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FACTORS INFLUENCING SURVIVAL OF TIGER AND LEOPARD IN THE HIGH-ALTITUDE ECOSYSTEM OF THE NILGIRIS, INDIA

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Abstract. Tiger conservation is a global initiative, and data on distribution, prey dynamics, competition, and range extension are critical factors in sustaining its fragile populations. We concentrated on evaluating the data pertaining to these variables in order to designate the high-altitude Nilgiri forest division as a tiger conservation unit. We gathered secondary data on animal density, mortality, and conflicts. We also conducted a people perception survey, a systematic grid-based prey species survey, and a tiger and leopard scat survey to assess the prey-predator relationship and understand human attitudes toward carnivore conservation. According to the findings, the Nilgiri forest division has a healthy prey base with positive or random prey-predator associations and a significant correlation between mammalian assemblages. Because the niche overlap between the tiger and the leopard is high, the latter broadens its niche and relies on wild prey in the shola fringes and tea estates. The tiger avoids human-dominated areas and prefers to stay in the shola, rarely venturing into tea estates. In contrast to previous considerations, we believe the Nilgiri forest division is an ideal tiger habitat. We specify that instead of being considered a connective corridor, the Nilgiri forest division may be merged with Mukkurthi National Park to form a high-altitude tiger reserve.

INTRODUCTION

The implementation of Project Tiger in the year 1973 made substantial progress in the Indian tiger conservation (Nayak et al. 2020). The extended efforts of the National Tiger Conservation Authority (NTCA) facilitated proper documentation of tiger abundance and occupancy in the different landscapes across India (Jhala et al. 2020). The implementation of Project Tiger also includes conservation with people participation and sustainably protecting their livelihood. New tiger reserves are coming into existence to broaden the endangered felid habitat, connectivity, and gene flow (Jhala et al. 2008; Hines et al. 2010; Yumnam et al. 2014; Singh et al. 2017; Kolipakam et al. 2019; Jhala et al. 2020). India's principal tiger conservation blocks are six major landscapes, including the high-altitude regions (Jhala et al. 2020), with major conservation units (tiger reserves) in lower altitudes. The tigers in the high-altitude pockets of the western Arunachal Pradesh were thought as extinct (Mishra et al. 2006), later Adhikarimayum and Gopi (2018) identified tiger presence in this region. Monitoring by the Global Tiger Forum (2019) identified the presence of tigers in high-altitude Himalayan regions of several Indian states (like Bengal, Sikkim, and Arunachal), as well as Nepal and Bhutan. The high-altitude tiger habitats have the potential to mitigate the issues related to climate change (Aggarwal 2019). In the approaching years of global warming, such habitats will become crucial conservation units and need to be protected with topmost priority. The high-altitude ecosystems of Nilgiris are less focused concerning predation and inter-species interactions of the tiger and its sympatric counterparts.

The problem of human-carnivore conflicts is a universal issue, where the people's attitude towards predators is vitally essential (Bhattarai and Fischer 2014). The conflicts with bigger carnivores can be fatal, ending in the retaliatory killing of predators (Wang and Macdonald 2006; Gurung et al. 2008; Inskip and Zimmermann 2009; Singh et al. 2015a, b). According to research from various landscapes, the rate of tiger and leopard mortalities varies, which may lead to a decline in the carnivore population in the landscape (Athreya et al. 2011; Singh et al. 2015a, b; Gubbi et al. 2021). Conflicts are primarily caused by predators' reliance on livestock due to a lack of wild prey, as well as inter-and intra-species competition (Bhattarai and Fischer 2014). The people's perception plays a significant role before drawing the conservative measure, otherwise it lacks local support (Graham et al.

2005). The people perception studies from the adjoining Mudumalai Tiger Reserve (Ramesh et al. 2019) indicate that attitudes differ among various local groups. The illiterate and those who depend on the firewood and forest products are hostile towards carnivore conservation efforts. Crop raiding intensity, the presence of wild herbivores in the village vicinity, and cattle picking are all indirect indicators of prey availability in the adjacent reserves. The negative human interactions directly or indirectly affect the trophic structure and transform the ecological communities (Woodroffe and Ginsberg 1998; Crooks 2002; Karanth et al. 2004).

The abundance of prey in an ecosystem determines the density of big cats (Carbone and Gittleman 2002; Treves and Karanth 2003; Karanth et al. 2004; Selvan et al. 2013). Prey availability, habitat suitability, and intra-guild competition all influence the presence of large predators (Gompper et al. 2016; Kafley et al. 2019). A good prey base, primarily ungulates, maintains a viable tiger population, whereas leopards consume a wide range of prey, including small and arboreal prey (Karanth and Sunquist 1995; Ramakrishnan et al. 1999; Karanth and Sunquist 2000; Harihar et al. 2007; Wegge et al. 2009; Karanth et al. 2011; Selvan et al. 2013; Thapa and Kelly 2017). Due to its larger body size than the leopard, the tiger includes prey of a higher weight class in its diet, allowing it to maintain a stable large prey population (Seidensticker 1976; Karanth et al. 2004). Tigers prefer relatively large and uninterrupted ranges with plenty of prey and avoid human settlements (Karanth et al. 2004; Wang and Macdonald 2009; Odden et al. 2010; Bhattarai and Kindlmann 2018). They prefer open grasslands, logged areas, and bordered areas as their primary habitats, whereas leopards are highly malleable and rely on human-modified landscapes such as croplands, tea estates, and agricultural plantations for movement, and the tiger avoidance varies depending on prey density (Johnsingh 1983; Bailey 1993; Linkie et al. 2003; Odden et al. 2010; Athreya et al. 2013; Bhattacharjee and Parthasarathy 2013; Navya et al. 2014; Odden et al. 2014; Sidhu et al. 2015; Kshettry et al. 2017). Studies demonstrated that when the tiger dominates in an ecosystem, the major co-predator (leopard) occupies the fringe and attempts to predate on livestock (Singh et al. 2013; Athreya et al. 2015; Gubbi et al. 2020; Puri et al. 2020). The co-existence of tiger and leopard is also influenced by landscape variability and human intervention (Gompper and Vanak 2008; Ripple et al. 2014; Karanth et al. 2017; Kshettry et al. 2017; Kafley et al. 2019; Thapa et al. 2021).

Sympatric predators can coexist, with limited competition, if the prey base is sufficient and resource portioning is effective (Selvan et al. 2013; Thapa and Kelly 2017). The people's perception of larger felid mortality, prey richness, and prey-predator relationship is not addressed in the upper Nilgiris, because the region is not considered a primary habitat for tigers and leopards. Population growth and activities such as urbanisation, agriculture, and tourism are on the rise in this landscape, with much of the shola region remaining fragmented and grasslands being replaced by tea plantations. The analysis of the trophic structure, conflict, mortality, and resource partitioning are of utmost importance to review the quality and suitability of the habitat in the NFD. The human-animal conflict is vital in understanding the prey base and prospects of sustainable conservation. The initial objective of our study was to assess the people's perception of wild animal presence and monitor the conflicts in the fragmented fringe areas and tea gardens. Secondly, we surveyed the prey encounter proportion and co-occurrence of tiger, leopard, and prey species in the forested and fringe areas. The final objective was to assess the prey utilisation by the co-predators in terms of dietary partitioning, niche breadth, and niche overlap.

MATERIALS AND METHODS

Study area

The Nilgiri forest division (NFD) is a new forest administrative unit formed by modifying the former Nilgiri South Forest Division (Figure 1). Tiger conservation units like Mudumalai, Sathyamangalam, Bandipur, and the Wayanad connects NFD from all sides (Jhala et al. 2020). The Nilgiri Hills are old mountain ranges and gain immense significance as they represent the point where the Eastern Ghats Mountain chain merges with the Western Ghats Mountain chain, reaching an altitude of ~ 2500 m asl. The Nilgiris is noted for its high level of endemism and is part of the Nilgiri Biosphere Reserve, a UNESCO recognized world heritage site. The Nilgiri North Division is located between 11^{o}10' and 11^{o}30' N latitude and 76^o 25' and 77^o 00' E longitude, includes the tehsils of Udhagamandalam (Ooty), Coonoor, Kotagiri, and Kunda. The NFD has eleven forest ranges (Paykara, Naduvattom, Parsons Valley, Korakundha, Udhagamandalam North and South, Kundha, Governor shola, Coonoor, Kattabettu, Kottagiri, and the Eastern Slopes of the Nilgiris) and 62 forest beats. The Nilgiri Forest Division shares boundary with the Mudumalai Tiger Reserve, Sathyamangalam Tiger Reserve, Mukkurthi National Park, Gudalur, Coimbatore Forest divisions (Tamil Nadu state), and the Silent Valley National Park (Kerala State).

The NFD has pine forests, *Eucalyptus* plantations, wattles, and fragmented shola regions interspersed with tea estates and agricultural lands. The total area of the forest division is 1,251.09 km^2, which includes 604.11 km^2 dense or medium forests, 359.59 km^2 open forests, 24.98 km^2 water bodies, and the remaining 262.42 km^2 non-forested region as per Bhuvan database, ISRO,

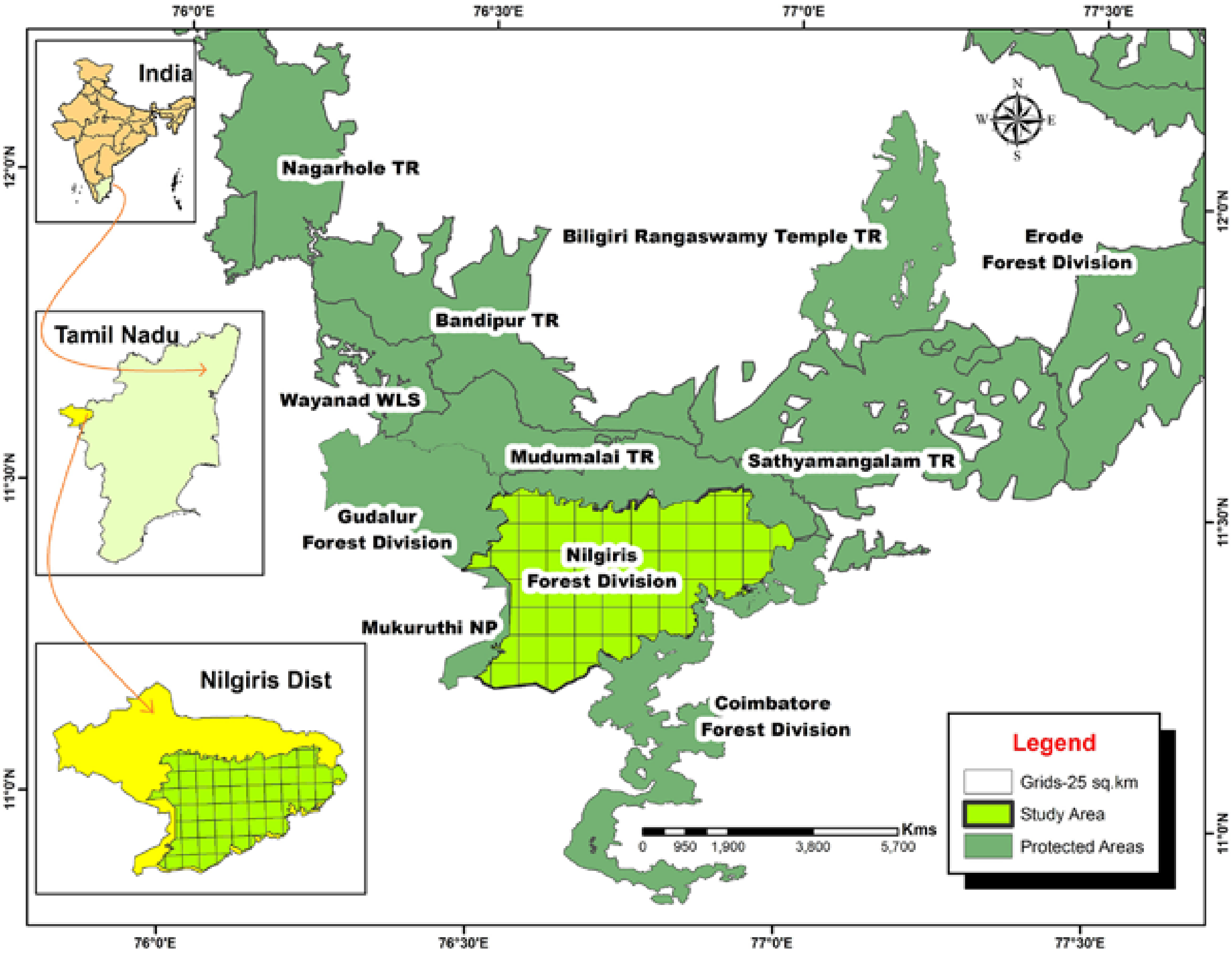

Figure 1. Study area map. The map shows the connectivity of the study area with other reserves. The sampled regions are presented as grids of 5 × 5 km which include both reserve and non-reserve areas.

India (http://bhuvan.nrsc.gov.in/). The existing natural vegetation is classified as southern montane wet temperate forests, Nilgiri sub-tropical hill forests, western sub-tropical hill forests, and southern dry mixed deciduous forests (Champion and Seth 1968). The temperature significantly rises to as high as 27ºC in April–May and drops to as low as -4ºC in winter during December–January. The plateau receives both the southwest and northeast monsoons, where the western rim (the Kundha region) gets the highest rainfall (~ 7,500 mm) during the southwest monsoon (June–August). The northeast monsoon is foremost in the western slopes (October–November), and the region is mainly human habituated. The Doddabetta range acts as a barrier to the free movement of the monsoon winds, dividing the plateau into two distinct climate zones.

Accession of secondary data

The general animal census data (2006–2016) of the Tamil Nadu Forest Department is accessed and used for our primary analysis. The ten years mortality and conflict data of tiger and leopard in the NFD was also obtained from the forest department. We also used the all-India tiger census data 2018 (Jhala et al. 2020) to assess the number of tigers, tiger density, and sex ratio in this region.

Questionnaire survey

We conducted a random questionnaire survey among the villagers/residents of houses /agriculturalists from the villages adjoined to the study location as a primary response. As the respondents are villagers from an agricultural background, we prepared the questionnaire in Tamil (the language of Tamil Nadu state) and orally explained it by the volunteers in the local language (Badaga), if needed. The questionnaire consists of 15 questions targeting the socio-economic status of respondents, details of wild herbivores, carnivores, and conflicts for the past ten years in their locality. We used the term livestock for domesticated ruminants and poultry for the domesticated fowls. The questions framed were short, direct, and simple to avoid response bias. We assessed the homogeneity of the responses by the chi-square test (χ^2) and ignored the skewed responses.

The survey helped us understand people's perception of tigers and leopards in their region, conflicts, crop-raiding, livestock, and cattle lifting.

Grid survey

We divided the entire NFD into a grid of 70 cells (5 × 5 km) of 25 km^2 using QGIS software (QGIS Development Team 2009) for systematic sampling. These grids are heterogeneous as they include the reserve areas (shola-grasslands), plantations, exotics, watershed regions, and human habituations. We surveyed the track paths and possible tracks of three segments comprising a 15 km walk in every grid cell. We sampled between 9.00 am and 3.00 pm from November to June in 2017–2018, and the effort taken was estimated as 3 × 70 = 210 sampling attempts in 5 km sampling segments for 70 grid cells (~15–20 km walk per day, which may cross multiple grids). We walked through the forest roads, track paths, and animal trails to record the direct and indirect signs. As a fragmented habitat, the track paths include shola vegetation, grasslands, *Eucalyptus*, *Pinus*, and wattle regions, tea gardens, other bushy forests, riparian regions, and agricultural areas. We use the term "shola region" to imply the shola forests, grasslands, forested areas, or forest plantations existing in the reserve forest areas and not actual shola vegetation alone. The scats, dungs, pellets, and signs were field identified and photographed for further confirmation. We collected the tiger and leopard scats in zip lock covers, with the details of GPS location.

Grid referencing and encounter ratio

According to the grids, the occurrence prints of various prey and predator species were plotted over the grid map in ArcGIS and tabulated further. The encounter proportion was estimated as the cumulative value of indirect signs and direct observations of a particular species per single effort (distance travelled in the grid through survey track). The prey species were classified as large prey (> 200 kg), medium prey (> 10 kg), and arboreal prey, and the cumulative encounter proportion, as well as the tiger and leopard, were mapped in the grid maps.

Scat identification

The tiger scat was differentiated from the leopard scats based on shape, size or diameter, endpoint, and presence of secondary evidence, i.e. pugmark (Norton et al. 1986; Rabinowitz 1989). The leopard and tiger scats are usually associated with tracks and signs, but some of the scat samples we collected were not associated with trails and signs. Tiger scats are less coiled with a more considerable distance between two successive constrictions (Johnsingh 1983). The herbivore dung and pellets were identified based on the shape and size and compared to the dried/preserved fecal specimens of herbivores maintained in our lab. Predator scat DNA was isolated using the QIAamp DNA Stool Mini Kit (QIAGEN, Cat No. / ID: 51504). We did the tiger and leopard identification using the AS-Nested method developed in our lab. (for detailed methodology, see Nittu et al. 2021).

Prey species identification

The complete hair samples or prey species were recovered in triplicate from the scat samples and washed in warm water. The hair samples were further fixed in formaldehyde (3% v/v), dehydrated in alcohol, cleared in xylene, and mounted using dibutylphthalate polystyrene xylene (DPX) in glass slides for trichological identification. The hair samples were observed for the proximal, distal, and middle regions to follow the cellular arrangement pattern. The length and breadth of the hair were also measured using micrometry, and we identified the prey species following the standard keys (Koppikar and Sabnis 1976; Easa 1995). We also compared the hair samples with the reference hair samples in the trichology collection of Molecular Biodiversity Lab., Ooty.

Frequency, rare resources, niche breadth, and overlap

The prey species frequency was calculated based on the scats collected, as the number of events of that prey species was divided by the total number of scats analyzed (Ackerman et al. 1984). Evenness measure (J)' of the Shannon-Wiener function (Colwell and Futuyma 1971; Hill 1973) scaled between 0 and 1 (scaled H') was used to understand the rare resources used by the predator. We estimated the niche breadth following the Levins (1968) equation by measuring distribution uniformity among the resource states. The niche breadth is standardized on a 0 to 1.0 scale by dividing the total number of resource states after correcting a finite number of resources (Hurlbert 1978). We followed Pianka's measure (Pianka 1986) to estimate the niche overlap between the tiger and the leopard.

Species co-occurrence

We used the 'co-occur' package (Griffith et al. 2016) in Rstudio (Rstudio Team 2020) to assess the spatial co-occurrence of the tiger and leopard with various prey species. This package helps to analyse the co-occurrence of the co-predators and prey using a probabilistic model described by Veech (2013). The package allows us to calculate the co-occurrence of two species at a lower (P_{lt}) or greater frequency (P_{gt}), which interprets it as a positive or negative co-occurrence (Shankar et al. 2020). We used the "ggpair" function of the GGally package in the RStudio to visualize the encounter scatter plot matrix.

RESULTS

Secondary data analysis

The available general census data (2006–2016) of the forest department (of the Nilgiri South Forest Division) indicated the presence of the sambar deer, Indian gaur, barking deer, wild pig, Nilgiri langur, bonnet macaque, giant squirrel, and Nilgiri tahr. The carnivores reported in the census were the tiger, leopard, hyena, wild dog, bear, jackal, and lesser cats. The report says there are not more than 2 or 3 tiger sightings during the entire period, and the most abundant number of carnivores reported was the wild dog, followed by the jackal and leopard. The ten-year census summary of the forest department is presented as an error bar and given as supplementary data (Supplementary Figure S1). The tiger census data of 2018 based on the camera trapping of NTCA (Jhala et al. 2020) shows 34 individual tigers in the Nilgiris forest division and four tigers in Mukurthi (a high-altitude National Park adjoined to the NFD). The tiger census of 2018 documented the tiger density in Nilgiris (NFD) as $3.04 \pm 0.52/\text{km}^2$ and the sex ratio as ~ 1:2.

According to the forest department's data (Supplementary Figure S2), five tigers (rate = 0.5/year) and eleven leopards (rate = 1.1/year) have died in the last ten years. Among the dead tigers, except one, all the others occurred in the reserve forest (shola regions). One death was reported due to poisoning as retaliation against livestock lifting. The case reports say that poisonous pesticides like fenvalerate were poured over the remaining carcass in the shola fringe. In contrast, all leopard deaths occurred outside the shola regions (one is a black panther) near human habituations or tea plantations. Two leopards died by accidentally getting entangled in the snare.

People perception analysis

We received 360 responses to the questionnaire from the fringe villages in the NFD. The respondents chiefly (74%) included males aged 30–60, finding their livelihood as tea leaf pickers (36%), firewood collectors (19%), and agriculturalists (45%). They primarily responded that the herbivores are a nuisance and not carnivores (84%). They complained about the carnivores as the reason for lifting livestock and poultry, but as an occasional one. Among the respondents, 47% opined that livestock lifting is rare (1 or 2 liftings/year), while 85% responded yes to the frequent poultry picking. The gaur (*Bos gaurus*) is a common occurrence in the tea estates (95% of respondents) and sometimes an annoyance to agriculturalists (43%). They identified the animals like sambar deer (*Rusa unicolor*) (47%), barking deer (*Muntiacus muntjac*) (82%), wild pig (*Sus scorfa*) (100%), bonnet macaque (*Maccaca radiata*) (73%), black langur (*Trachipithicus johni*) (21%), porcupine (*Hystrix* sp.) (89%) as very common crop raiders. The carnivores like jungle cat (*Felis chaus*) (63%), mongoose (*Herpestes* sp.) (91%), bear (*Ursus* sp.) (54%), and leopard (48%) are frequently sighted in the tea plantations and fringe villages. Villagers rarely sighted a tiger (7%) and opined that it would remain only in the shola and never sighted in the fringe areas and tea plantations. The survey indicates (~ 85% of respondents) that people do not like the leopard or the tiger in their locality. Regarding the question to human-animal conflict, 82% opined major conflict is with crop raiding herbivores and 5% opined of human-carnivore conflicts.

Co-occurrence and distribution

We identified the tiger presence from 45 (61%) grid cells and the leopard from 56 (68%). In 44 (59%) grids, we observed the coexistence of the tiger and leopard. The grids surveyed include tea plantations, shola regions, social forestry sites, hydro-electrical sites, revenue lands and village suburbs. The areas surveyed towards the southern and western sides have pristine shola regions with grassland and are protected from human disturbances. Much of the forested areas adjoined to the shola have exotic weeds like *Lantana*, *Parthenium,* and *Eupatorium*. The results of positive, random, and negative interactions analyzed using the "co-occur" R package are given in Figure 2. Please refer to supplementary material for the grid-wise consolidated results of the prey, predator, and co-occurrence (Supplementary Table S3). Most of the observed associations are positive, indicating a harmonious co-existence of both the predators and the prey. The positive associations indicate prey abundance, lesser competition, and resource partitioning in the NFD. None of the species pairs (prey-predator) showed negative interaction. At the same time, we observed random associations between the gaur and livestock (sheep and goat), feral buffalo, livestock, and mouse deer with elephant, and notably mouse deer-tiger. The categorized geo-referenced encounter rates (Figure 3) showed that the tiger distribution is located explicitly in forested regions. At the same time, the leopard has a comparatively wide range of distribution, including the dominant human habituations. The leopard seems to coexist with the tiger in the shola regions, where large prey and arboreal prey are abundant. The distribution of the leopards in the other areas follows the distribution pattern of the medium-small range prey, predominantly in the plantations (majorly tea gardens) and grasslands.

The correlation scatter plots matrix of encounter proportion of the tiger and the leopard with various prey and between prey species (Figure 4) shows tiger-sambar and gaur-sambar significantly correlate ($r \geq +0.75$, $p \leq 0.05$).

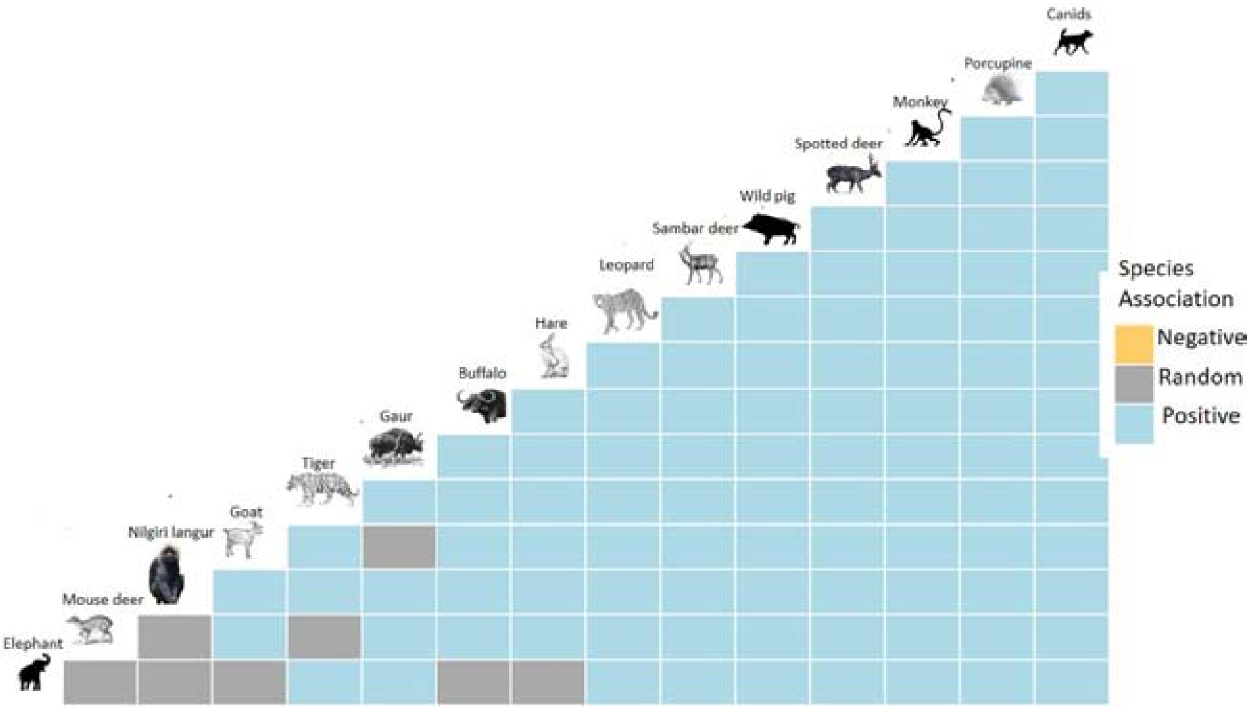

Figure 2. Species co-occurrence in NFD. The grey indicates random associations, and the blue indicates positive association, no negative associations were observed.

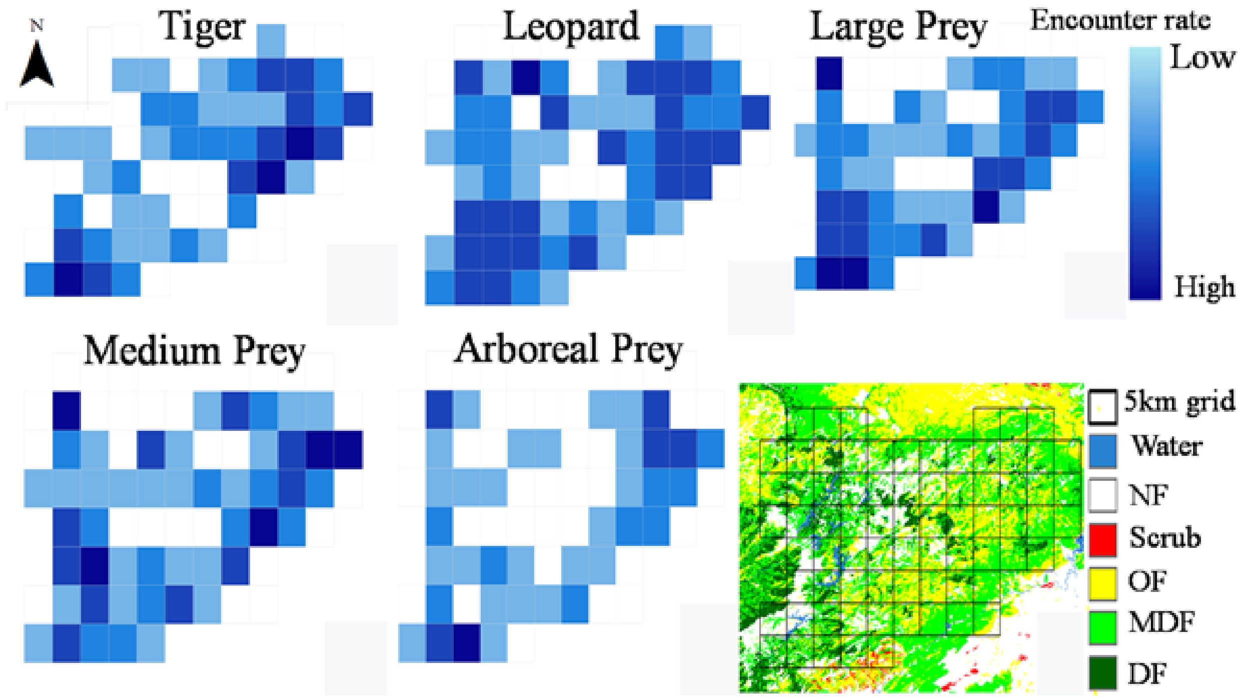

Figure 3. Grid-wise density of tiger, leopard, various categories of prey. The topography of grids laid in the reserve is shown in the right side bottom. NF: Non Forest, MDF: Moderate Dense Forest DF: Dense Forest..

Most prey species exhibited a moderate correlation (r = 0.50–0.75) with the tiger and the leopard. The average correlation shown by the tiger is with the leopard (+0.658), wild pig (+0.684), gaur (+0.606), porcupine (+0.677), Nilgiri langur (+0.627), black napped hare (+0.627), barking deer (+0.618), and bonnet macaque (+0.556) in sequential order. The leopard also shows a moderate correlation with the barking deer (+0.699), wild pig (+0.677), gaur (+0.648), bonnet macaque (+0.609), black napped hare (+0.607), and porcupine (+0.614). The other considerable high degree of significant correlation is between the wild pig-barking deer (+0.898), porcupine-black napped hare (+0.848), and sambar-gaur (+0.77) pairs.

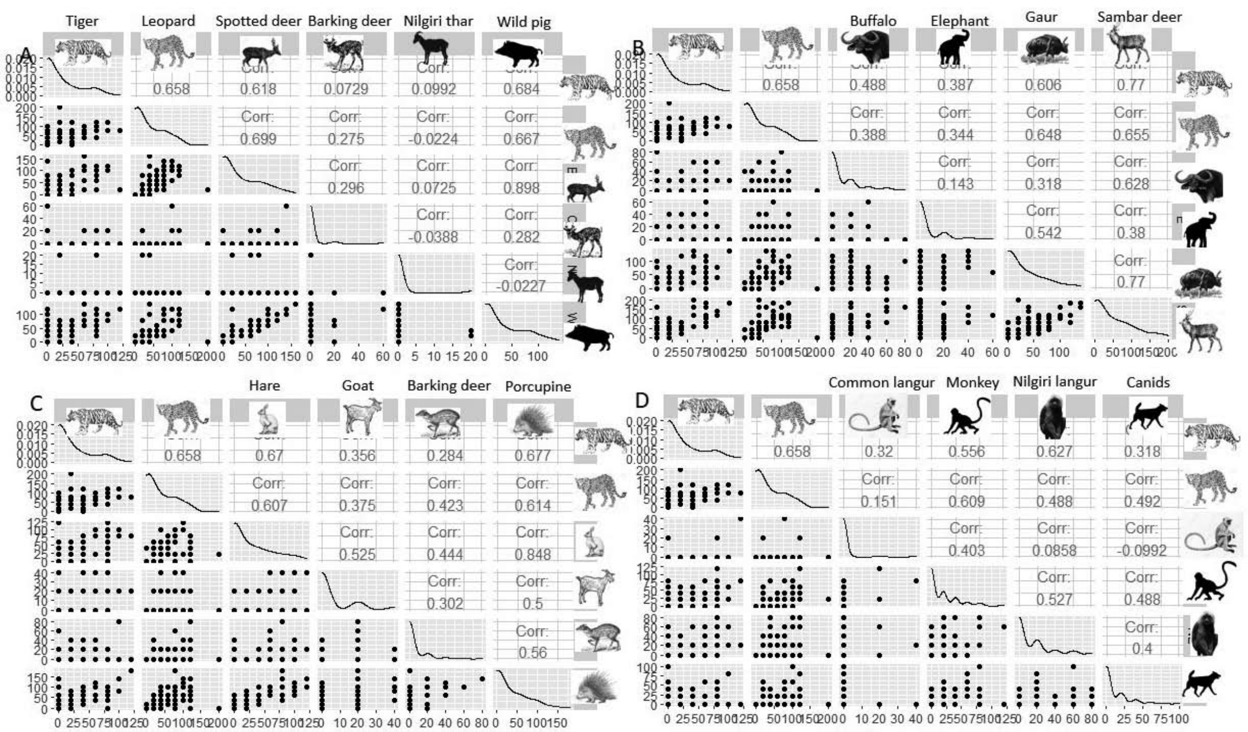

Figure 4. Correlation of encounter proportion of tiger and leopard with various mammalian species. The scatter plot is shown in the lower half, the Pearson coefficient (r) is shown in the upper half, and in the middle is the slope line.

Table 1. Prey species, prey proportion and prey biomass of tiger (N = 67) and leopard (N = 95). Mann Whitney U (U = 65.5, z-score = -1.92873) indicates there is a significant difference between the prey of tiger and leopard ($p \leq 005$).

Prey species	No of prey specimens in scat		Prey proportion (%)		Prey biomass (kg)	
	Tiger	Leopard	Tiger	Leopard	Tiger	Leopard
Rusa unicolor	41	12	61.19	12.63	368.18	107.76
Muntiacus mutjac	06	30	08.96	31.58	014.82	074.10
Lepus nigricollis	02	19	02.99	20.00	004.31	040.95
Ratufa indica	00	04	00.00	04.21	000.00	008.20
Petaurista philippensis	00	01	00.00	01.05	000.00	002.05
Trachypithecus johnii	00	01	00.00	01.05	000.00	002.26
Macaca radiata	00	03	00.00	03.16	000.00	006.57
Loris lydekkerianus	00	02	00.00	02.11	000.00	003.99
Aves	00	02	00.00	02.11	000.00	004.00
Bos gaurus	06	02	08.96	02.11	158.88	052.96
Axis axis	01	04	01.49	04.21	003.03	012.12
Moschiola indica	02	04	02.99	04.21	004.14	008.27
Sus scrofa	08	09	11.94	09.47	029.00	032.63
Bubalus bubalis	01	00	01.49	00.00	013.15	000.00
Ovis aries	00	02	00.00	02.11	000.00	005.71
Total	**67**	**95**	**100**	**100**	**595.50**	**361.55**

Scat identification

We collected 182 scats from the reserve during the survey. The molecular analysis showed 67 scats belong to the tiger and 95 belong to the leopard. The remaining scats remain unidentified, hence ignored.

Prey analysis

Table 1 shows the details of prey and its proportion in tiger and leopard scats. The prey species observed in the leopard scats are the sambar deer (*Rusa unicolor*), barking deer (*Muntiacus mutjac*), black napped hare (*Lepus nigricollis*), giant squirrel (*Ratufa indica*), flying squirrel (*Petaurista philippensis*), Nilgiri langur (*Trachypithecus johnii*), bonnet macaque (*Macaca radiata*), slender loris (*Loris lydekkerianus)*, birds (Aves), gaur (*Bos gaurus)*, spotted deer (*Axis axis)*, mouse deer (*Moschiola indica*), wild pig (*Sus scrofa*), and domestic goat (*Ovis aries*). The prey species obtained from the tiger scats are the sambar deer, buffalo (*Bubalus bubalis*), barking deer, black napped hare, gaur, spotted deer, mouse, deer, and wild pig. Our comparison of tiger and leopard prey proportions with non-parametric Mann Whitney U indicated that the prey vary significantly (U = 65.5, z-score = -1.92873, $p \leq 0.05$). Sambar seems to be the chief prey of the tiger and the leopard, while barking deer, arboreal prey, and hare observed more in the leopard diet. The mouse deer and livestock are solely restricted to the leopard scat, while the wild boar was observed to be present in both tiger and leopard scats. The buffalo seems to be present only in the tiger scat, while the gaur dominates in the tiger scat.

Niche breadth, diversity and overlap

We represented the niche breadth, prey diversity, and prey overlap in a Venn diagram (Figure 5), which confirms that the leopard has a broader niche (0.29) than the tiger (0.19). The Shannon Index of Diversity (Scaled H) shows that the leopard's prey diversity was 0.65 (included more prey states), while the tiger's was 0.5. This is an indirect example of resource partitioning because one includes a greater diversity of prey than the counterpart. A significant niche overlap (0.84) indicates that the two co-predators eat similar species considerably.

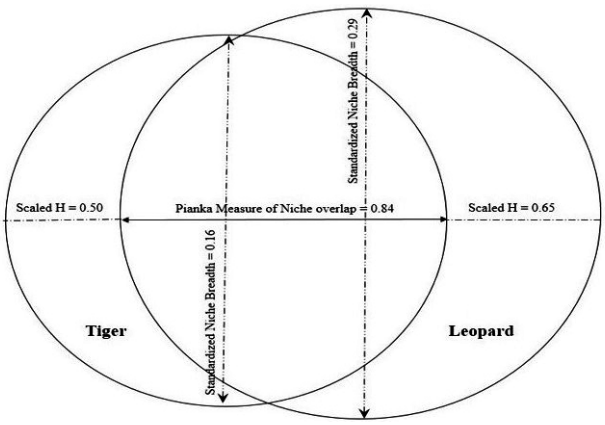

Figure 5. Venn diagram demonstrating niche breadth, niche overlap, and prey diversity of tiger and leopard. Leopard has more niche breadth and includes more prey states in the diet than tiger.

DISCUSSION

The NFD embraces an exceptionally high-altitude ecosystem having pristine montane shola-grasslands with remarkably high endemism and diversity. Due to massive human exploitation for plantation and developmental activities in the post-Indian independence, the continuity of shola-grasslands shrank and became patchy. The conservation pace increased in India by the end of the last and start of this century, with the declaration of sanctuaries, national parks, and tiger reserves. The report of 34 individual tigers in the 2018 all-India tiger census report (Jhala et al. 2020) raised curiosity, as the NFD is not considered a prime tiger habitat. As given in the present study, the previous direct census observed only one or two tigers from the reserve. According to Johnsingh et al. (2010), most large mammals in this region occupy the previously identified protected areas. They also did not prioritize the NFD as a tiger conservation unit but as a high-altitude corridor or migratory path connecting the adjoined reserves. We argue the camera-trapped tigers in the Nilgiris cannot be a spillover population (see the sex ratio of 1:2) or migratory tigers, but belong to a resident population. Even tigers with leucism were reported from the high altitude of the Nilgiris (Jhala et al. 2021). Leucism in felids is an expression of the recessive allele (Sanil et al. 2014) and happens in a population due to inbreeding or a stabilized trait as in the Sundarbans or Simlipal (Jhala et al. 2021; Sagar et al. 2021). The presence of such trait ascertains the fact that a resident population of tigers exists in the NFD and adjoining areas.

The people perception survey clearly indicates that they have never or rarely sighted a tiger in human habituations or agricultural areas, but are aware that the tiger is inside the shola forest. The case of the leopard is different, where villagers frequently sight the leopard in tea estate and shola fringes. The villagers are mostly bothered about the herbivores than the carnivores, as they are the major crop destroyers. According to them, herbivores like the gaur, wild pig, sambar deer, barking deer, and porcupine are very common in the tea estates. Sheep and buffalo rearing are common practices, and the reports of the livestock picking is comparatively less than from other landscapes (Singh et al. 2013; Athreya et al. 2015; Gubbi et al. 2020; Puri et al. 2020). When plenty of resources are available in the forest, the big cats, especially tiger, never venture in human habituations (Karanth et al. 2004; Wang and Macdonald 2009; Odden et al. 2010; Bhattarai and Kindlmann 2018). In disturbed habitats, the leopard partially relies on domestic prey, while the tiger depends solely on wild prey (Odden et al. 2010; Athreya et al. 2016). To the question "do the carnivores in tea estates can control the wild herbivore problem?" villagers responded "we know how to control the crop raiders, for that we don't need another risk". Thus, the primary questionnaire survey gives a clear idea regarding the various prey species and the predators present in their locality and the people's perception towards the wild animals.

The co-occurrence analysis and scat-based prey analysis confirm the above assumptions that diverse prey species are present in the forested shola regions and adjoining tea plantations. The tea gardens may buffer human habitation and the forested shola regions (Sidhu et al. 2015). The continuous stretch of the tea gardens in the NFD also effectively connects the fragmented shola regions. The co-occurrence of co-predators and prey species without negative interaction shows a diverse and robust prey base in the NFD. The dietary pattern of predators indicates effective resource partitioning of the leopard with the tiger. We observed tiger - leopard coexistence in 44 grid cells, and both co-predators have a significant correlation with the sambar deer. The habitat suited for a tiger is also a habitat suited for the leopard, depending on the same prey resources (Kafley et al. 2019). The tiger exhibited only random associations with small prey like barking deer, while the leopard had positive associations. Large-bodied wild ungulates such as the sambar, wild boar, gaur, and chital are a chief constituent of the tiger diet (Mondal et al. 2011; Hayward et al. 2012; Basak et al. 2020). The proportion of the domestic prey is almost zero in the tiger diet, and the buffalo hairs observed in the scat can be feral or free-ranging. The NFD has a large feral buffalo (Toda buffalo breed) population established from a free-ranging domestic breed. These buffalos are a unique breed maintained by the Toda tribes, a primitive tribal group in the Nilgiri Hills. The nominal proportion of domestic prey in the leopard diet also validates the availability of wild prey and sustainable competition in this region. Puri et al. (2020) reported from the fragmented forested landscape of central India that the free-ranging dogs and the domestic prey together constitute only 3% of the leopard diet. We hypothesize that when there is competition from the tiger in the shola region, leopards find it easy to prey on wild herbivores in shola fringes and tea estates.

The overlap of humans and wild animal necessities in an area leads to human-wildlife conflict, which peaks in fragmented regions with high human density (Ogada et al. 2003; Shankar et al. 2020). Tiger occupancy negatively correlates to the intensity and the magnitude of human disturbance (Harihar and Pandav 2012; Barber-Meyer et al. 2013; Steinmetz et al. 2013; Kafley et al. 2016). The observed tiger/leopard mortality rate in the NFD indicates that in the past ten years around five tigers and ten leopards were killed or died. The tiger mortality indicates that the NFD also faces threat due to human-induced mortality as reported previously (Sunquist 1981; Smith 1993; Singh et al. 2015a). The studies from Rathambore (Singh et al. 2015a) recorded an annual animal death of 2.4/year, which is quite large in comparison to the NFD. Exploitation (e.g., poaching, killing) and the presence of prey in high density determine the fine-scale existence of the tiger in a human-dominated landscape (Carter et al. 2012). Tiger killing/mortality occurred only in the shola regions, while that of the leopard was in tea gardens. The frequent reports of leopard conflicts (e.g., human attack, cattle lifting, poisoning in retaliation, poaching, mob killing, and killing for self-defence) are from the tea gardens (Bhattacharjee and Parthasarathy 2013). The snares are generally being placed in the tea estates to trap the wild herbivores by the villagers. This is a common trapping practice since snares are easy to setup and place in the animal's path (Aziz et al. 2017). Although snares are generally used to trap wild herbivores, they can also cause serious injuries or mortality to unintended targets (Gubbi et al. 2021). Reports of killing tigers/leopards by poisoning the left-out carcass exist from many localities (Gopal et al. 2010; Tilson et al. 2010; Kalaivanan et al. 2011; Saif and MacMillan 2016; Aziz et al. 2017). It should be assumed that the NFD is an important tiger habitat with an ample prey base, even though reports of livestock picking are less, the conflicts with big cats are common.

Tiger research in the Nilgiris focused mainly on the surrounding lower elevations like Mudumalai (Ramakrishnan et al. 1999), Silent Valley (Balakrishnan 1984), and Bandipur (Johnsingh 1992). The recent identification of tiger habitat in the sub-Himalayan region increased attention towards high-altitude conservation units, but is more prioritized in the northeast (Sarkar et al. 2018). The entire stretch of the Western Ghats shows a 32% increase in tiger population in ten years (Jhala et al. 2020). This considerable increase indicates the need to expand tiger conservation areas with an ample prey base and minimum disturbance. The increased population leads to intraspecific competition in established reserves and forces the submissive adults to occupy new territories. The high density of tigers in the neighbouring tiger reserves and prey availability can also account for the increased density of tigers in the NFD. The continuous reserve forest ranges of the Wayanad, Mudumalai, Bandipur and the Nagarhole form a major tiger conservation block and acclaim for > 300 tigers as per the latest tiger population assessment. The high-altitude NFD is situated between other major tiger conservation units and has a significant tiger population and prey base, making it eligible for its designation as a tiger reserve.

CONCLUSIONS

In conclusion, the present study suggests that the NFD may be merged with the Mukkurthi National Park to form a new high-altitude tiger reserve. The study finds that the reserve has a good prey base, and the region fulfils all the essential criteria to be considered a tiger reserve. The elevation to a tiger reserve would improve the habitat quality, continuity, prey density, action plans and would reduce human-wildlife conflicts, ensuring the free movement of big cats between the reserves, thereby maintaining genetic stability between demes or meta-populations.

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DECLARATION OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

AUTHOR CONTRIBUTIONS

GM, JY, GN, SJB, SN done the field work investigation, data curation, and wrote a preliminary script. JM and BR done data curation, formal analysis and manuscript editing. TTS done software works and conceptualization, RS gathered resources, permissions, supervision and finalization of the script.

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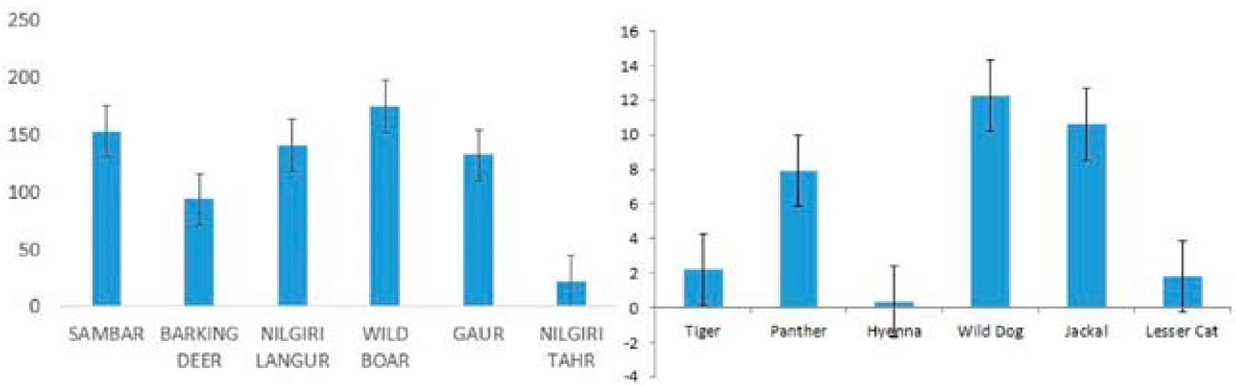
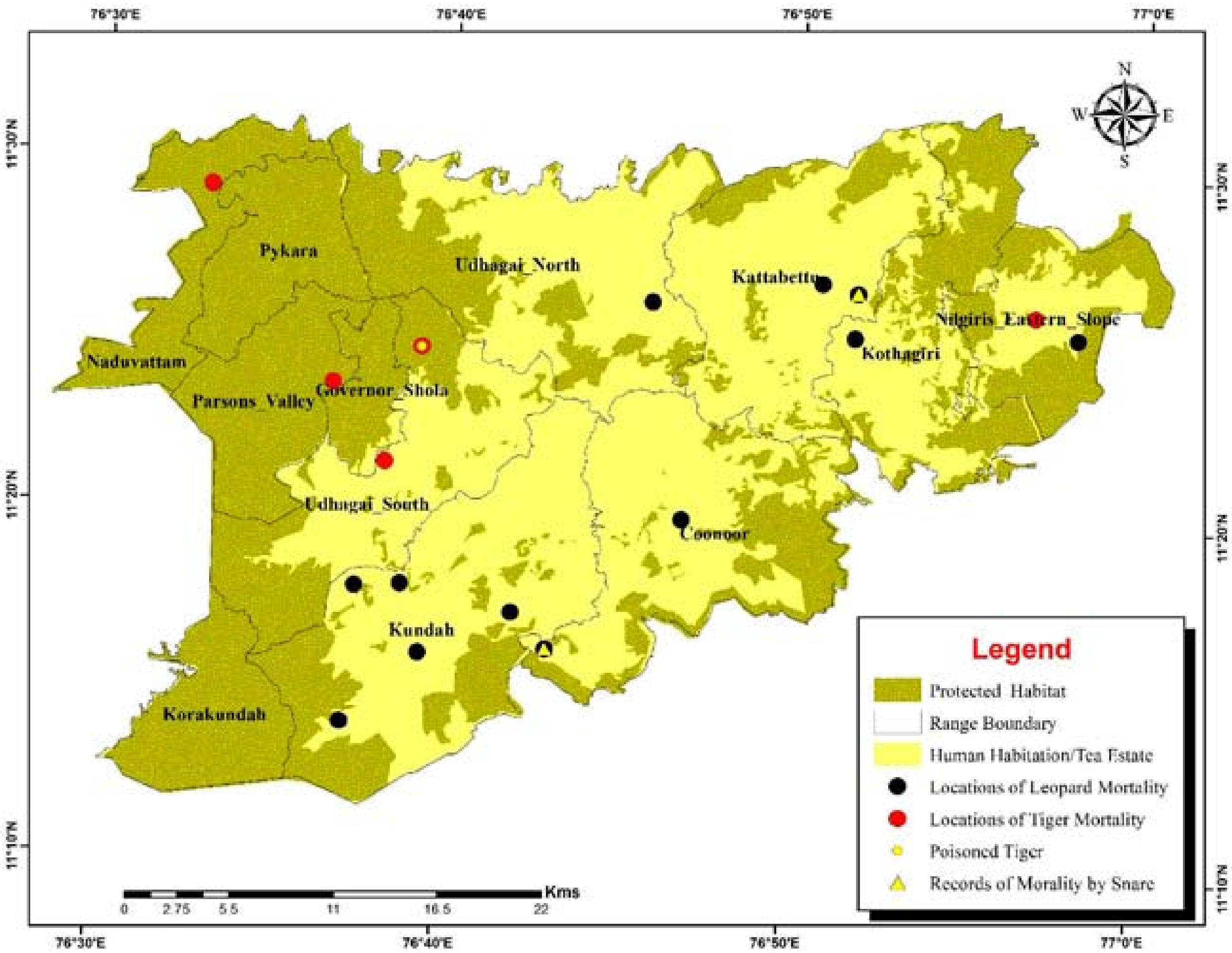
LIST OF SUPPLEMENTARY MATERIALS



Supplementary Figure S1. Carnivore population assessment in the study area by the Tamil Nadu Forest Department from the years 2005–2016. The value represented here is the mean ± standard deviation of the random survey done by the forest department with the help of an NGO. This data gives an idea of the prey and predator species present in the reserve.



Supplementary Figure S2. The geo-referenced tiger and leopard mortality data for 10 years. The data shows the rate of leopard mortality is 1/year and of tiger is 0.5/year. Tiger mortality mostly happened inside the reserves and leopard mortality in the non-reserve areas. Two records of leopard mortality are due to snare and one mortality of tiger is due to poisoning.

Supplementary Table S3. Co-occurrence analysis indicating species co-occurrence. *Plt* < 0.05 and *Pgt* < 0.05 indicate spatial segregation and positive association.

Species A	Species B	Species A	Species B	Observed co-occurrence	Probability of co-occurrence	Expected co-occurrence	*Plt*	*Pgt*
Tiger	Leopard	45	56	44	0.473	34.5	1	0
Tiger	Elephant	45	18	15	0.152	11.1	0.99496	0.02558
Tiger	Gaur	45	50	39	0.422	30.8	1	0.00003
Tiger	Sambar	45	53	42	0.448	32.7	1	0
Tiger	Chital	45	5	3	0.042	3.1	0.64091	0.71619
Tiger	Wild pig	45	47	40	0.397	29	1	0
Tiger	Barking deer	45	51	42	0.431	31.4	1	0
Tiger	Feral buffalo	45	28	24	0.236	17.3	0.99991	0.00072
Tiger	Common langur	45	3	2	0.025	1.8	0.77185	0.67384
Tiger	Bonnet macaque	45	40	32	0.338	24.7	0.99994	0.00042
Tiger	Mouse deer	45	16	12	0.135	9.9	0.94071	0.17099
Tiger	Nilgiri langur	45	37	33	0.312	22.8	1	0
Tiger	Nilgiri tahr	45	3	3	0.025	1.8	1	0.22815
Tiger	Porcupine	45	48	39	0.405	29.6	1	0
Tiger	Canids	45	30	23	0.253	18.5	0.99359	0.02389

Species A	Species B	Species A	Species B	Observed co-occurrence	Probability of co-occurrence	Expected co-occurrence	*Plt*	*Pgt*
Tiger	Black napped hare	45	47	38	0.397	29	1	0.00001
Tiger	Livestock	45	20	16	0.169	12.3	0.98992	0.04089
Leopard	Elephant	56	18	18	0.189	13.8	1	0.00386
Leopard	Gaur	56	50	47	0.525	38.4	1	0
Leopard	Sambar	56	53	52	0.557	40.7	1	0
Leopard	Chital	56	5	5	0.053	3.8	1	0.25431
Leopard	Wild pig	56	47	46	0.494	36.1	1	0
Leopard	Barking deer	56	51	51	0.536	39.1	1	0
Leopard	Feral buffalo	56	28	27	0.294	21.5	0.99994	0.00109
Leopard	Common langur	56	3	3	0.032	2.3	1	0.44569
Leopard	Bonnet macaque	56	40	40	0.42	30.7	1	0
Leopard	Mouse deer	56	16	16	0.168	12.3	1	0.0079
Leopard	Nilgiri langur	56	37	37	0.389	28.4	1	0
Leopard	Nilgiri thar	56	3	3	0.032	2.3	1	0.44569
Leopard	Porcupine	56	48	47	0.504	36.8	1	0
Leopard	Canids	56	30	30	0.315	23	1	0.00002
Leopard	Black napped hare	56	47	46	0.494	36.1	1	0
Leopard	Livestock	56	20	20	0.21	15.3	1	0.00183
Elephant	Gaur	18	50	17	0.169	12.3	0.99967	0.00445
Elephant	Sambar	18	53	17	0.179	13.1	0.99882	0.01293
Elephant	Chital	18	5	3	0.017	1.2	0.98822	0.09245
Elephant	Wild pig	18	47	16	0.159	11.6	0.99862	0.01026
Elephant	Barking deer	18	51	17	0.172	12.6	0.99949	0.00642
Elephant	Feral buffalo	18	28	10	0.095	6.9	0.97682	0.07462
Elephant	Common langur	18	3	2	0.01	0.7	0.98688	0.14842
Elephant	Bonnet macaque	18	40	15	0.135	9.9	0.99934	0.00465
Elephant	Mouse deer	18	16	7	0.054	3.9	0.98776	0.05062
Elephant	Nilgiri langur	18	37	10	0.125	9.1	0.77226	0.41942
Elephant	Nilgiri tahr	18	3	2	0.01	0.7	0.98688	0.14842
Elephant	Porcupine	18	48	16	0.162	11.8	0.99794	0.01436
Elephant	Canids	18	30	11	0.101	7.4	0.98795	0.04406
Elephant	Black napped hare	18	47	14	0.159	11.6	0.9542	0.13868
Elephant	Livestock	18	20	5	0.068	4.9	0.6428	0.59441
Gaur	Sambar	50	53	48	0.497	36.3	1	0
Gaur	Chital	50	5	5	0.047	3.4	1	0.14106
Gaur	Wild pig	50	47	44	0.441	32.2	1	0
Gaur	Barking deer	50	51	45	0.479	34.9	1	0
Gaur	Feral buffalo	50	28	25	0.263	19.2	0.99973	0.0021
Gaur	Common langur	50	3	3	0.028	2.1	1	0.31513
Gaur	Bonnet macaque	50	40	35	0.375	27.4	0.99999	0.00013
Gaur	Mouse deer	50	16	15	0.15	11	0.99907	0.01075
Gaur	Nilgiri langur	50	37	33	0.347	25.3	0.99999	0.00011
Gaur	Nilgiri tahr	50	3	3	0.028	2.1	1	0.31513
Gaur	Porcupine	50	48	44	0.45	32.9	1	0
Gaur	Canids	50	30	28	0.281	20.5	0.99999	0.00009
Gaur	Black napped hare	50	47	42	0.441	32.2	1	0

Species A	Species B	Species A	Species B	Observed co-occurrence	Probability of co-occurrence	Expected co-occurrence	*Plt*	*Pgt*
Gaur	Livestock	50	20	16	0.188	13.7	0.94706	0.15438
Sambar	Chital	53	5	5	0.05	3.6	1	0.19105
Sambar	Wild pig	53	47	47	0.467	34.1	1	0
Sambar	Barking deer	53	51	49	0.507	37	1	0
Sambar	Feral buffalo	53	28	27	0.278	20.3	0.99999	0.00017
Sambar	Common langur	53	3	3	0.03	2.2	1	0.37665
Sambar	Bonnet macaque	53	40	38	0.398	29	1	0
Sambar	Mouse deer	53	16	16	0.159	11.6	1	0.00282
Sambar	Nilgiri langur	53	37	37	0.368	26.9	1	0
Sambar	Nilgiri thar	53	3	3	0.03	2.2	1	0.37665
Sambar	Porcupine	53	48	48	0.477	34.8	1	0
Sambar	Canids	53	30	30	0.298	21.8	1	0
Sambar	Black napped hare	53	47	46	0.467	34.1	1	0
Sambar	Livestock	53	20	20	0.199	14.5	1	0.00047
Chital	Wild pig	5	47	4	0.044	3.2	0.89788	0.41087
Chital	Barking deer	5	51	4	0.048	3.5	0.84361	0.52242
Chital	Feral buffalo	5	28	2	0.026	1.9	0.71619	0.64091
Chital	Common langur	5	3	0	0.003	0.2	0.80578	1
Chital	Bonnet macaque	5	40	3	0.038	2.7	0.75541	0.5919
Chital	Mouse deer	5	16	3	0.015	1.1	0.9928	0.0667
Chital	Nilgiri langur	5	37	3	0.035	2.5	0.81269	0.51321
Chital	Nilgiri tahr	5	3	0	0.003	0.2	0.80578	1
Chital	Porcupine	5	48	4	0.045	3.3	0.886	0.43786
Chital	Canids	5	30	4	0.028	2.1	0.99051	0.08794
Chital	Black napped hare	5	47	4	0.044	3.2	0.89788	0.41087
Chital	Livestock	5	20	3	0.019	1.4	0.98187	0.12271
Wild pig	Barking deer	47	51	45	0.45	32.8	1	0
Wild pig	Feral buffalo	47	28	26	0.247	18	1	0.00004
Wild pig	Common langur	47	3	3	0.026	1.9	1	0.26071
Wild pig	Bonnet macaque	47	40	34	0.353	25.8	0.99999	0.00006
Wild pig	Mouse deer	47	16	16	0.141	10.3	1	0.00029
Wild pig	Nilgiri langur	47	37	35	0.326	23.8	1	0
Wild pig	Nilgiri tahr	47	3	3	0.026	1.9	1	0.26071
Wild pig	Porcupine	47	48	44	0.423	30.9	1	0
Wild pig	Canids	47	30	29	0.265	19.3	1	0
Wild pig	Black napped hare	47	47	42	0.415	30.3	1	0
Wild pig	Livestock	47	20	19	0.176	12.9	0.99998	0.00044
Barking deer	Feral buffalo	51	28	27	0.268	19.6	1	0.00004
Barking deer	Common langur	51	3	3	0.029	2.1	1	0.33483
Barking deer	Bonnet macaque	51	40	39	0.383	27.9	1	0
Barking deer	Mouse deer	51	16	16	0.153	11.2	1	0.00136
Barking deer	Nilgiri langur	51	37	36	0.354	25.8	1	0
Barking deer	Nilgiri tahr	51	3	3	0.029	2.1	1	0.33483
Barking deer	Porcupine	51	48	46	0.459	33.5	1	0
Barking deer	Canids	51	30	30	0.287	21	1	0
Barking deer	Black napped hare	51	47	44	0.45	32.8	1	0

Species A	Species B	Species A	Species B	Observed co-occurrence	Probability of co-occurrence	Expected co-occurrence	*Plt*	*Pgt*
Barking deer	Livestock	51	20	20	0.191	14	1	0.00018
Feral buffalo	Common langur	28	3	2	0.016	1.2	0.94733	0.32616
Feral buffalo	Bonnet macaque	28	40	22	0.21	15.3	0.99981	0.00122
Feral buffalo	Mouse deer	28	16	11	0.084	6.1	0.99903	0.00595
Feral buffalo	Nilgiri langur	28	37	25	0.194	14.2	1	0
Feral buffalo	Nilgiri tahr	28	3	1	0.016	1.2	0.67384	0.77185
Feral buffalo	Porcupine	28	48	25	0.252	18.4	0.99993	0.00065
Feral buffalo	Canids	28	30	18	0.158	11.5	0.99971	0.00164
Feral buffalo	Black napped hare	28	47	25	0.247	18	0.99996	0.00035
Feral buffalo	Livestock	28	20	12	0.105	7.7	0.99517	0.02009
Common langur	Bonnet macaque	3	40	3	0.023	1.6	1	0.15885
Common langur	Mouse deer	3	16	1	0.009	0.7	0.88102	0.52955
Common langur	Nilgiri langur	3	37	2	0.021	1.5	0.87507	0.51042
Common langur	Nilgiri tahr	3	3	0	0.002	0.1	0.88012	1
Common langur	Porcupine	3	48	2	0.027	2	0.72191	0.73149
Common langur	Canids	3	30	0	0.017	1.2	0.19842	1
Common langur	Black napped hare	3	47	1	0.026	1.9	0.2874	0.9582
Common langur	Livestock	3	20	2	0.011	0.8	0.98167	0.18024
Bonnet macaque	Mouse deer	40	16	16	0.12	8.8	1	0.00001
Bonnet macaque	Nilgiri langur	40	37	28	0.278	20.3	0.99996	0.00029
Bonnet macaque	Nilgiri tahr	40	3	2	0.023	1.6	0.84115	0.57271
Bonnet macaque	Porcupine	40	48	35	0.36	26.3	1	0.00002
Bonnet macaque	Canids	40	30	23	0.225	16.4	0.99971	0.00165
Bonnet macaque	Black napped hare	40	47	33	0.353	25.8	0.99994	0.00041
Bonnet macaque	Livestock	40	20	15	0.15	11	0.99274	0.02947
Mouse deer	Nilgiri langur	16	37	11	0.111	8.1	0.97368	0.08746
Mouse deer	Nilgiri tahr	16	3	0	0.009	0.7	0.47045	1
Mouse deer	Porcupine	16	48	15	0.144	10.5	0.99957	0.00561
Mouse deer	Canids	16	30	14	0.09	6.6	1	0.00003
Mouse deer	Black napped hare	16	47	14	0.141	10.3	0.99601	0.02505
Mouse deer	Livestock	16	20	9	0.06	4.4	0.9991	0.00581
Nilgiri langur	Nilgiri tahr	37	3	3	0.021	1.5	1	0.12493
Nilgiri langur	Porcupine	37	48	35	0.333	24.3	1	0
Nilgiri langur	Canids	37	30	22	0.208	15.2	0.99979	0.00123
Nilgiri langur	Black napped hare	37	47	34	0.326	23.8	1	0
Nilgiri langur	Livestock	37	20	17	0.139	10.1	0.99997	0.00029
Nilgiri thar	Porcupine	3	48	3	0.027	2	1	0.27809
Nilgiri thar	Canids	3	30	1	0.017	1.2	0.63398	0.80158
Nilgiri thar	Black napped hare	3	47	3	0.026	1.9	1	0.26071
Nilgiri thar	Livestock	3	20	0	0.011	0.8	0.37665	1
Porcupine	Canids	48	30	30	0.27	19.7	1	0
Porcupine	Black napped hare	48	47	44	0.423	30.9	1	0
Porcupine	Livestock	48	20	19	0.18	13.2	0.99996	0.00071
Canids	Black napped hare	30	47	28	0.265	19.3	1	0.00001
Canids	Livestock	30	20	14	0.113	8.2	0.99961	0.00246
Black Napped Hare	Livestock	47	20	17	0.176	12.9	0.9961	0.02048