(EVI)	52.47	7525.48	49.27	7930.60
	s(x,y)+s(EVI)	49.71	7540.82	46.92	7941.92
	s(x,y)+s(ruggedness)+s(distance from Human settelements)+s(EVI)	60.43	7543.48	46.32	7949.09
	s(x,y)+s(elevation)	43.50	7569.07	53.23	7953.12
	s(x,y)+s(ruggedness)	41.19	7578.51	43.45	7959.48
	s(x,y)	37.67	7584.78	42.35	7959.68
	s(x,y)+s(distance from Human settelements)	40.92	7585.77	45.76	7961.61
	s(x,y)+s(moistness)	41.71	7592.01	43.47	7961.64
sambar	s(x,y)+s(elevation)+s(EVI)	28.56	6162.89	28.01	6084.55
	s(x,y)+s(EVI)	29.68	6164.64	30.79	6088.58
	s(x,y)+s(ruggedness)+s(distance from Human settelements)+s(EVI)	29.59	6165.05	32.39	6089.05
	s(x,y)+s(elevation)	31.80	6166.31	32.28	6090.02
	s(x,y)+s(ruggedness)	32.81	6168.23	31.17	6090.20
	s(x,y)	32.92	6168.97	31.94	6091.27
	s(x,y)+s(distance from Human settelements)	35.95	6171.61	34.93	6093.94
	s(x,y)+s(moistness)	37.25	6175.08	38.54	6099.16
gaur	s(x,y)+s(elevation)+s(EVI)	25.40	5685.40	31.55	5693.71
	s(x,y)+s(EVI)	27.68	5687.78	35.94	5698.21
	s(x,y)+s(ruggedness)+s(distance from Human settlements)+s(EVI)	27.58	5697.21	34.80	5699.15
	s(x,y)+s(elevation)	29.84	5697.89	37.38	5701.03
	s(x,y)+s(ruggedness)	29.04	5698.57	35.97	5701.34
	s(x,y)	30.55	5701.04	36.88	5701.87
	s(x,y)+s(distance from Human settlements)	31.34	5703.49	39.37	5706.48
	s(x,y)+s(moistness)	34.07	5703.86	46.92	5716.04
Wild pig	s(x,y)+s(elevation)+s(EVI)	---	---	--	---
	s(x,y)+s(EVI)	29.13	5214.68	41.21	5214.35
	s(x,y)+s(ruggedness)+s(distance from Human settlements)+s(EVI)	--	---	---	---
	s(x,y)+s(elevation)	28.84	5208.21	43.63	5220.43
	s(x,y)+s(ruggedness)	25.67	5209.41	40.69	5213
	s(x,y)	27.38	5207.15	39.89	5211.37
	s(x,y)+s(distance from Human settlements)	26.70	5211.21	42.70	5218.62
	s(x,y)+s(moistness)	26.73	5210.32	42.97	5221.97
Barking deer	s(x,y)+s(elevation)+s(EVI)	---	---	--	---
	s(x,y)+s(EVI)	24.22	6381.04	46.48	6169.42
	s(x,y)+s(ruggedness)+s(distance from Human settlements)+s(EVI)	---	---	--	---
	s(x,y)+s(elevation)	25.33	6383.07	39.08	6169.42
	s(x,y)+s(ruggedness)	30.30	6383.79	45.32	6172.67
	s(x,y)	22.12	6376.64	41.70	6165.88
	s(x,y)+s(distance from Human settlements)	28.25	6387.02	44.90	6172.38
	s(x,y)+s(moistness)	25.84	6378.69	41.99	6167.07

Edf-Effective degree of freedom; EVI- Enhanced vegetation Index; '---' represents that complex models does not show any effect on distribution of wild pig and barking deer.

Appendix

1. **Glimpses of field work pertaining to observations on scan and focal animal sampling, vegetation sampling done on line transects, documentation of bite counts and foraging activity pattern and monitoring of ungulates through camera trapping in Kanha Tiger Reserve.**

2. **Co-occurrence of major ungulates (Chital, Sambar and Gaur) in Kanha forest provided me opportunity to study mechanisms through which they share space, time and food.**

3. List of Palatable plant species eaten by chital, sambar and gaur in Kanha Tiger Reserve

Plant species	Local name	Palatable parts	Chital	Sambar	Gaur
Acacia pennata	unidentified	leaves	no	no	yes
Aegle marmelos	bel	leaves	no	no	yes
Aristedae setacea	garmi shukra	leaves and stem	no	no	yes
Arthraxon spp.	unidentified	whole plant	yes	no	no
Bauhinia malabarica	amti	leaves	yes	yes	yes
Bauhinia racemosa	dadhera	leaves	no	no	yes
Bauhinia vahlii	mahulbela	leaves	no	yes	yes
Bothrichlora odorata	kaandi	whole plant	yes	no	yes
Buchcnania lanzan	char	leaves	yes	no	yes
Careya arborea	kumbhi	leaves	no	no	yes
Chloris barbata	sikka	whole plant	yes	yes	yes
Coix lakryma	unidentified	whole plant	yes	no	no
Cordia myxa	lasoda	leaves	yes	no	yes
Cynodon dactylon	doob	whole plant	yes	no	no
Cynodon viveri	doob	whole plant	yes	no	no
Dendrocalamus strictus	bamboo	leaves	yes	yes	yes
Desmotachya bipinnata	kush	stem and leaves	yes	no	yes
Diaspyros melanoxylon	tendu	leaves	yes	yes	yes
Dicanthium annulatum	Kaandi	whole plant	yes	no	yes
Dicanthium coricosum	Kaandi	whole plant	yes	no	no
Dicanthium persutium	Kaandi	whole plant	yes	no	no
Dimeria arnothopoda	Kaandi	whole plant	yes	no	no
Eragrostis uniloides	unidentified	whole plant	yes	no	no
Ficus benghalensis	bargad	fruit and leaves	yes	no	yes
Ficus racemosa	umar	leaves and fruit	yes	no	yes
Ficus religiosa	Peepal	leaves	no	no	yes
Ficus virens	Pakhri	fruit	yes	no	yes
Flamingia microphylla	banchana	leaves	yes	yes	yes
Gardenia latifolia	paniabillo	leaves	yes	no	no
grewia eriocarpa	dhamin	leaves	yes	no	yes
Haldinia cordifoila	Haldu	leaves	yes	no	yes
Heteropogon contortus	shukra	whole plant	yes	no	no
Holarrhena antidysentrica	dudhiya	leaves	yes	no	no
Impereta cylindrica	chir	leaves and stem	yes	no	yes
Ischimum indicum	Kaandi	whole plant	yes	no	yes
Lagerstomia perviflora	lendia	leaves	yes	no	yes
Lannea coromandelica	Ghari	leaves	yes	no	no
Lantana camara	lantana	leaves	yes	yes	yes
Madhuca indica	Mahua	leaves	yes	yes	yes

Plant species	**Local name**	**Palatable parts**	**Chital**	**Sambar**	**Gaur**
Mallotus philipinnes	sendur	leaves	no	yes	yes
Mangifera indica	aam	leaves	yes	no	no
Miliusa tomentosa	kaari	leaves	yes	no	no
Mitragyna parviflora	Mundi	leaves	yes	no	no
Pavetta crassicaulis	papdi bela	leaves	no	yes	no
Penicitum annulatum	moa	leaves	yes	no	no
Phoenix acualis	chind	leaves	yes	no	yes
Sacchrum spontaneum	Kaansi	whole plant	yes	no	yes
Shorea robusta	sal	leaves	yes	yes	yes
Syzygium cumini	jamun	leaves and fruits	yes	no	yes
Terminalia alata	saja	leaves	yes	yes	yes
Themeda triandra	bhond	whole plant	yes	no	yes
unidentified	banmirchi/musapuchi	leaves	yes	no	no
unidentified	basin	whole plant	yes	no	no
unidentified	bhuichippa	whole plant	yes	no	no
unidentified	dhudsibhaji	whole plant	yes	no	no
unidentified	khattabhaji	whole plant	yes	no	no
Unidentified	madhiya	whole plant	yes	no	no
Ziziphus rugosa	churna	fruit and leaves	no	yes	yes
zizyphus xylophyrus	ghatia	leaves	no	yes	yes
Phyllanthus emblica	Amla	fruit and leaves	yes	no	yes
Casearia graveolens	Girchi	fruit and leaves	yes	no	yes
Terminalia chebula	Harra	leaves	no	no	yes

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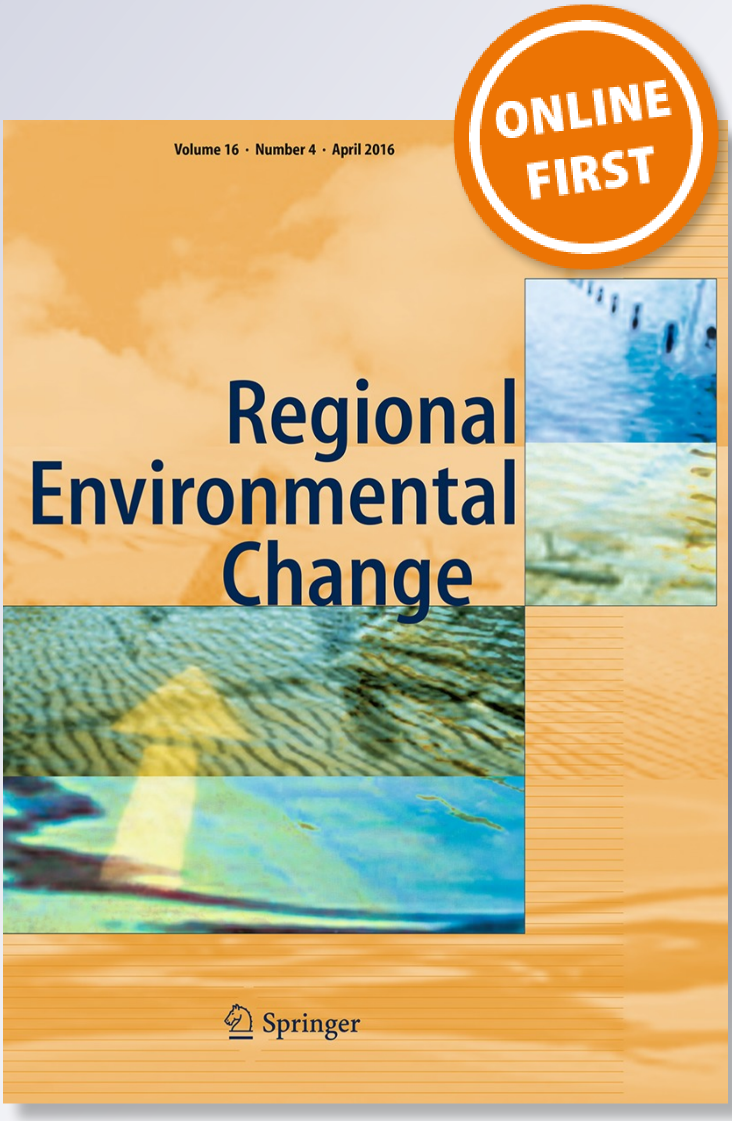

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ORIGINAL ARTICLE

Effect of human use, season and habitat on ungulate density in Kanha Tiger Reserve, Madhya Pradesh, India

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Abstract Conservation practitioners require strata specific, seasonal species densities for habitat management. Herein, we use stratified distance sampling in Kanha Tiger Reserve (KTR) with 200 spatial transects and an effort of 1200 km walk in the year 2013. Analysis was done to access (a) impact of human use and (b) effect of habitat and season on ungulate densities in KTR. While a single detection function for each species was used for estimating density within human-restricted core and multiple use buffer of KTR, species-specific seasonal detections were modelled for each habitat. Ungulate biomass was 4.8 times higher in the core area compared with the buffer zone. The core supported a herbivore density and biomass of 50 ± 4.80/km^2 and 26,806 ± 2573 kg/km^2, respectively. Chital were found to be most abundant, having a density of 30.1 ± 4.34/km^2 and contributing 33 % of the biomass with a habitat preference for grasslands (106 ± 39/km^2) in summer and winter. Sambar had highest density (15.4 ± 3.34/km^2) in bamboo-mixed habitat, in both seasons. Gaur contributed 39 % of the ungulate biomass and showed a seasonal shift in density from sal forests (9.65 ± 3.55/km^2) in summer to miscellaneous forests (8.13 ± 1.94/km^2) in winter. Barasingha were restricted to grasslands with similar summer and winter densities of 1.56 ± 0.76/km^2. Chousingha were rare (0.1 ± 0.04/km^2), found mostly in miscellaneous forests and plateau grasslands. Grassland and bamboo-mixed forests supported 58 % of the total ungulate biomass. Management for an optimal habitat mosaic that maintains ungulate diversity, addresses the specific needs of endangered species and maximizes ungulate biomass is recommended.

Keywords Distance sampling · Habitat management · Habitat mosaic · Protected areas · Tropical forest · Ungulate biomass

Introduction

Tropical deciduous forests are capable of supporting high density of ungulates due to their high productivity and nutrient availability (Field et al. 1998; Melillo et al. 1993). Subsequently, due to a high prey abundance, these forests are important refuges for conserving large carnivores. Land for conservation comes at a high premium in tropical countries with burgeoning human populations (Dinerstein et al. 2010). Severe biotic pressure such as bush meat consumption, use of non-timber forest products, and livestock grazing has likely resulted in an unprecedented reduction in ungulate abundance in these forests. Protected areas in the tropics are relatively small compared with other biomes (Schmitt et al. 2008). Often large carnivore populations in the tropics, such as those of tigers, are primarily restricted to protected areas (Jhala et al. 2015). Rarely does a single reserve harbour a tiger population of sufficient size required for its long-term persistence (Yumnam et al. 2014). Density of large carnivores is primarily dictated by the density of their prey (Hayward et al. 2007). Therefore, managing them optimally to serve both

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the purpose of conserving biodiversity and harbouring viable large carnivore populations becomes crucial. The Tiger Reserves in India are legally mandated to delineate a core area where large investments by the Government are made to resettle human habitations from within the core area through an incentivised, voluntary, relocation scheme (Wild life (Protection) Amendment Act 2006). The core is subsequently declared 'inviolate' with extremely restricted human activity (Gopal et al. 2007). Scientific data that document the effectiveness of these investments in achieving the desired conservation objectives would encourage Governments to invest further in such schemes that benefit both the local communities through better livelihood options and biodiversity conservation (Secretariat of the Convention on Biological Diversity 2008).

Ungulates meet their food and cover needs from a wide range of resources and habitats. Food quality, plant productivity and water regime vary in availability with seasons (Prins and Loth 1988; Beever et al. 2000), which often force ungulates to expand their home ranges, or shift their use of habitats in a seasonally predictable fashion. Distance sampling (Buckland et al. 2001) has opened up the field of estimating forest dwelling ungulate abundance. However, current application of distance sampling has been done on random foot transects that typically traverse multiple habitat types. Although estimates from such studies are unbiased to the region of inference, they fail to provide information on how ungulate abundance responds to different habitats, a vital requirement for management. Precision of estimates from distance sampling on foot transects depends on variability of effective strip width (ESW), encounter rate and cluster size (Buckland et al. 2001). For a given sample size, habitat-specific distance sampling would provide more precise density estimates compared with the same number of transects that traverse habitat mosaics (Thomas et al. 2010). Estimating abundance by habitat stratification is a sensible approach to improve the precision of estimates and ensure proper coverage of habitats (Sutherland 2000).

Herein, we use stratified line transect sampling in Kanha Tiger Reserve, Madhya Pradesh, India, and analyse our data with conventional distance sampling to assess the effect of a) extractive anthropogenic use and b) habitat and season on ungulate densities. Our results showed that ungulate densities were significantly depressed in "multiple use" forests of the buffer zone compared with the "human-restricted" core area of KTR. Some ungulates of KTR showed significant seasonal shifts in their habitat-specific densities, while others seemed to be habitat specialists and maintained high habitat-specific densities in summer and winter. We attempt to interpret our results in the context of nutritional and cover requirements of ungulates and thereby provide management options for specific ungulate species and for the overall conservation objectives of KTR.

Materials and methods

Study Area

Kanha Tiger Reserve is located in the state of Madhya Pradesh (latitudes 22° 7′ N and 22°27′ N and longitudes 80° 26′ E and 81° 3′ E) in the Maikal chain of hills in the eastern Satpura mountains of the Central Indian Highlands. The Tiger Reserve comprises of two distinct management strata: the core which covers an area of 940 km^2, devoid of human settlements and has the prime objective of biodiversity conservation and a 1134 km^2 of buffer zone which is a multiple use area, having human settlements where tourism-based resorts and hotels, small-scale industries like rice mills, agriculture practices, and infrastructure development for village people are permitted although activities adverse to conservation such as mining and large polluting industries are not permitted in the buffer zone. The area of forest or wild ungulate habitat available within the buffer zone is 585 km^2, and thus, the conservation unit totals an area of 2074 km^2, and is designated as a Tiger Reserve.

Kanha is a tropical moist deciduous forest interspersed with grasslands of anthropogenic origin, arrested in succession by management activities of annual burning and woody plant removal (Kanoje 1999). The undulating terrain and variation in the altitude (450–950 m above mean sea level) has resulted in a diversified floral composition (Champion and Seth 1968). In general, four different habitat types, viz. grassland, pure sal forest, miscellaneous forest and bamboo-mixed forest, are present in the reserve. The higher elevation sites consist of extensive plateau-capped hills supporting sparse or little tree growth of miscellaneous forest and are primarily grasslands. The depressions, gorges and streams, just below these plateaux, support bamboo (*Dendrocalamus strictus*), while the low-altitude sites comprise valleys with grassy meadows interspersed with groves of sal (*Shorea robusta*) and the lower slopes carry dense stands of sal with bamboo which also occur in miscellaneous stands in the upper slope. The faunal assemblage consists of endangered carnivores like tiger (*Panthera tigris*), leopard (*Panthera pardus*), wild dog (*Cuon alpinus*) and sloth bear (*Melursus ursinus*), and nine species of ungulates such as hard ground barasingha (*Rucervus duvaucelii*), chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*), barking deer (*Muntiacus vaginalis*), wild pig (*Sus scrofa*), chousingha (*Tetracerus quadricornis*), nilgai (*Boselaphus tragocamelus*) and mouse deer (*Moschiola indica*). Among small carnivores, jungle cat (*Felis chaus*) and rusty spotted cat (*Prionailurus* *rubiginosus*) are present in the reserve. The climate is monsoon type with marked seasonal variations in temperature and rainfall. The mean annual rainfall is 1623 mm, most of it restricted to the monsoon months (Negi and Shukla 2011). Three seasons are observed in the area: namely winter (December–February), summer (March–May) and rainy seasons (June–September). October and November are a transition period from monsoon to winter.

Habitat mapping and validation

Extensive ground truthing was done by sampling 900 vegetation plots of 707 m^2 size in the field by trained personnel. Each vegetation plot was classified to its dominant vegetation community to record major habitat types (Fig. S7). Plots (1) with >70 % sal were considered as "pure sal"; (2) having <70 % sal and >30 % other tree species were considered as "miscellaneous forests"; (3) with miscellaneous forests having >20 % bamboo were considered as "bamboo-mixed forests"; and (4) having <10 % tree cover and ground vegetation dominated by grasses were defined as "grasslands". The other habitat categories were (5) agriculture/fallow fields, (6) barren areas and built-up human habitation area and (7) water bodies. We used 70 % of ground plots for modelling vegetation classification, while 30 % were used for model validation to assess the performance of our image classification. Unsupervised classification of LANDSAT-8 satellite imagery (pixel size = 30 metres; acquisition date; April and November 2013) was carried out. The results of the unsupervised classes were merged by supervised classification to adhere to field identifiable classes mentioned above. Digital image processing, geo-referencing and digital classification of remotely sensed data were done using ERDAS imagine 2010 (Earth Resources Data Analysis System, Leica Geosystems, Atlanta, Georgia, USA).

We built an error matrix that compared the habitat classes identified in the field for independent, randomly selected 450 vegetation plot locations against their corresponding classified pixels on the image using kappa coefficient (Cohen 1960). Kappa indicates to what extent classification accuracy is due to the true agreement of the field data with classified data (Lillesand et al. 2004). Its values generally range from 1 for perfect agreement to 0 for no agreement (Rosenfield and Fitzpatrick-Lins 1986). Habitat classification was assessed as accurate if kappa coefficient was greater than 0.6 (Landis and Koch 1977).

Sampling design and data collection

Ungulate density is likely to respond to regimes of protection as well as to vegetation types. Hence, we used a stratified design in the core area of the Tiger Reserve, where the number of transects in each habitat was approximately in proportion to the area of the habitat. Thus, grassland had 12 transects, sal forest had 36 transects, bamboo-mixed forest had 29 transects, and miscellaneous forest had 73 transects. Based on management zones, the core area had 150 transects, while the forest of buffer zone had 50 transects (Fig. 1). Line transects of 2 km were marked within each strata and walked during early morning (6:00 a.m. to 8:00 a.m.), for three consecutive mornings in summer and winter of 2013. In each season, sampling was completed within 30 days. The total transect survey effort comprised 1200 km of walk along 200 spatial replicates in both seasons. Radial distance, animal bearing and group size were recorded with encounter of each ungulate species. We surveyed the entire reserve with 20 observers who were well versed with field craft and species identification. We trained and tested each observer in the use of laser range finder (Bushnell RX 1000), see through compass (Suunto KB-20) and GPS (Garmin eTrex 10).

Data analysis

Ungulate abundance estimates were derived from 200 line transect samplers placed across 1945 km^2 of the study area using conventional distance sampling (CDS) approach (Buckland et al. 2001) in program Distance (version 6.2; Thomas et al. 2010). Densities of six major ungulates (chital, sambar, gaur, wild pig, barasingha and barking deer) were recorded for each management and habitat strata. Chousingha and nilgai were analysed only for management strata as the number of observations recorded for these species was insufficient to separately estimate detection functions and densities for each habitat type.

For the first analysis, we were interested in finding out whether density of specific species differed between two regimes of management, i.e. the core area, devoid of human settlement and the buffer zone, a multiple use area with extractive use by local communities. For this analysis, we developed detection functions for each species from all transects pooled across management zones and subsequently estimated density for each species for each management zone by post-stratification. Since habitat types between core and buffer areas were similar, we did not expect detection functions for each species to differ between the core and buffer zones. We tested this premise for species that had a large number of detections in both management strata (chital and barking deer), by comparing the effective strip width (ESW) and detection probability obtained from independent fitting of detection functions for core and buffer habitats. Since ESWs and detection probability did not differ between core and buffer, we pooled

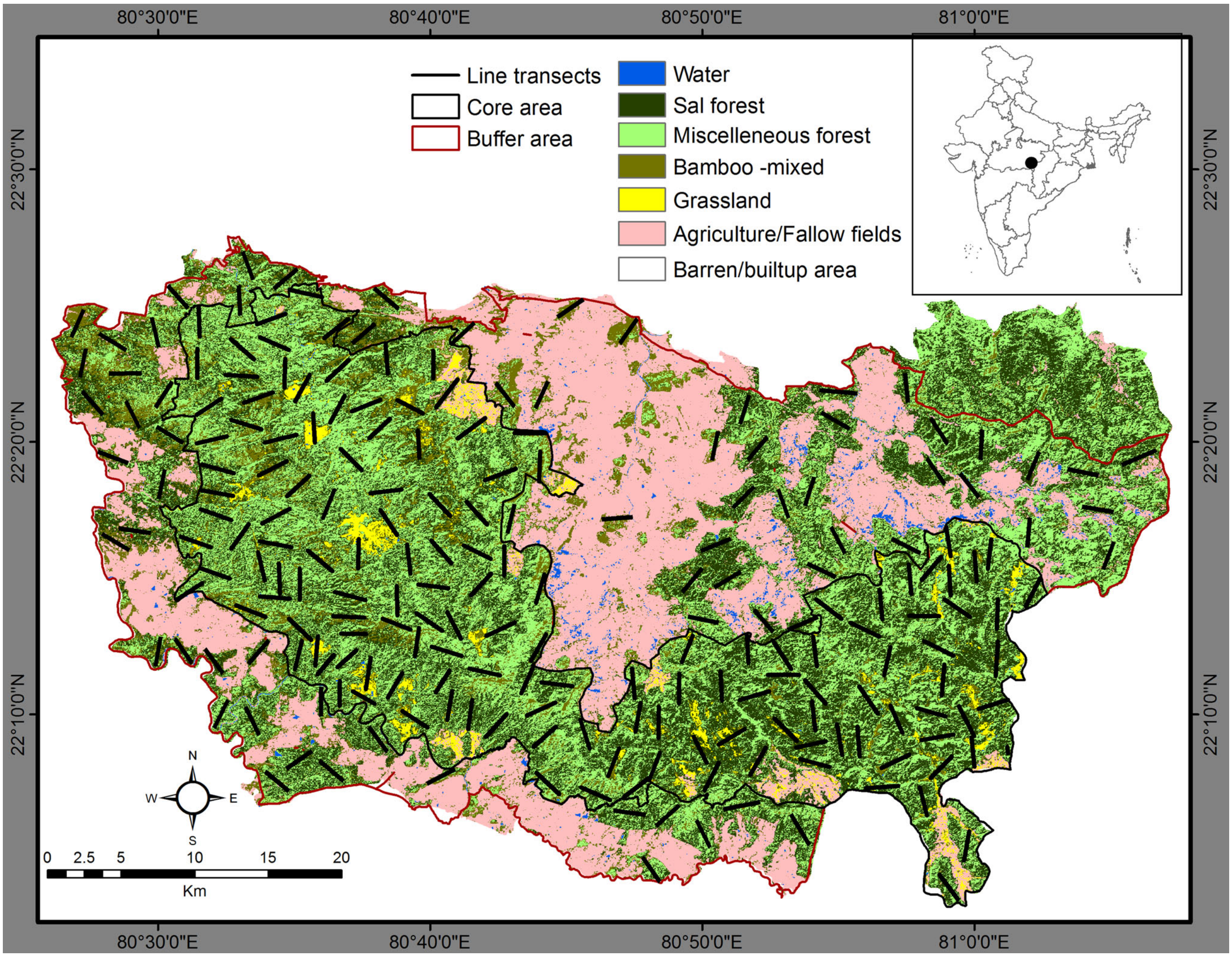

Fig. 1 Vegetation cover map of Kanha Tiger Reserve showing the spatial distribution of habitat-specific line transects

data separately for individual species between core and buffer zones to obtain a more robust and precise estimate of ESW for each species and estimated density separately for core and buffer using a common detection function (Figs. S1 and S2).

In our second analysis, we were interested in the effect of habitat type and season on ungulate densities. We restricted our analysis to the core of the Tiger Reserve since transects in the buffer area were not habitat specific. This was because habitat patches in the buffer were too small to lay a transect of reasonable length. Since there were few detections of sambar, gaur and wild pig in grassland for both seasons and few detections of gaur within sal forests and bamboo-mixed forests for winter season to permit the modelling of detection functions, we pooled individual species detection data for these species from our transect walks in these habitats for the years 2012 and 2013. A detection function was then modelled for each species for a particular habitat in a specific season by combining the 2-year data. This detection function was then used to obtain the species density for the year 2013 by post-stratification by years, for a particular habitat in a specific season. Shape criteria were examined for heaping and any outliers were right-hand truncated where necessary (Buckland et al. 2001). Three key functions (uniform, half-normal and hazard rate all with cosine series adjustment) were considered for each analysis. Model selection was evaluated using Akaike's information criteria (AIC), while Kolmogorov–Smirnov statistics were used to assess the goodness of fit of each model (Buckland et al. 2004).

Considering ungulate abundance in a habitat type to be the use by that species, we computed Ivlev index of electivity (1961). Ivlev index measures the utilization of habitat types (U) by species in relation to their availability (A) in the landscape (Dyke 2008). Ivlev index of selection is determined as U-A/U + A. It is an algorithm for identifying the strength of selection for habitats (Yeo and Peek 1992). The selection index will be zero whenever animals use the habitat in the same proportion as its availability. It will approach the value of one when use is proportionately much higher than availability suggesting the strong preference for that habitat. Alternatively, it will approach a value of negative one when use is less than availability (Dyke 2008). Ivlev index was only used for graphical representation (Fig. 2). Following Byers et al. (1984), we first tested for overall seasonal habitat preference by an ungulate species through a Chi-square test, and subsequently, we used simultaneous Bonferroni confidence intervals that control for an overall experiment wise error rate, to check for preference of each habitat type. We computed ungulate biomass for each habitat in each season by multiplying species density with the 3/4th of the adult female body mass (Schaller 1972) (Table S1 and S2).

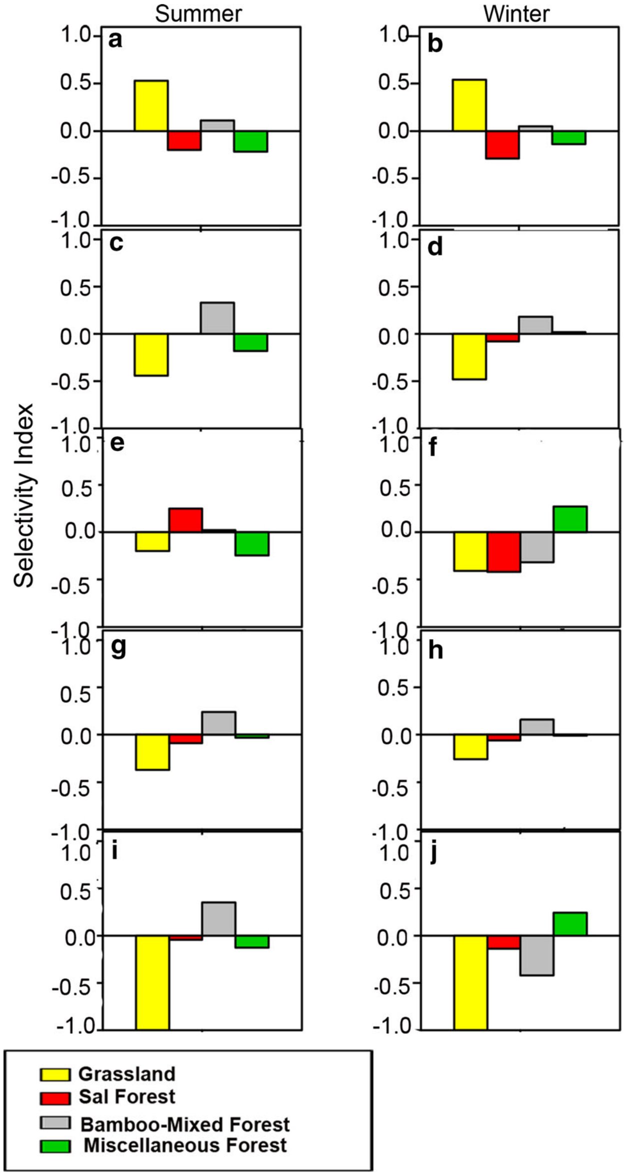

Fig. 2 Seasonal habitat selection by chital **a** summer **b** winter; sambar **c** summer **d** winter; gaur **e** summer **f** winter; wild pig **g** summer **h** winter and barking deer **i** summer **j** winter in Kanha Tiger Reserve depicted by Ivlev's selectivity index

Results

A kappa statistics value of 0.8 ($p < 0.001$) suggested good agreement of validation plots with the vegetation map (Fig. S7). As per the habitat classification map prepared in this study, the area under (1) pure sal was 426 km^2, (2) miscellaneous forests was 648 km^2, (3) bamboo-mixed forests was 425 km^2, (4) grassland was 88 km^2, (5) agriculture/fallow fields were 268 km^2, (6) barren and built-up areas were 218 km^2, and (7) water bodies were 16 km^2. Chital was the most commonly sighted ungulate followed by sambar, barking deer, gaur and wild pig (Tables 1, 2 and 3).

Human use and ungulate density

Species densities differed between core and buffer zones (Table 1). The results showed that among all ungulates, chital was the most abundant with much higher density in the core area (30.1 ± 4.34) compared with the buffer zone (8.45 ± 2.37) of the Tiger Reserve. The next most abundant were sambar and gaur, with a consistent trend between core and buffer areas, in both summer and winter seasons. Only in the case of wild pig and barking deer, densities were comparable between both management strata and seasons. Only nilgai had higher densities in buffer zone compared with the core zone (Table 1) while barasingha and chousingha were not detected in the multiple use buffer zone. Group size of all ungulates except nilgai was larger in the core zone (Table 1). Detection probabilities and ESWs for chital and barking deer did not differ between core, buffer and combined analysis (Figs. S1 and S2).

Habitat-specific densities and preference by ungulates

All species of ungulates showed preference for certain habitats ($\chi^2 > 7.85$, $p < 0.05$). Chital was most abundant among all ungulates, across all four habitats and in both summer and winter seasons. Chital densities were highest in grassland followed by bamboo-mixed forest with little seasonal variation (Tables 2 and 3). Chital consistently showed a high preference for grassland in both summer and winter seasons (Figs. 2a and b; Tables S3 and S4). Sambar had the highest densities in the bamboo-mixed forest in summer followed by sal forest and miscellaneous forest. The seasonal densities of sambar show a little habitat shift from bamboo-mixed forest in summer season to

Table 1 Density of ungulates in the core and buffer area of Kanha Tiger Reserve in 2013

Species	season	Management site	Best model	Detection probability $\hat{P}$ (SE)	KS test *p* value	No of observation (n)	Mean Cluster size E(s) (SE)	Group density $\widehat{DS}$ (SE)	Density $\hat{D}$ (SE)
Chital	Summer	Core	HRC	0.25 (0.01)	0.892	357	9.62 (0.52)	3.14 (0.48)	30.3 (4.9)
		Buffer				51	5.8 (0.65)	1.35 (0.28)	7.9 (1.88)
	Winter	Core	HNC	0.18 (0.01)	0.823	326	8.35 (0.47)	3.59 (0.40)	29.9 (3.7)
		Buffer				55	5.93 (0.66)	1.51 (0.43)	9.0 (2.79)
Sambar	Summer	Core	HRC	0.29 (0.01)	0.727	250	2.86 (0.10)	2.76 (0.33)	7.90 (0.99)
		Buffer				15	2.58 (0.43)	0.49 (0.13)	1.29 (0.42)
	Winter	Core	HNC	0.13 (0.01)	0.721	258	2.33 (0.08)	3.58 (0.36)	8.38 (0.89)
		Buffer				18	2.24 (0.37)	0.54 (0.17)	1.22 (0.43)
Gaur	Summer	Core	HRC	0.21 (0.03)	0.712	102	5.25 (0.63)	0.92 (0.21)	4.83 (1.25)
		Buffer				10	2.75 (0.82)	0.30 (0.15)	0.83 (0.49)
	Winter	Core	HRC	0.28 (0.02)	0.810	98	3.59 (0.42)	1.18 (0.17)	4.27 (0.81)
		Buffer				8	4.9 (1.12)	0.29 (0.14)	1.44 (0.76)
Wild pig	Summer	Core	HRC	0.21 (0.01)	0.858	91	4.94 (0.53)	1.0 (0.15)	5.29 (0.95)
		Buffer				17	7.66 (2.92)	0.53 (0.14)	4.11 (1.92)
	Winter	Core	HRC	0.21 (0.02)	0.772	90	4.74 (0.55)	1.31 (0.22)	6.22 (1.27)
		Buffer				19	9.44 (4.07)	0.53 (0.14)	5.07 (2.58)
Barking deer	Summer	Core	HRC	0.20 (0.01)	0.821	124	1.22 (0.03)	1.36 (0.16)	1.66 (0.20)
		Buffer				51	1.25 (0.06)	1.68 (0.30)	2.11 (0.40)
	Winter	Core	HRC	0.23 (0.03)	0.897	127	1.12 (0.02)	1.99 (0.22)	2.23 (0.26)
		Buffer				56	1.31 (0.08)	1.80 (0.35)	2.37 (0.49)
Barasingha	Summer	Core	UC	0.3 (0.02)	0.810	32	15.9 (3.54)	0.10 (0.03)	1.59 (0.70)
		Buffer	–	–		–	–	–	–
	Winter	Core	UC	0.6 (0.08)	0.882	40	7.5 (1.42)	0.20 (0.10)	1.52 (0.81)
		Buffer	–	–		–	–	–	–
Chousingha	Summer	Core	HRC	0.25 (0.01)	0.892	8	1.39 (0.26)	0.06 (0.02)	0.09 (0.04)
		Buffer				–	–	–	–
	Winter	Core	HNC	0.18 (0.01)	0.823	10	1.37 (0.07)	0.08 (0.03)	0.11 (0.04)
		Buffer				–	–	–	–
Nilgai	Summer	Core	HRC	0.20 (0.01)	0.727	4	1.41 (0.45)	0.04 (0.03)	0.06 (0.05)
		Buffer				16	2.69 (0.45)	0.19 (0.10)	0.52 (0.28)
	Winter	Core	HNC	0.13 (0.01)	0.721	12	5.08 (1.13)	0.06 (0.03)	0.33 (0.20)
		Buffer				14	2.5 (0.38)	0.17 (0.05)	0.44 (0.16)

A single global detection function was modelled for each species by pooling data from the entire study area, while density for each management strata was estimated subsequently in program DISTANCE

SE standard error, *KS* Kolmogorov–Smirnov test. Best models are *UC* uniform cosine, *HNC* half-normal cosine, *HRC* hazard rate cosine

miscellaneous forest in winter (Tables 2 and 3). Sambar exhibited preference for bamboo-mixed habitat in both summer and winter seasons (Fig. 2c and d; Tables S3 and S4). Sambar clustered in similar size groups across habitats and seasons. Gaur densities were highest in sal forest in summer and miscellaneous in winter. Gaur showed a major seasonal shift in density from bamboo-mixed and sal forest in summer to miscellaneous forest in winter (Tables 2 and 3). They preferred sal in summer, whereas in winter, gaur showed preference for miscellaneous forests (Fig. 2e and f; Tables S3 and S4). Wild pig density was also found to be higher in bamboo-mixed habitat, and seasonal densities were similar across all habitats (Tables 2 and 3). Wild pig showed preference for bamboo-mixed habitat in both summer and winter (Fig. 2g and h; Tables S3 and S4). Barking deer had highest densities in bamboo-mixed and miscellaneous forests (Tables 2 and 3) and also showed preference for these habitat types (Fig. 2i and j; Tables S3 and S4). Barasingha being obligate to grassland were only detected in grassland habitat (Tables 2 and 3), while

Table 2 Habitat-specific summer densities and biomass of major ungulates in Kanha Tiger Reserve 2013

Habitat type	species	Best model	KS test p value	No of observations (n)	Effective strip width (ESW) [SE] m	Encounter rate(n/l)	Detection probability $\hat{P}$ (SE)	Group Density $\widehat{DS}$ (SE)	Mean Cluster size E(S) (SE)	Density $\hat{D}$ (SE)	Biomass Kg/km^2 (SE)
Grassland	Chital	UC	0.831	82	122.5(14.2)	1.13	0.56 (0.05)	4.64 (1.63)	23.7 (2.99)	110.09 (41.15)	5174 (1934)
	Sambar[a]	UC	0.869	36	86.08 (6.62)	0.20	0.55 (0.04)	1.21 (0.39)	2.93 (0.26)	3.55 (1.22)	483 (166)
	Gaur[a]	UC	0.869	21	86.08 (6.62)	0.11	0.55 (0.04)	0.57 (0.22)	7.5 (1.88)	3.88 (1.91)	2177 (1072)
	Wild pig[a]	UC	0.831	20	122.5 (14.2)	0.11	0.56 (0.05)	0.88 (0.37)	5.12 (1.35)	3.01 (1.52)	81 (41)
	Barasingha	UC	0.882	32	182 (24.4)	0.40	0.6 (0.08)	1.10 (0.35)	14.34 (2.19)	15.8 (5.59)	2512 (889)
	Barking deer	–	–	–	–	–	–	–	–	–	–
Sal forest	Chital	HRC	0.619	91	74.05 (8.56)	0.42	0.41 (0.04)	2.84 (0.75)	7.94 (0.61)	22.61 (6.24)	1063 (293)
	Sambar	HRC	0.963	56	41.32 (5.81)	0.25	0.40 (0.05)	3.13 (0.83)	2.86 (0.25)	9.0 (2.52)	1224 (343)
	Gaur	HNC	0.795	29	48.44 (9.56)	0.13	0.42 (0.08)	1.38 (0.45)	6.96 (1.11)	9.65 (3.55)	5414 (1992)
	Wild pig	HNC	0.623	21	43.8 (5.90)	0.09	0.47 (0.06)	1.10 (0.34)	4.88 (1.26)	5.42 (2.17)	146 (59)
	Barking deer	HNC	0.829	24	39.37 (6.74)	0.11	0.69 (0.11)	1.41 (0.39)	1.41 (0.09)	1.99 (0.57)	36 (10)
Bamboo-mixed forest	Chital	HNC	0.615	71	46.72 (6.67)	0.4	0.18 (0.02)	4.36 (1.08)	8.04 (1.00)	42.56 (12.3)	2000 (578)
	Sambar	HRC	0.916	90	39.8 (5.09)	0.5	0.40 (0.05)	6.49 (1.34)	2.76 (0.16)	17.9 (3.88)	2434 (528)
	Gaur	HNC	0.675	22	47.22 (13.03)	0.12	0.20 (0.05)	1.33 (0.53)	4.52 (0.99)	6.05 (2.76)	3394 (1548)
	Wild pig	HRC	0.685	23	48.3 (13.2)	0.13	0.29 (0.08)	1.36 (0.53)	7.78 (1.90)	10.64 (4.89)	287 (132)
	Barking deer	HRC	0.939	34	28.6 (4.67)	0.19	0.22 (0.03)	3.4 (0.85)	1.33 (0.07)	4.55 (1.16)	82 (21)
Miscellaneous forest	Chital	HRC	0.601	115	54.5 (8.2)	0.26	0.35 (0.05)	2.41 (0.6)	9.08 (0.88)	21.97 (6.04)	1033 (284)
	Sambar	HRC	0.871	89	46.9 (5.09)	0.20	0.38 (0.04)	2.17 (0.47)	2.87 (0.19)	6.25 (1.42)	850 (193)
	Gaur	HRC	0.923	32	48.1 (14.6)	0.07	0.29 (0.01)	0.76 (0.30)	4.61 (1.04)	3.51 (1.62)	1969 (909)
	Wild pig	HRC	0.629	50	46.6 (3.62)	0.11	0.57 (0.04)	1.23 (0.23)	4.93 (0.73)	6.07 (1.47)	164 (40)
	Barking deer	HRC	0.670	62	48 (5.78)	0.14	0.38 (0.04)	1.47 (0.28)	1.14 (0.04)	1.69 (0.33)	30 (6)

UC uniform cosine, *HNC* half-normal cosine, *HRC* hazard rate cosine, *KS test* Kolmogorov–Smirnov test, *SE* standard error

[a] Indicates that we used pooled detection data for 2012 and 2013 to fit a detection function but report density, group density, cluster size and biomass only of 2013

Table 3 Habitat-specific winter densities and biomass of major ungulates in Kanha Tiger Reserve

Habitat type	species	Best model	KS Test p value	No of observations(n)	Effective strip width (ESW) (SE) m	Encounter rate (n/l)	Detection probability $\hat{P}$ (SE)	Cluster size Density $\widehat{DS}$ (SE)	Mean Cluster size E(S) (SE)	Density $\hat{D}$ (SE)	Biomass (kg/km^2) (SE)
Grassland	Chital	UC	0.679	84	81.7 (6.74)	1.16	0.40 (0.03)	7.15 (2.36)	14.74 (2.02)	103.5 (36.9)	4865 (1734)
	Sambar[a]	UC	0.909	26	67.68 (10.31)	0.18	0.22 (0.03)	1.33 (0.43)	2.38 (0.28)	3.18 (1.10)	432 (150)
	Gaur[a]	HNC	0.909	20	88.8 (20.95)	0.06	0.75 (0.17)	0.39 (0.20)	5.0 (1.30)	1.95 (1.13)	1094 (634)
	Wild pig[a]	UC	0.679	23	81.73 (6.74)	0.12	0.39 (0.09)	0.49 (0.18)	9.55 (1.47)	4.7 (1.8)	127 (49)
	Barasingha	UC	0.932	40	115.4 (17.09)	0.51	0.71 (0.10)	2.22 (1.06)	7.97(1.37)	17.7 (9.0)	2814 (1431)
	Barking deer	–	–	–	–	–	–	–	–	–	–
Sal forest	Chital	HRC	0.708	60	53.04 (12.54)	0.27	0.38 (0.09)	2.61 (0.93)	6.58 (0.60)	17.23 (6.33)	810 (298)
	Sambar	HRC	0.711	62	42.5 (39.23)	0.28	0.26 (0.02)	3.71 (0.7)	2.08 (0.14)	7.73 (1.66)	1051 (226)
	Gaur[a]	HNC	0.711	22	44.99 (11.71)	0.05	0.34 (0.08)	0.56 (0.23)	3.36 (1.40)	1.90 (1.11)	1066 (623)
	Wild pig	HNC	0.624	21	33.2 (8.11)	0.09	0.18 (0.04)	1.46 (0.47)	4.64 (1.27)	6.78 (2.9)	183 (78)
	Barking deer	HNC	0.764	31	36.9 (4.05)	0.14	0.59 (0.06)	1.94 (0.44)	1.01 (0.05)	1.97 (0.46)	35 (8)
Bamboo-mixed forest	Chital	HNC	0.611	75	47.09 (7.20)	0.43	0.25 (0.03)	4.57 (1.09)	7.6 (0.57)	34.74 (8.74)	1633 (411)
	Sambar	HRC	0.620	72	42.6 (15.9)	0.41	0.26 (0.09)	5.8 (1.16)	2.22 (0.15)	12.97 (2.7)	1764 (367)
	Gaur[a]	HRC	0.620	34	37.46 (7.93)	0.08	0.22 (0.04)	1.07 (0.39)	2.26 (0.68)	2.43 (1.15)	1363 (645)
	Wild pig	HRC	0.712	21	26.3 (10.7)	0.11	0.24 (0.09)	2.18 (1.15)	4.82 (1.26)	10.53 (6.24)	284 (168)
	Barking deer	HRC	0.670	20	51.2 (13.26)	0.10	0.46 (0.12)	1.0 (0.3)	1.0 (0.05)	1.01 (0.40)	18 (7)
Miscellaneous forest	Chital	HRC	0.744	103	51.8 (3.77)	0.23	0.47 (0.03)	2.29 (0.44)	10.15 (0.91)	23.33 (4.98)	1095 (234)
	Sambar	HRC	0.722	110	34.2 (2.91)	0.25	0.43 (0.03)	3.72 (0.64)	2.49 (0.14)	9.29 (1.69)	1263 (230)
	Gaur	HRC	0.747	68	47.9 (6.11)	0.15	0.40 (0.05)	1.64 (0.32)	4.95 (0.65)	8.13 (1.94)	4561 (1088)
	Wild pig	HRC	0.685	40	36.07 (7.13)	0.09	0.55 (0.11)	1.28 (0.39)	5.82 (1.02)	7.47 (2.63)	202 (71)
	Barking deer	HRC	0.600	69	31.22 (2.77)	0.15	0.61 (0.05)	2.55 (0.38)	1.60 (0.04)	4.07 (0.50)	73 (9)

UC uniform cosine, *HNC* half-normal cosine, *HRC* hazard rate cosine, *KS test* Kolmogorov–Smirnov test, *SE* standard error

[a] Indicates that we used pooled detection data for 2012 and 2013 to fit a detection function but report density, group density, cluster size and biomass only of 2013

chousingha were detected on transects in miscellaneous forests and plateau grasslands. Detection probabilities were highest for grassland habitat and lowest for bamboo forests for all species in both seasons (Fig. S5).

Discussion

By sampling habitats in proportion to their availability, our sampling design permits the conventional global analysis as well as habitat-wise analysis. The precision of density estimates depends on the variability in effective strip width, encounter rates and the cluster size (Thomas et al. 2010; Ogutu et al. 2005). We believe that by laying habitat-specific transects and subsequently analysing the data separately for each habitat type, we can minimize the variability contributed by ESW. However, sample size and encounters obtained in each habitat strata were small in comparison with the global analysis. The stratified analysis provides more ecologically meaningful results. Unfortunately, homogenous habitat patches of sufficient size to mark independent transect line within each habitat patch were not available in the human dominated buffer zone. We, therefore, could not extend the habitat-specific analysis to the buffer zone.

Core and buffer densities

Our study unambiguously demonstrates the impact of even low human use on wild ungulate densities. The core area, where there were no human habitations and had minimal use by humans, had higher densities of all ungulates except wild pig, barking deer and nilgai. The core had 4.8 times higher wild ungulate biomass compared with the buffer zone. This higher biomass density in the core area was due to both increased encounter rate and larger cluster size. It is well known that larger cluster sizes are found in resource-rich areas (Pulliam and Caraco 1984), suggesting that habitat quality was better in the core area for most ungulates. More importantly, barasingha and chousingha were found only within the core area of the Tiger Reserve and were either absent or occurred in very low densities in the multiple use buffer zone forests, highlighting the importance of undisturbed areas for endangered and rare ungulates. The depression of wild ungulates in the forests of the buffer zone was likely due to competition with livestock (Loveridge et al. 2010), extraction of minor forest produce and biomass, and subsistence level poaching (Steinmetz et al. 2010). In countries like India, with high human densities and associated high demand for land, protected areas are small by global standards (Lopoukhine et al. 2012). Harbouring viable populations of apex carnivores such as tigers in such small reserves is a major conservation concern. Our study lends support to the conservation strategy of relocating human habitation by incentivised voluntary relocation from core areas of Tiger Reserves; as such, areas would then support a much higher density of prey and subsequently the carnivore community, including tigers.

Habitat-specific seasonal densities

Seasonal habitat selection by ungulates is influenced by metabolic and nutritional requirements for maintenance, growth, rut, gestation and lactation (OwenSmith 1994). These physiological needs combined with predation risks vary across habitat types (Kie 1999) and determine animal distribution. Tropical India is highly seasonal due to the effect of monsoon. Ungulate densities are likely to respond to varying seasonal nutrient availability in different habitats.

Grasses grow during monsoon (July–September), mature and flower in October and November, and become senescent in summer (March–June). However, due to high soil moisture and management practice of late winter burn, most grasses produce a fresh flush of new shoots during early summer. Thus, protein and nutrient availability are maximum in monsoon and in a month of early summer after the annual late winter burn (February–March) in grasslands. In forested habitats, new flush of leaves, flowers and fruits emerge prior to monsoon in the peak of the dry summer season (May and June). Bamboo (*Dendrocalamus strictus*) produces new shoots at the beginning of summer and growth declines by October and November (Liese and Kohl 2015). Patterns of ungulate distribution may change in different times of the year because of plant growth, and thus, food availability changes between the seasons.

In our study, chital used grassland habitat throughout the year and maintained large herd size and high densities over other habitat types. Due to smaller mouth parts, chital could possibly obtain the required nutrients by selective foraging (Schaller 1967) even when the nutrient quality of grasslands declined in summer. Chital fawns have a “lying out” stage wherein they remain hidden in tall grass clumps and bushes for the initial few weeks of their life in winter (Schaller 1967). Thus, the requirement of food and cover by chital could potentially be achieved by living within grassland and bamboo-mixed forests in both the seasons.

Maximum densities of sambar were recorded in bamboo-mixed habitat throughout the year, and sambar also showed a high preference for this habitat type. Sambar are primarily browsers and prefer undulating to steep terrain (Hofmann 1989). Bamboo-mixed forests provide the maximum diversity of browse species, and this habitat type occurs on hill slopes, explaining the high density and preference shown by sambar for this habitat mainly in summer. The cluster size of sambar was small and similar across habitats.

Gaur are known for their seasonal movements (Imam 1985). Unlike other ungulates, there was a distinct difference in their seasonal densities between different habitats. During the summer, their density, as well as preference, was higher for sal forest. Plants such as *Flamingia spp*. and *Mallotus philippensis* sprout in sal forest during this season and are a significant source of food for gaur. During winter season, gaur mainly shift to areas with more browse and having dense plant cover. Gaur herds were observed to be larger in summer compared with winter in all habitats. During summers, water becomes a limiting factor in the higher elevations and gaur descend to valley habitats where they calve and rut (Schaller 1967). This results in larger aggregations of gaur in summer.

Conclusion and management implications

Our study stresses the importance of inviolate core areas for achieving high wild ungulate densities and for maintaining populations of endangered and rare species. We show the relevance of different habitat types for differential seasonal use by ungulates and attempt to interpret these in the context of nutrition and cover needs by wild ungulates. Much of the Kanha forest was worked for enhancing timber production in the past, and the current stands of sal forests are a result of selective thinning of non-timber species (Blakesley1905). Now the thrust of management within protected areas is for the conservation of diversity, endangered species and ungulate biomass to sustain viable populations of large carnivores. Maximum diversity and ungulate biomass were supported by grassland followed by bamboo-mixed habitat. Furthermore, endangered species like barasingha and blackbuck were found only in the grassland habitat. Grasslands account for 9 % of the KTR core area, most of which originated due to the anthropogenic activity of agriculture and livestock grazing. Most grasslands of KTR are currently maintained by management of woody plant removal and fire in this arrested stage of succession. Enhancing this habitat along with its appropriate management would help maintain ungulate diversity, cater to the needs of the only surviving population of the endangered hard ground barasingha and increase ungulate biomass so as to sustain a source population of tigers in this landscape. In historic times, a dynamic habitat mosaic was maintained in the larger landscape by natural processes of fire, flood and anthropogenic activities (Hansen and DeFries 2007). However, now these forces no longer operate at such a scale and wildlife populations of most species have become insular within protected areas. Therefore, interventions that manage these habitat mosaics in optimal conditions would be in the interest of achieving the conservation objectives of the protected area.

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Do conservation strategies that increase tiger populations have consequences for other wild carnivores like leopards?

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Most large carnivore populations are declining across their global range except in some well managed protected areas (PA's). Investments for conserving charismatic apex carnivores are often justified due to their umbrella effect on biodiversity. We evaluate population trends of two large sympatric carnivores, the tiger and leopard through spatially-explicit-capture-recapture models from camera trap data in Kanha PA, India, from 2011 to 2016. Our results show that the overall density (100 km^{-2}) of tigers ranged between 4.82 ± 0.33 to 5.21 ± 0.55SE and of leopards between 6.63 ± 0.71 to 8.64 ± 0.75SE, with no detectable trends at the PA scale. When evaluated at the catchment scale, Banjar catchment that had higher prey density and higher conservation investments, recorded significant growth of both carnivores. While Halon catchment, that had lower prey and conservation investments, populations of both carnivores remained stable. Sex ratio of both carnivores was female biased. As is typical with large carnivores, movement parameter sigma (an index for range size), was larger for males than for females. However, sigma was surprisingly similar for the same genders in both carnivores. At home-range scale, leopards achieved high densities and positive growth rates in areas that had low, medium or declining tiger density. Our results suggest that umbrella-species conservation value of tigers is likely to be compromised at very high densities and therefore should not be artificially inflated through targeted management.

The tiger, once widely distributed across Asia has now lost 93% of its former range[1] and currently occurs only in 11 countries[2]. India holds the largest wild tiger population estimated at about of 70% of the global population[3]. Due to its charisma, the tiger attracts conservation investments from Governments and civil society. Being an apex predator, it also serves as an umbrella for conserving Asia's forest biodiversity[4]. The leopard is more widely distributed across much of Africa and parts of Asia. Its status is less precarious compared to tigers, with whom the leopards are sympatric in Asia. However, despite being a generalist, capable of exploiting a multitude of habitats, prey, and adapted to live in close proximity with people[5] the leopard is still on the decline globally[6].

India has made large investment in the form of Protected Areas, human resettlement, law enforcement and habitat management to conserve tigers so as to reap their benevolent umbrella effect in protecting biodiversity[7] and ecosystem services[8]. Tigers being apex predators out-compete and often kill other predators like leopards, dhole, and sloth bear[9]. In areas of high tiger densities, leopard are likely out-competed[10]. High tiger density areas like Corbett and Kaziranga National Parks though having abundant prey, have very few leopards[3,11]. Habitats without refuge from tigers are devoid of leopards e.g. the mangrove swamp forests of Sundarbans. Understanding population response of leopards at various ecologically relevant spatial scales to tigers would provide insights on thresholds of the benevolent effect of tigers on sympatric large carnivores and at what densities tigers become detrimental to other threatened carnivores.

Often abundance estimates and population trends of threatened species are required for evaluating the success of management actions and prioritising conservation investments[12]. Despite their ecological importance, there are limited studies on long-term population trends of large carnivores[13]. Development of camera trap based classical capture-recapture[14,15] is the method of choice for estimating abundance of uniquely identifiable individuals of a species e.g. tiger[15], jaguar[16], leopard[10] and ocelots[17]. Most studies on tigers and leopards are limited

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Site	Sampling Year	Tiger						Leopard					
		Density ($100\,km^{-2}$)	g_0 Female	g_0 Male	σ (km) Female	σ (km) Male	Sex Ratio (M: F)	Density ($100\,km^{-2}$)	g_0 Female	g_0 Male	σ (km) Female	σ (km) Male	Sex Ratio (M: F)
Banjar Catchment	2011	6.34 ± 0.80	0.07 ± 0.003	0.05 ± 0.001	1.59 ± 0.05	2.56 ± 0.08	0.55 ± 0.03	4.36 ± 0.76	0.003 ± 0.001	0.003 ± 0.001	1.39 ± 0.09	2.98 ± 0.2	0.45 ± 0.09
	2012	6.99 ± 0.64			1.86 ± 0.07	3.00 ± 0.10		5.30 ± 0.66			1.64 ± 0.12	2.71 ± 0.08	0.37 ± 0.08
	2013	7.70 ± 0.53			1.64 ± 0.06	2.64 ± 0.09		6.10 ± 0.57			1.30 ± 0.08	2.58 ± 0.08	0.35 ± 0.08
	2014	8.49 ± 0.54			1.41 ± 0.02	2.27 ± 0.05		7.03 ± 0.59			0.79 ± 0.04	1.66 ± 0.07	0.54 ± 0.08
	2015	9.36 ± 0.74			1.39 ± 0.03	2.25 ± 0.05		8.09 ± 0.80			0.78 ± 0.05	1.68 ± 0.09	1.86 ± 0.09
	2016	10.32 ± 1.09			1.27 ± 0.03	2.04 ± 0.04		9.30 ± 1.26			1.04 ± 0.04	2.23 ± 0.08	0.54 ± 0.07
Halon Catchment	2011	2.27 ± 0.50	0.05 ± 0.003	0.04 ± 0.003	2.64 ± 0.16	3.74 ± 0.28	0.66 ± 0.06	4.98 ± 0.97	0.04 ± 0.004	0.03 ± 0.002	1.21 ± 0.11	2.48 ± 0.20	0.46 ± 0.04
	2012	2.24 ± 0.37			2.30 ± 0.12	3.25 ± 0.23		5.32 ± 0.80			1.23 ± 0.12	2.54 ± 0.21	
	2013	2.21 ± 0.29			2.46 ± 0.15	3.58 ± 0.23		6.00 ± 0.67			1.17 ± 0.09	2.41 ± 0.20	
	2014	2.19 ± 0.29			2.21 ± 0.89	3.13 ± 0.14		6.59 ± 0.64			1.05 ± 0.08	2.16 ± 0.20	
	2015	2.16 ± 0.36			2.40 ± 0.16	3.39 ± 0.19		7.24 ± 0.82			1.01 ± 0.06	2.08 ± 0.13	
	2016	2.13 ± 0.47			2.08 ± 0.87	2.95 ± 0.13		7.95 ± 1.19			1.34 ± 0.07	2.76 ± 0.13	
Kanha National Park	2013	5.21 ± 0.55	0.04 ± 0.001	0.03 ± 0.0008	2.60 ± 0.50	3.03 ± 0.75	0.66 ± 0.03	6.63 ± 0.71	0.018 ± 0.001	0.02 ± 0.001	1.40 ± 0.06	2.52 ± 0.09	0.50 ± 0.02
	2014	5.01 ± 0.34			1.59 ± 0.23	2.37 ± 0.45		7.24 ± 0.49			1.34 ± 0.04	2.44 ± 0.06	
	2015	4.87 ± 0.33			1.95 ± 0.35	2.91 ± 0.52		7.90 ± 0.46			1.59 ± 0.63	2.86 ± 0.08	
	2016	4.82 ± 0.33			1.85 ± 0.30	2.76 ± 0.44		8.64 ± 0.75			1.84 ± 0.50	2.92 ± 0.07	

Table 1. Density (±SE at $100\,km^{-2}$), detection probability (g_0), spatial scale of detection (σ km), and detection corrected sex ratio of tigers and leopards in Kanha National Park, Halon and Banjar Catchments.

to assessment of their abundance[3,10,15,18], while studies that address other demographic parameters are rare[19–22]. Most population trend studies on tigers use either classical non-spatial closed capture-recapture models[21,23] or statistically less rigorous track counts[24]. Herein, we use spatially explicit capture recapture (SECR)[25,26] to estimate tiger and leopard spatial densities, sex ratios[27] and their trends over a six-year period in Kanha National Park, a major stronghold for both species in Central India. We demonstrate the importance of monitoring, both at local and PA scales, so as to gain an understanding of spatial population dynamics and guide conservation management with site specific information. We analyse our data at home-range scales to gain insights into how leopards and tigers interact over time and space.

Results

With an annual effort ranging between 3992 to 34868 trap nights we photo-captured 125 adult tigers that included 61 males and 64 females; 217 adult leopards that included 78 males, 120 females and 19 of unknown gender. Total annual photo-captures for tigers for the PA were between, 122 to 1584 and for leopard between, 57 to 935. The mean number of captures for an individual tiger were 9 (range 1 to 45) photo-captures, while for leopards were 3.8 (range 1 to 20) photo-captures. None of the individuals in the study were photo-captured in Banjar as well as Halon catchments within the same year, suggesting a clear separation between sites in the short-term. However, 04 tigers and 01 leopards were observed to have dispersed between catchments between sampling periods (years). The mean maximum (±SE) distance moved by tigers was 6.5 ± 0.48 km (Max 25 km), for leopards the estimate was 5.16 ± 0.60 km (Max 28.6 km; Table S1). The gender of all tigers and 91% of leopards were identified from camera trap photos.

The best model for both tigers and leopards for the entire data representing Kanha National Park as well as for individual catchments was the same, wherein variation in g_0 and σ were explained by sex as well as sampling years (Table S2 & S3). Tiger density (±SE) of Kanha PA (at $100\,km^{-2}$) ranged between 4.82 ± 0.33 to 5.21 ± 0.55 and leopard densities (at $100\,km^{-2}$) between 6.63 ± 0.71 to 8.64 ± 0.75 (Table 1). Since variation in sex ratio between years did not contribute to explaining our data and was therefore not selected in the top model, we report the overall sex ratio for each catchment (except for leopard estimates in Banjar catchment, Table 1). Overall sex ratios in Kanha National Park (M:F) was biased towards females for both tigers (0.66 ± 0.03) and leopards (0.50 ± 0.02).

Mean abundance of tigers at the PA scale showed an annual decline of 2% ($R^2 = 0.94$; $P = 0.002$) and leopards showed an annual increase of 8.8% ($R^2 = 0.99$, $P < 0.001$) between 2013 to 2016. However, after considering the variability in the abundance estimates, the 95% confidence intervals on λ showed no detectible trends for both carnivores (95% CI on tiger $\lambda = 0.86$ to 1.07 and (95% CI on leopards $\lambda = 0.99$ to 1.20). Density for both tigers and leopards in Banjar catchment showed growth with a $\lambda = 1.10$ ($CI_{95\%}$ 1.02–1.18; $R^2 = 0.99$, $P < 0.001$) for tigers and $\lambda = 1.15$, ($CI_{95\%}$ 1.05–1.27; $R^2 = 0.99$, $P < 0.001$) for leopards. For the Halon catchment tiger density remained stable at $\lambda = 0.98$ ($CI_{95\%}$ 0.86–1.14) while leopard density increased at $\lambda = 1.09$ but was statistically insignificant ($CI_{95\%}$ 0.98–1.22).

Sigma, which is an index of home-range size was higher in males compared to females in both tigers and leopards (Table 1). Interestingly σ's of tigers and leopards were similar for the same sex (Table 1). Average σ, the scale parameter estimated by SECR, showed a declining trend with increasing density for both genders of tigers (♂, $r = -0.93$ *&* ♀, $r = -0.94$; $P < 0.001$) and leopards (♂ $= r - 0.56$, $P = 0.056$; ♀ $= r - 0.57$, $P = 0.05$) (Fig. 1). Simulation results of 100 regression analysis showed that in all cases (both genders) for tigers and leopards the slope of the regression was negative (Table S4). The 95% confidence interval for the slope of the regression

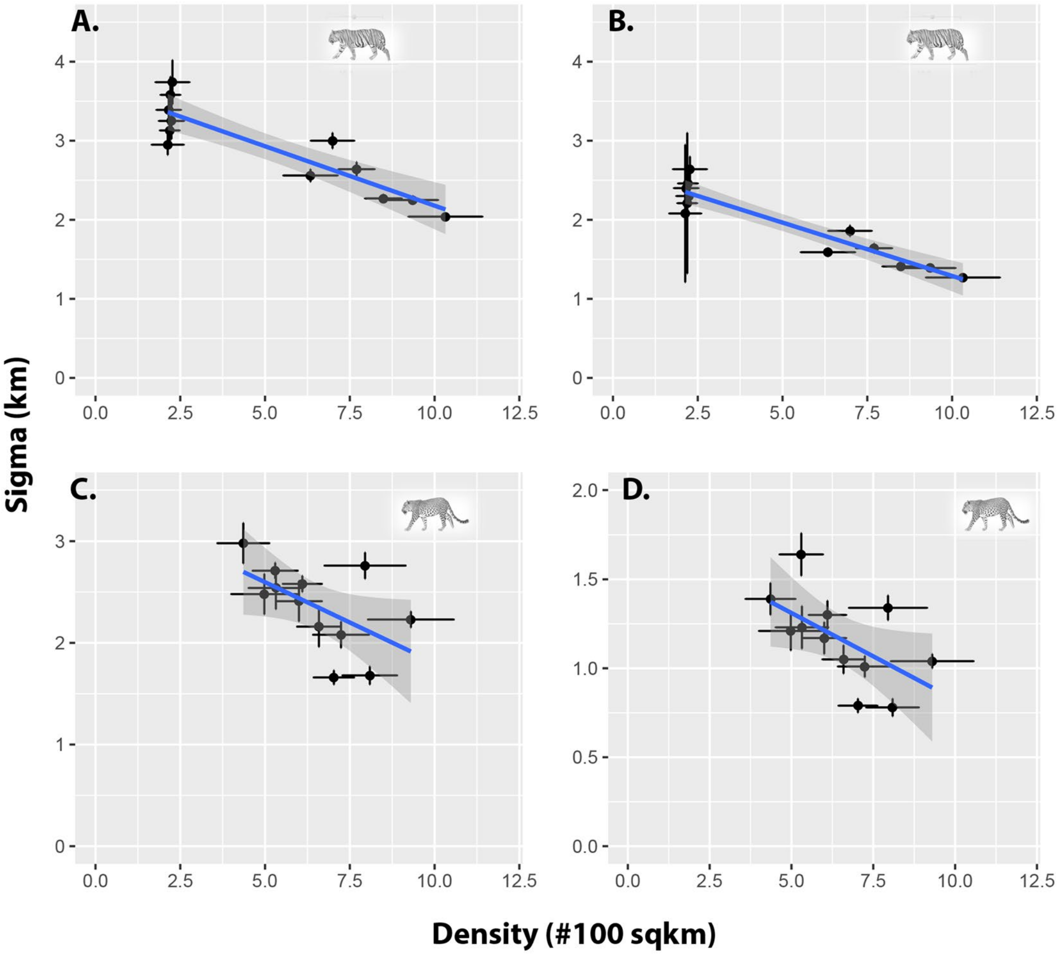

Figure 1. Relationship between Sigma σ (km ± SE), an index of home-range *vs* Density (at 100 km^{-2} ±SE), (**A**) female tigers, (**B**) male tigers, (**C**) female leopards and (**D**) male leopards.

for both genders of tigers and leopards was negative and did not include zero. Therefore, we concede that the observed declining trend in σ with increasing density was genuine and not an artefact of sample variability.

At tiger home range scale (10 km^2 grids), leopards achieved high density in areas with low, medium or declining tiger density. Leopard populations showed positive growth in areas with low to medium-stable or declining tiger density (Fig. 2).

Discussion

Often placement of cameras is such that they attempt to maximize photo-captures of the target species, in our case the tiger. However, such placement that results in enhanced precision for tigers (more frequent recaptures) does not enhance photo-captures of leopards that often avoid the most frequented paths used by tigers[28]. The use of one sampling design, which can accommodate precise density estimates for both tigers and leopard, was initially a challenge. This was addressed by increasing camera density and placement of some cameras away from large trails and dirt tracks that tigers often use and leopards avoid. The SECR based density estimates are mostly robust to bias but require a proper sampling design for achieving good precision[29,30]. Based on the recommended sampling design[29,30] for an unbiased density estimate, placement of camera traps should be at distances less than the home-range radius of the target species, while the size of the sampled area should be greater than 1.5 times the home-range size of the target species. Our study met these minimal criteria for both, tigers and leopards. The high density and small inter-camera distances ensured that each tiger/leopard had the potential to be exposed from one to several cameras and there were no "holes" in the study design.

The overall density of tigers and leopards in Kanha National Park did not show any trend. Density of leopards was significantly higher than tigers. The two sampling blocks, Banjar and Halon catchments, were selected based on substantial differences in prey densities and conservation investments with the objective of studying the response of large carnivores to these differences. Contrary to our expectation, both predators occurred at reasonably high densities and both showed positive growth in the Banjar catchment. Here, tigers density (at 100 km^{-2}) significantly increased from 6.34 to 10.32, while leopard density (at 100 km^{-2}) increased from 4.36 to 9.30 (Table 1). While in Halon catchment that had lower prey density and less investment in conservation management, both carnivores did not show a detectable increase. Tigers are more K-selected when compared to leopards[31] and should exhibit slower life history traits manifesting in slower population growth when compared

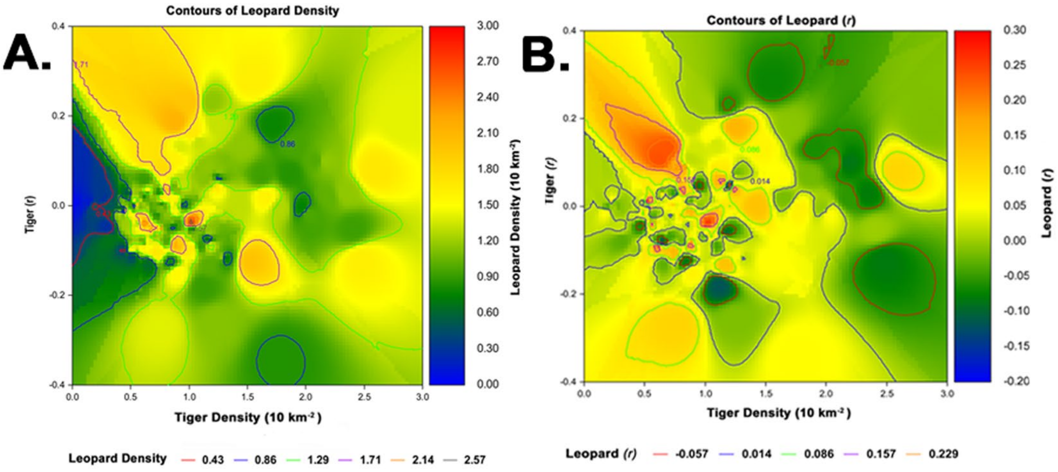

Figure 2. (**A**) Heat and contour map of leopard density plotted against tiger density and tiger growth rate (r). (**B**) Heat and contour map of leopard growth rate (r) plotted against tiger density and tiger growth rate. Density of both tiger and leopard was estimated by SECR and growth rate estimated for each 10 km^2 pixel by regressing Ln(Density) against years.

to leopards. But contrary to our expectations, the growth rate of leopards was comparable to that observed for tigers. This result is suggestive of competitive inhibition of leopards by the larger tiger. Besides competing for food (which was plentiful), tigers are known to pursue and kill leopards[9]. Leopard densities were significantly higher compared to tiger densities in Halon catchment and both carnivore populations did not show growth here. We believe that this was a due to high human disturbance and possibly due to poaching of prey and carnivores. Leopards fare better than the tiger when faced with poaching, since there is higher illegal demand for tiger body parts compared to leopards, and leopards have faster life history traits compared to tigers[31]. This was reflected in Halon catchment that had more leopards compared to tigers.

Home-range scales to body size[32]. Smaller carnivores are expected to have smaller ranges compared to larger carnivores especially when both have similar food habits and foraging strategy[33]. We therefore, expected leopards to have smaller σ compared to tigers. Our study showed contrary results where σ was similar for tigers and leopards. This suggests that leopards in Kanha Tiger Reserve had to invest almost as much in movement as tigers, that are three times larger in size. This further points to the high adaptability of leopards that not only survive well in human dominated landscapes[5] but also do well in areas with high tiger density through higher investments (e.g. maintaining large home-ranges).

Efford *et al.*[34] showed an exponential decline in σ with increasing tiger density at landscape scales[34]. Density dependent home range sizes have been published for many species[22,35,36]. These suggest that home-range size adjusts like an elastic disk to changes in density[37] and when nearing carrying capacity the rate of decrease in home-range size is no longer possible (reaches an asymptote). Our local scale data for σ of both tigers and leopards showed a linear decline with density suggesting that the population of both tigers and leopards was not yet at carrying capacity and could potentially increase further.

In SECR the density surface depicted by the model (without covariates) is of the realized capture process and not the actual density estimated after correcting for capture probability[38]. In our case, since we had a high density of camera traps and a reasonable number of trap nights the difference between the photo-captured individuals (M_{t+1}) and the population estimate $\hat{N}$ were close (see Table 2) and therefore the surface depicting tiger and leopard photo-captures would be very close to the actual density. At the fine scale of home-range, our heat and contour plots clearly show that though leopards coexisted with tigers, they paid a price for this coexistence and achieved high density only in areas that had either low tiger density or where tiger density showed declines. Growing leopard populations were found in low tiger density areas or areas with declining tiger density (Fig. 2). All of the above independent population response assessments (large home-ranges, regions with high leopard density and growth at fine home range scale) point to the costs to leopards for being sympatric with tigers.

Earlier estimates using non-spatial CMR as well as most SECR estimates rarely take into account local variations in density, and population well-being is usually inferred from the overall response in density and its trends for a PA or catchment. This could mislead policy and management decisions[39]. Our study highlights the importance of estimating densities at various scales since diverse responses to differential management, prey populations and demography of apex carnivores are possible within the same PA. The low-density area of Halon catchment would benefit substantially by an increased protection regime and reduction of human disturbance. SECR when employed with a proper study design provides results required for site specific management of endangered species populations.

Often charismatic large carnivore populations, like those of Asiatic lions (*Panthera leo*) and tigers are intensively managed through habitat manipulations, health care interventions, baiting, and regulating social mortality in PA's of India[22,40]. Such well-meaning management interventions can inflate local or PA densities of these apex carnivores that can often be detrimental to other carnivores, prey, and even alter the natural selection processes

					Tiger			Leopard		
Site	Sampling Year	Camera Locations	Effort(Trap nights)	Average Trap distance (Km)	No. detections	Unique Tigers (M, F)	Population Estimate Realised ($\hat{N}$)	No. detections	Unique Leopards (M, F, UN)	Population Estimate Realised ($\hat{N}$)
Banjar Catchment	2011	58	2842	1.8	314	33 (13, 20)	35 ± 1.5	84	20 (9, 10, 1)	22 ± 1.66
	2012	58	2092	1.8	253	33 (13, 20)	34 ± 1.3	86	21 (9, 11, 1)	24 ± 2.0
	2013	58	2610	1.8	291	41 (16, 25)	44 ± 1.71	100	24 (9, 12, 3)	30 ± 2.76
	2014	279	8129	0.5	965	53 (23, 30)	54 ± 0.98	129	29 (13, 16, 0)	36 ± 2.70
	2015	140	4848	1.0	686	45 (19, 28)	48 ± 1.73	75	30 (23, 7, 0)	39 ± 3.34
	2016	140	6468	1.0	849	47 (23, 24)	51 ± 2.01	257	37 (17, 18, 2)	42 ± 2.43
Halon Catchment	2011	38	1368	1.8	122	10 (2, 8)	10 ± 0.19	61	15 (8, 7, 0)	17 ± 1.72
	2012	38	1900	1.8	192	12 (5, 7)	12 ± 0.17	57	14 (8, 6, 0)	16 ± 1.69
	2013	38	1824	1.8	121	10 (5, 5)	10 ± 0.13	72	16 (7, 8, 1)	19 ± 1.87
	2014	191	3831	0.5	276	14 (8, 6)	14 ± 0.08	91	19 (8, 11, 0)	21 ± 1.53
	2015	98	2346	1.0	165	12 (8, 4)	12 ± 0.09	115	25 (10, 14, 1)	27 ± 1.53
	2016	98	4280	1.0	206	9 (4, 5)	09 ± 0.08	269	28 (11, 17)	29 ± 0.85
Kanha National Park	2013	155	7595	1.8	542	60 (26, 34)	61 ± 0.9	250	57 (22, 28, 7)	71 ± 4.35
	2014	758	34868	1.8	1584	74 (37, 37)	74 ± 0.48	520	84 (35, 48, 1)	91 ± 2.71
	2015	384	15360	1.8	1179	62 (27, 35)	62 ± 0.49	335	85 (41, 40, 4)	91 ± 2.49
	2016	384	18816	0.5	1477	62 (27, 35)	62 ± 0.46	935	105 (38, 62, 5)	109 ± 2.17

Table 2. Sampling effort, detections and population estimates of tigers and leopards within Kanha National Park, Banjar and Halon catchments between 2011 to 2016. M- male, F- female, UN- unidentified sex.

operating within these apex carnivores[40]. Our data shows that leopards can coexist with tigers, but with potentially high costs, we believe that similar response would be seen for sloth bear and dhole. The benevolent role of tiger conservation as an umbrella species would be best achieved by allowing natural process to which these species have adapted for sympatric coexistence, management should attempt to reduce human impacts within PA's and refrain from the urge to increase the population of the apex carnivore by population and habitat manipulation beyond a point. In this study, using camera trap SECR with sex based heterogeneity models[27,41] we have gained significant ecological insights on the likely role interactions, prey, and good protection play on population response of two sympatric large carnivores. Leopards response to tigers varied with scale, at PA and catchment scale, prey and protection regime were dominant factors determining the response of both carnivores. While at home-range scale, tiger density and demography depressed leopard demography.

Methods

Study area. Kanha National Park is one from the first group of seven tiger reserves established in 1973. It is situated in Mandla and Balaghat districts of Madhya Pradesh state in India. The Kanha National Park is 940 km^2 and encompasses the catchments of two rivers, the Banjar and Halon. A narrow ridge of Bhaisanghat separates these two catchments. Since its inception as a National Park in 1955, the Banjar catchment gained considerable conservation investment where majority of the villages were relocated prior to 1998. Additionally control of poaching, law enforcement and habitat restoration in the form of water and grassland management by woody and invasive species removal is being practiced here. In the Halon catchment, which was added to the National Park in 1976, there was far less investment and human habitation resettlement was done more recently (last village resettled in 2017).

We believe, that as a result of higher interventions in the Banjar catchment, it has higher prey densities and biomass (33,963 kg/km^2) and less anthropogenic pressure due to the absence of villages. While the Halon catchment has an ungulate biomass of 7257 kg/km^2 [42,43]. By 2017, most of the villages from Halon catchment were also relocated and conservationists are hopeful of prey recovery. The ungulate density of Kanha National Park was 50 ± 4.80/km^2, which is one of the highest prey densities in Asian PA's with a biomass of 26,806 ± 2,573 kg/km^2 [44].

Methodology. We used camera trap based mark-recapture framework[15] to estimate spatially explicit densities of tigers and leopards[25]. We divided our survey area in two regions i.e. Banjar catchment and Halon catchment based on prey densities and logistical reasons. In the initial 2 years 2011 to 2012 our sampling areas were smaller, an area of 280 km^2 in Banjar catchment and 180 km^2 in Halon catchment with average trap spacing of 1.8 km (Table 2). Later, from 2013 to 2016, with availability of additional resources, we were able to sample the entire National Park of 916 km^2 (Fig. 3). We conducted extensive sign surveys to select the best possible location of camera traps. Two camera traps were placed at a single location to photo-capture both flanks of each animal that passed between them. Cameras were placed on forest roads, animal trails and dry streams that were intensively used by tigers and leopards to maximize their detections[15]. We identified individual tigers and leopards from their pelage pattern and prepared capture histories for each individual using Program Extract Compare[45] and Hotspotter[46].

We used maximum likelihood based spatially explicit capture recapture (SECR) to estimate densities[25].The basic parameters for this model are detection probability at the home-range centre, g_0 and spatial scale of detection, σ. For SECR animals are assumed to be distributed independently in space and occupy home-ranges. The

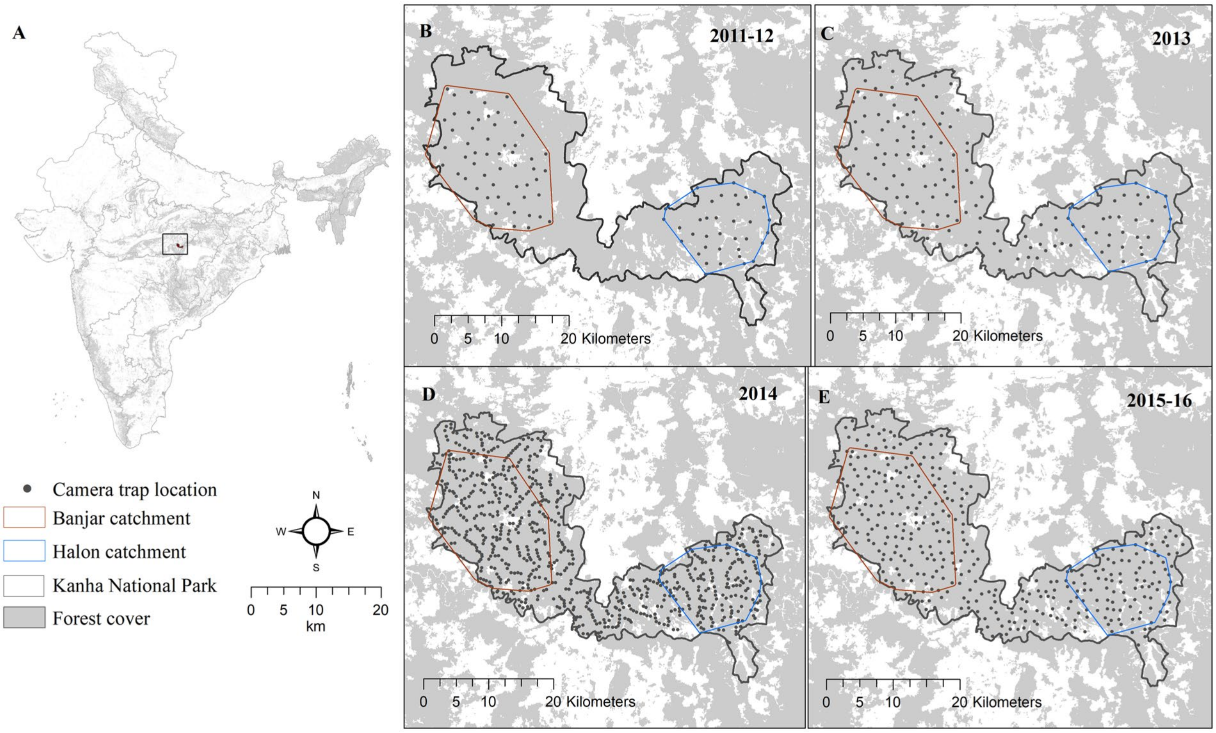

Figure 3. Study area and study design at Kanha National Park (**A**) Map showing location of Kanha National Park in India, Sampling design (**B**) in 2011 & 2012, (**C**) in 2013, (**D**) in 2014, and (**E**) in 2015 & 2016. Data from areas that were consistently sampled across all years (Banjar catchment -brown polygon, Halon catchment -blue polygon) were used for trend analysis.

model incorporates spatial locations of captures to estimate detection probability (g) as a declining function of increasing distance (σ) from the animal's activity centre[47] akin to distance sampling[48]. We analysed our data using package "secr" (version 3.1.8)[38] on R platform. For estimating trends in density, we used data from the area that was consistently sampled across all years. Capture histories for tigers and leopards were recorded for both blocks separately between 2011 to 2016 as well as for the entire Kanha National Park between 2013 to 2016. We used multisession model of SECR to estimate densities and their trends across all sessions (years), to compute the finite rate of increase (λ) by fitting session as a predictor in the model[38]. We used an 8 km buffer around the outermost trap locations as model space. The buffer width was decided based on our data, using "suggest.buffer" argument of secr 3.1.8[38]. The suggested buffer was between 7–8 km for both species, hence we choose 8 km buffer width for both tigers and leopards. We removed non-habitat (human settlements) from the buffer to get the final region of model integration, i.e. the habitat mask for estimating density.

Males and females of large felids have different home-range sizes[49]. Hence, sex specific movement could potentially be a source of variability in capture probability[41]. We identified genders of tigers and leopards based on genitalia and secondary sexual characters (nipples) from our long-term dataset. We accounted for potential sources of variability in our data by modelling g_0 and σ as a function of gender and sampling year (as density was likely to change between years and potentially alter σ).

We used hybrid mixture models of SECR ("hcov" argument in secr) using full likelihood approach to accommodate the unsexed individuals and allocate them to gender classes based on their detection (g_0) and movement (σ) parameters. The mixing parameter *pmix* indicates and models the detection parameters to the two sexes (male & female) as a two-class mixture. The parameter *pmix* gives us the detection corrected sex ratio as a mixing proportion of the sexes. We selected the best model based on Akaike information criteria corrected for small samples (AICc)[50].

Movement parameter σ, is often used as a surrogate for home range size[34]. At landscape scale, home-range as indexed by σ, was shown to be density dependent as it declined exponentially with tiger densities[34]. We test this premise at the PA scale[22] by modelling σ as a declining function of tiger and leopard density. For regression analysis a prerequisite is that x values (independent variables) are known with certainty[51]. In our case, the independent variable i.e. tiger and leopard density were estimates, where leopard densities in particular had large variances (see results) making inference from simple regression analysis questionable. To address this discrepancy, and ascertain that the pattern we observed from our regression model (σ versus density) was not due to chance variation in our data, we simulated 100 values of σ and density for both sexes of tigers and leopards for each year using the mean and standard deviation of our estimates. We ran 100 regression models by randomly choosing from this simulated data of σ and density and computed the average slope, R^2 values, and their 95% confidence intervals. If our hypothesis of declining sigma with increasing density were true, then the 95% confidence intervals on the slope of the regressions would be negative.

Since SECR models are spatially explicit in nature, they produce fine scale density maps[52]. We generated spatial variation maps of tiger and leopard densities within the sampled area and a buffer of 3 km width (equal to one σ of tiger and leopard). We also estimated population size of both tigers and leopards within this same region[53].

To understand how leopard population responds to the density and growth of tigers at the scale of a home-range (10 km^2) of breeding tigresses[54], we extracted the density and computed growth rates (r) of tigers and leopards in each grid of 10 km^2 from data between 2013 to 2016 for entire Kanha National Park. For each grid, we estimated the growth rate (r) for both carnivores by regressing Natural log of density against years[55]. We plotted leopard density and growth rates (heat and contour plots) against tiger density and tiger growth rates to evaluate the demographic response of leopards to tiger demography.

Data Availability

Photo-capture matrices of tigers and leopards are not publicly available due to threat of poaching. All other data are either in the main paper or in the Supplementary Material.

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Author Contributions

Y.J. and Q.Q. conceived, supervised, and secured resources for the study. U.K. and N.A. conducted the fieldwork. U.K. and Y.J. did the data analysis, U.K. and Y.J. wrote the M.S., and all authors reviewed and approved the M.S.

Additional Information

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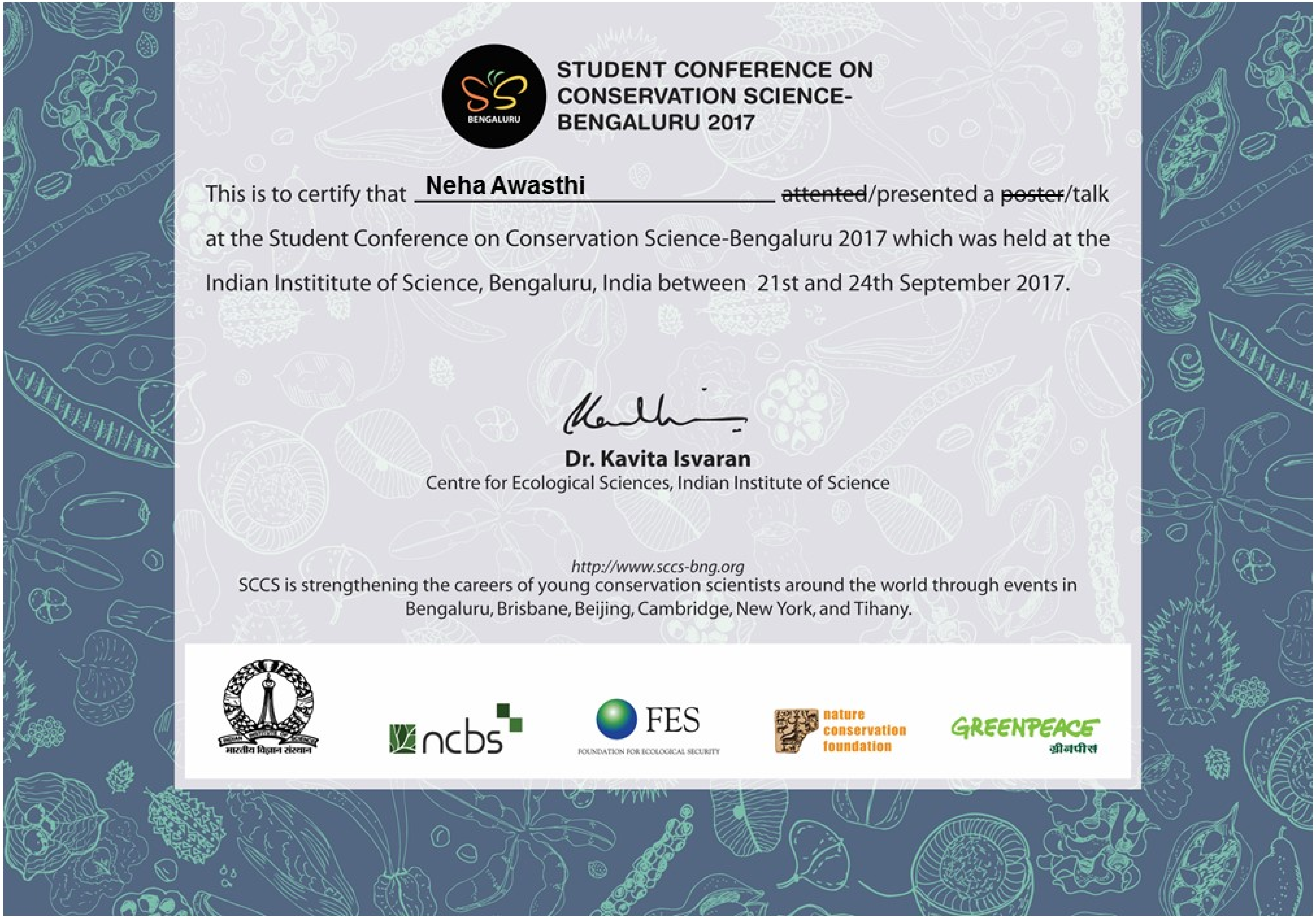

BENGALURU

STUDENT CONFERENCE ON CONSERVATION SCIENCE-BENGALURU 2017

This is to certify that **Neha Awasthi** ~~attented~~/presented a ~~poster~~/talk at the Student Conference on Conservation Science-Bengaluru 2017 which was held at the Indian Instititute of Science, Bengaluru, India between 21st and 24th September 2017.

Dr. Kavita Isvaran
Centre for Ecological Sciences, Indian Institute of Science

http://www.sccs-bng.org
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CERTIFICATE

OF EXCELLENCE

This Certifies that

Neha Awasthi

had distinction for the Best Oral Presentation/ ~~Speed talk cum Poster~~/ ~~Poster~~/ ~~Nature Film~~ in YETI 2017 - Tezpur held at Tezpur University, Assam from 4th January 2017 to 7th January 2017

YOUNG ECOLOGISTS TALK AND INTERACT

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Student Conference on Conservation Science

Department of Zoology
UNIVERSITY OF CAMBRIDGE

Conservation Science Group
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Web: www.sccs-cam.org

This is to certify that

Neha Awasthi

has attended the Student Conference on Conservation Science, 26-28 March 2019,

at the University of Cambridge, Downing Street, Cambridge, UK

and presented a poster entitled

"Factors affecting group-size of ungulates"

Administrator SPGreen

Date: 28 March 2019

Building links among young conservation scientists and practitioners