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Article

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ARTICLE

Prey selection and food habits of the Tiger *Panthera tigris* (Mammalia: Carnivora: Felidae) in Kalakkad-Mundanthurai Tiger Reserve, southern Western Ghats, India

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Abstract: The Endangered Tiger *Panthera tigris* is the largest felid, distributed over 1.1 million km^2 globally. Conservation of Tigers largely depends on the preservation of its natural prey base and habitats. Therefore, the availability of prey and its selection play a major role in the sustainable future of Tigers in the given landscape. The current study assesses the prey selection patterns by Tigers in tropical evergreen forest of the Kalakkad-Mundanthurai Tiger Reserve (KMTR), southern Western Ghats, India. Density of ungulates was assessed by distance sampling (line transect, N = 21) and diet composition of Tigers was evaluated by analysing their faecal samples (N = 66). The study estimated very low ungulate density (26.87 ± 7.41 individuals km^{-2}) with highest density of Gaur *Bos gaurus* (9.04 individuals km^{-2}) followed by Wild Boar *Sus scrofa* (8.79 ± 2.73 individuals km^{-2}), whereas, primate density was quite high (45.89 ± 12.48 individuals km^{-2}), with Nilgiri Langur *Semnopithecus johnii* having the highest density (38.05 ± 10.22 individuals km^{-2}). About 74.62% of the biomass of Gaur constituted in the Tiger's diet, consumed lesser than its availability, whereas Sambar constituted 16.73% of the Tiger diet consumed proportionally to its availability. Chital *Axis axis*, Muntjac *Muntiacus muntjak*, and Indian Chevrotain *Moschiola indica* were not represented in the Tiger's diet. The current study is the first scientific information on prey selection of the Tiger in KMTR landscape, which will serve as a baseline for its conservation planning and management.

Keywords: Faecal analysis, food habits, line transect, prey abundance, prey selection.

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Ministry of Environment, Forest and Climate Change
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INTRODUCTION

The Tiger *Panthera tigris*, is the largest among five big cats in the genus (Sunquist 2010), distributed across the heterogeneous habitats of Asia (Hayward et al. 2012). Globally, Tiger population has precipitously declined, and its range has extensively diminished over the past century (Kerley et al. 2015). Poaching for Tiger body parts, habitat loss, and degradation and depletion of prey base have been the major causes for its decline (Karanth et al. 2004; Miquelle et al. 2010). Despite existence of large tracts of suitable habitats across Asia, Tigers are absent in many of the areas, probably due to lack of adequate prey base (Rabinowitz 1993; Check 2006), however, previous studies have emphasised that Tigers are flexible and recover when their habitat and adequate prey species are well protected (O'Brien et al. 2003).

Tigers are obligate terrestrial carnivores, generally preying upon ungulates (Seidensticker 1997), including diverse ranges of species that differ in size such as cervids, bovids, and suids (Andheria et al. 2007; Miquelle et al. 2010; Hayward et al. 2012). Prey availability, season, topography, and forest types are some of the significant ecological variables that influence the dietary habits of Tigers (Sunquist & Sunquist 1999). Studies have also suggested that predators play a major role in regulating the abundance of herbivore population in an environment of tropical forest (Karanth et al. 2004), which further results in the cascading effect at each trophic level (Polis & Strong 1996). Therefore, understanding of the dietary habits of the Tiger in relation to its prey base availability is essential for efficient management of wildlife and natural habitats (Biswas & Sankar 2002; Bagchi et al. 2003). Most of the information on prey selection of Tiger comes from studies carried out in semi-arid dry thorn and dry deciduous forests of central India (Bagchi et al. 2003; Biswas & Sankar 2002; Sankar et al. 2010) and tropical moist deciduous forests of southern India (Karanth & Suquist 1995; Ramesh et al. 2012a; Kumaraguru et al. 2011). In those areas, Chital was the dominant prey species in the Tiger's diet (Johnsingh 1992; Karanth & Sunquist 1995; Venkataraman et al. 1995; Andheria et al. 2007), however, no comprehensive study has been conducted to estimate the abundance of prey and its selection by Tigers in their distribution range in the southern Western Ghats. There is scanty information about predator-prey selection at Kalakkad-Mundanthurai Tiger Reserve (KMTR) and the lack of such information can be a major limitation in designing and implementing site-specific conservation measures (Karanth et al. 2003). Understanding the principal constituents of the Tiger diet is essential for planning effective conservation policies (Kerley et al. 2015). Thus, the current research aims to assess the prey selection patterns by the Tiger in the tropical evergreen forest of KMTR.

STUDY AREA

The current study was carried out between July 2015 and May 2018 in four administrative ranges, namely, Mundanthurai, Papanasam, Ambasamudram, and Upper Kodhayar (Intensive study area, henceforth ISA) of 588km^2 in KMTR (900km^2), located in the southern Western Ghats (8.357–8.883 ^{0}N & 77.169–77.574 ^{0}E) in Tamil Nadu, India (Figure 1). The terrain KMTR is mountainous (the elevation ranges 100–1,866 m), and the vegetation ranges from dry thorn scrub to montane wet tropical forest and grassland at high altitudes (Ramesh et al. 2012b). KMTR receives rainfall from both the south-west (June to September) and the north-east (October to January) monsoons (Sarkar 2012). The annual rainfall is about 3,000mm, and the temperature fluctuates between 17°C and 37°C during the year. This reserve is bordered by agricultural lands with human settlements (about 145 villages) in the east (Arjunan et al. 2006), and with forest tracts of the Neyyar, Peppara, and Shendurni wildlife sanctuaries in the Ashambu Hill range (Naniwadekar & Vasudevan 2006) in the west. The rivers Peyar, Karaiyar, Kavuthalaiyar, Servalar, Chithar, and Pambar and their tributaries drain into a perennial river called Tamiraparani. The sympatric carnivore species found here are the Tiger, the Leopard *Panthera pardus*, and the Wild Dog *Cuon alpinus*. Sambar, Gaur, Chital, Wild Boar, Barking Deer, and Indian Chevrotain are some of the major prey species that occur in this reserve. In addition, Asian Elephant *Elephas maximus*, Indian Hare *Lepus nigricollis*, Bonnet Macaque *Macaca radiata*, Tufted Grey Langur *Semnopithecus priam*, Lion-tailed Macaque *Macaca silenus*, Nilgiri Tahr *Hemitragus hylocrius*, Indian Crested Porcupine *Hystrix indica*, Indian Giant Squirrel *Ratufa indica*, Grey Jungle Fowl *Gallus sonneratii*, Red Spurfowl *Galloperdix spadicea*, and Indian Peafowl *Pavo cristatus* are also found in the reserve.

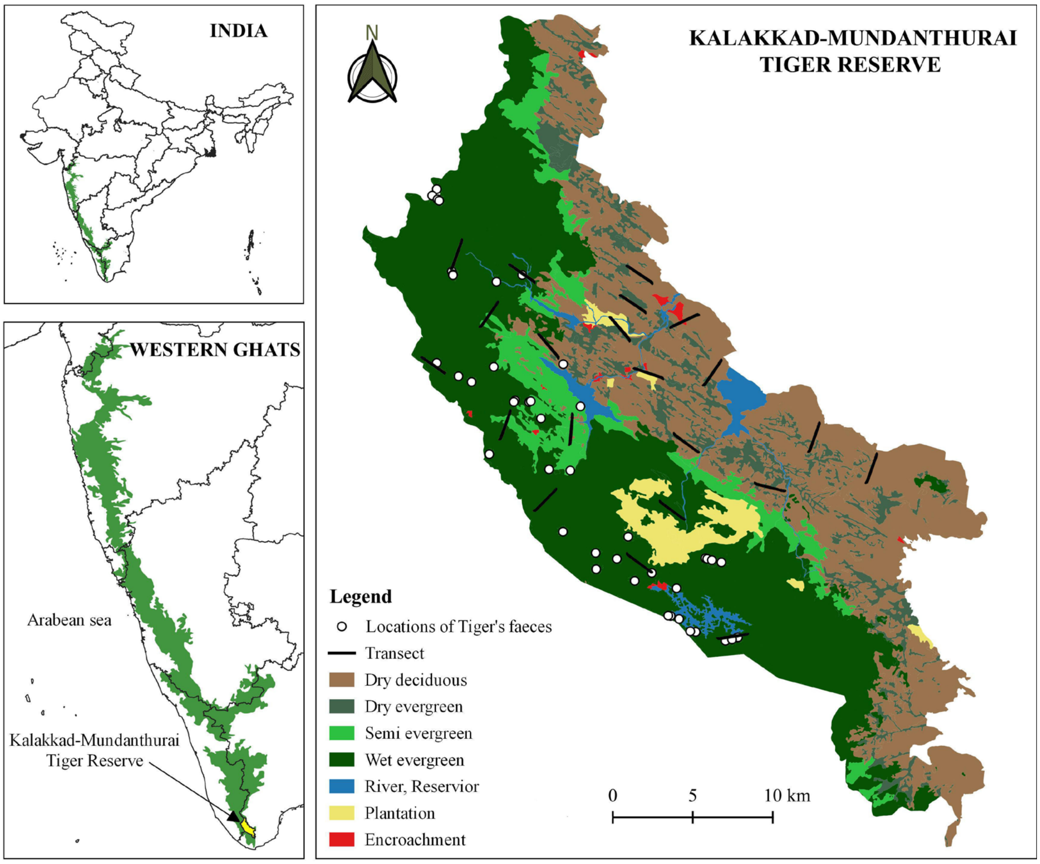

Figure 1. Study area depicting the locations of the line transects and Tiger faeces in Kalakkad-Mundanthurai Tiger Reserve.

Field Methods

Density and biomass estimation of prey species

The densities of wild prey were estimated by using the line transect sampling technique (Burnham et al. 1980; Buckland et al. 1993, 2001). The line transect method has been extensively applied to estimate animal densities in the tropical forests of southern Asia (Karanth & Sunquist 1992, 1995; Biswas & Sankar 2002; Jathanna et al. 2003; Bagchi et al. 2003; Edgaonkar 2008; Paliwal 2008; Malla 2009). Permanent transect lines (n=21) were randomly laid across different habitat types of KMTR by the Tamil Nadu Forest Department. The transect length vary from 1.5 (n=3) to 2 (n=18) km. The total length and sampling effort was 40.50 and 243km, respectively. Six replicates of 21 transects were walked at dawn (06.30–08.30 h) between January and May 2016 and at dusk (16.30–18.30 h) between January and May 2017 within the ISA area. Data were collected by a researcher and two trained observers on every transect walk. For each detection, the animal bearings were recorded using a look through compass (KB 20, SUNNTO, Vantaa, Finland), while angular sighting distance were recorded using a laser range finder (Yardage Pro 850, Bushnell, Overland Park, Kansas USA). Group size was also recorded during the transect sampling. Necessary care was taken while walking on transects to maximize detectability of animals before they disappeared from sight.

Faecal sample collection

As cryptic and nocturnal behaviour of the carnivores limit the direct observation of their predatory behaviour in the wild, faecal samples were collected to determine their food habits. Large carnivores generally prefer to travel along forest roads and trails, and as they travel they defecate to mark their presence and passage (Sunquist 1981; Johnsingh 1983; Smith et al. 1989; Karanth & Sunquist 2000). Therefore, faecal samples of Tiger were collected by intensively searching along such trails, river beds, and open glades from July 2015 to May 2017. All trails were revisited after about two months for consecutive collection. Faeces of Tigers were collected only when they were associated with scraps and tracks. We distinguished faecal samples between Leopard and Tiger by their diameter and supplementary evidence such as pugmarks and scrapes (Karanth & Sunquist

1995). Leopard faeces are much larger, twisted, more coiled between constriction and deposited on the grassy stripes at the centre or the edges of forest road (Andheria et al. 2007), whereas, Tiger faeces appear to be less coiled and have larger distance between two successive constrictions within a single piece of a faeces (Ramesh 2010). Once a faeces was encountered, a large portion was collected in a paper envelope for diet analysis. One-fourth of the faeces was left uncollected to avoid disturbances in Tigers' territorial marking. The collected faecal samples were washed in running water through a nylon mesh (<1mm), later sun-dried in thin paper pages (Andheria et al. 2007). Following that, the dried faecal samples were stored in airtight bags individually labelled with date and location for further identification.

Analytical Methods

Density and biomass estimation of prey species

The density of major prey species of Tiger was estimated using the program 'DISTANCE' version 7.2 (Thomas et al. 2010). To maximise the number of the sighting, the temporal replicates of each of the line transects were pooled together and were considered as a single spatial sample (n=21). Different detection functions were fitted to the observed data and the appropriate model was selected based on the lowest Akaike information criterion (AIC) values (Burnham et al. 1980; Buckland et al. 1996). Parameters such as effective strip width (ESW), cluster density (D_g), cluster size (G_s), and animal prey individual density (D_i) were also estimated using program DISTANCE 7.2 (Burnham et al. 1980; Buckland et al. 1993).

The density of ungulate commonly represented as the biomass of ungulates available in the ecosystem. The biomass (kg km^{-2}) of major prey species was calculated by multiplying the individual density (D_i) of prey species by its average estimated unit weight (Tamang 1982; Wegge et al. 2009) from the available information for major prey species (Karanth & Sunquist 1992, 1995) (see Appendix 1).

Identification of prey species

Examination of indigestible parts of animals and plants found in a predator's faeces is the primary source of information about its food habits (Andheria et al. 2007). The prey species were identified by microscopic examination of the medullary pattern (colour, length, and thickness of the medulla) in 20 hairs, collected randomly from each faecal sample (Mukherjee et al. 1994), and later corroborated with reference guides of Bahuguna et al. (2010) and Chakraborty & De (2010).

Estimation of frequency of occurrence and relative biomass of prey consumed

A most commonly used measure of the frequency of occurrence (henceforth FO) for each prey type was to estimate the prey intake and composition (Andheria et al. 2007). The FO, however, does not provide the best approximation of the true dietary patterns of a predator, as the biomass consumed to faeces excreted is not alike for all prey species due to their variation in surface area: volume ratio, described by Floyd et al. (1978) and Ackerman et al. (1984). To preclude such bias, we have used the biomass calculation model recently developed for obligate carnivores by Chakrabarti et al. (2016).

$$Y = ((0.033- (0.025 \times \exp(-4.284(X/PBM)))) \times PBM$$

Where, Y is the mass of prey consumed per collectable faecal sample, X is the prey body mass, and PBM is the predator body mass. The mean body weight of each prey consumed by Tiger was based on Karanth & Sunquist (1995).

The adequacy of the sample size was calculated using the Brillouin diversity index (Brillouin 1956).

$$HB = \ln N! - \sum \ln n_i!/N$$

Where HB is diversity, N is the number of the prey taxa in all the samples, and n_i is the number of individual prey taxa in the i th category.

Analysis of prey selection

To assess the prey selection patterns of Tigers for different prey species in KMTR, Jacobs' index (1974) of preference (D) was used:

$$D = (ri-pi) / (ri + pi - 2ripi)$$

Where, ri is the proportion of a prey remains in faecal sample, and pi is the proportional density of prey species in the population. The resulting values ranges from +1 (strongly selected) to -1 (strongly avoided). Prey selection assessment was restricted to those prey species whose density information was available.

RESULTS

Density and biomass of prey species

The overall densities of ungulates and primates were 26.87± 7.41 km^{-2} and 45.89 ± 12.48 km^{-2}, respectively, whereas, densities of Indian Giant Squirrel and Grey Jungle Fowl were 3.20 ± 1.32 km^{-2} and 25.32 ± 5.09 km^{2}, respectively. The estimated individual and cluster density for potential prey species of a large carnivore is given in Table 1 along with cluster size and their percentage of the coefficient variation, and effective stripe width (Appendix 2). Half-normal-cosine was the

Table 1. Estimated density of major prey species of large carnivore in Kalakkad-Mundanthurai Tiger Reserve. Total sampling effort was 243km.

Species	Model (AIC)	Min AIC	Cluster size (SE)	ESW in meter (SE)	D_i km^{-2} (SE)	%CV (D) (km^{-2}) 95%	95% CI	Dg km^{-2} (SE)	Biomass kg km^{-2}
Bonnet Macaque	Half-normal / Cosine	15.913	7.88 (2.79)	48.77 (8.46)	1.70 (0.53)	21.15	0.50 – 5.81	0.22 (0.11)	6.8
Tufted Grey Langur	Half-normal / Cosine	9.272	30.74 (10.22)	31.52 (6.77)	6.14 (1.73)	23.34	1.12 – 33.74	0.20 (0.01)	55.26
Nilgiri Langur	Half-normal / Cosine	212.77	7.82 (0.97)	34.93 (2.86)	38.05 (10.22)	26.82	22.33 – 64.87	4.86 (1.15)	342.45
Total primates					45.89				404.51
Chital	Half-normal / Cosine	15.982	2.65 (0.70)	15.61 (4.37)	2.50 (0.92)	18.44	0.65 – 9.60	0.94 (0.32)	117.5
Sambar	Half-normal / Cosine	40.157	1.72 (0.24)	15.03 (2.50)	4.80 (1.04)	21.70	2.06 – 11.17	2.80 (0.57)	643.2
Mouse Deer	Half-normal / Cosine	7.79	*	(8.42) (2.65)	1.74 (0.69)	19.82	0.42 – 7.35	*	5.22
Gaur	Half-normal / Cosine	37.98	4.79 (1.31)	25.55 (4.08)	9.04 (2.03)	28.55	3.08 – 26.52	1.88 (0.47)	4068
Wild Boar	Half-normal / Cosine	33.95	2.70 (0.43)	12.87 (2.18)	8.79 (2.73)	31.07	2.72 – 28.42	3.26 (1.29)	281.28
Total ungulates					26.87				5115.20
Indian Giant Squirrel	Half-normal / Cosine	46.82	1.57 (0.19)	19.33 (3.27)	3.19 (1.32)	20.8	1.42 – 7.20	2.03 (0.81)	
Grey Jungle Fowl	Half-normal / Cosine	201.98	1.6 (0.43)	15.38 (0.79)	25.32 (5.09)	20.12	16.82 – 38.11	15.82 (3.07)	

CV—Coefficient of Variation | Dg—Density of cluster size | D—Density of individuals | ESW—Effective Stripe Width | Min AIC—Minimum Akaike information criterion | SE—Standard Error | CI—95% Confident Interval | *—data not analysed.

best fit model that had resulted in the lowest AIC value for all the species. The major prey species of Tigers are classified into groups such as ungulates (Chital, Sambar, Mouse Deer, Gaur, Wild Boar) and primates (Tufted Grey Langur, Nilgiri Langur, Bonnet Macaque), while Grey Jungle Fowl was also consumed by them. In terms of density of clusters in ungulates, Wild Boar (3.26 ± 1.29 km^{-2}) were most abundant, followed by Sambar (2.79 ± 0.57km^{-2}), Gaur (1.88± 0.47 km^{-2}), and Chital (0.94± 0.32 km^{-2}), whereas density of individual Gaur (9.04 ± 2.03 km^{-2}) was the highest among all the ungulates, followed by Wild Boar (8.79± 2.73 km^{-2}), Sambar (4.80± 1.04 km^{-2}), Chital (2.50± 0.92 km^{-2}) and Mouse Deer (1.74± 0.69 km^{-2}). The number of detections for elephants was too low to permit useful analysis. Total estimated biomass for ungulates and primates in KMTR was 5,115.20 kg km^{-2} and 404.51 kg km^{-2}, respectively.

KMTR harboured high density of primates as individual densities for Nilgiri Langur, Tufted Grey Langur and Bonnet Macaque were 38.05 ± 10.22 individuals km^{-2}, 6.14 ± 1.73 individuals km^{-2}, and 1.70 ± 0.53 individuals km^{-2}, where the density of cluster was 4.86 ± 1.15, 0.20 ± 0.01, and 0.22 ± 0.11 clusters km^{-2}, respectively. Substantial observations of Indian Giant Squirrel (3.20 ± 1.32 km^{-2}) and Grey Jungle Fowl (25.32 ± 5.09 km^{-2}) were obtained on transects during the study period.

Prey composition and selection

After excluding faecal samples (n = 6) which had an unidentifiable object and were loose/viscous in consistency, we had a total of 66 Tiger faecal samples. The Brillouin diversity index value for the estimation of adequacy of the sample size reached 15th faecal, indicating that we had sampled adequately (Figure 2). Four species of mammals were identified in the Tiger faecal sample (Table 2). All faecal samples contained single prey items. Out of the prey species identified in the Tiger faeces, Gaur constituted 74.2% followed by Sambar (16.6%), Sloth Bear (6.06%), and Nilgiri Tahr (3.0%). No remains of Chital, Muntjac, Mouse Deer, Wild Boar, and primates were found in the Tiger faeces.

The prey selectivity of a Tiger was tested by comparing with the individual density of the prey species. Prey selection analysis was restricted to seven prey species (Gaur, Sambar, Chital, Mouse Deer, Wild Boar, Nilgiri Langur, and Tufted Grey Langur), whose density information was available. The Jacobs' index value showed that Tigers displayed strongest selection of Gaur followed by Sambar (Figure 3) and apparently avoided other prey in KMTR.

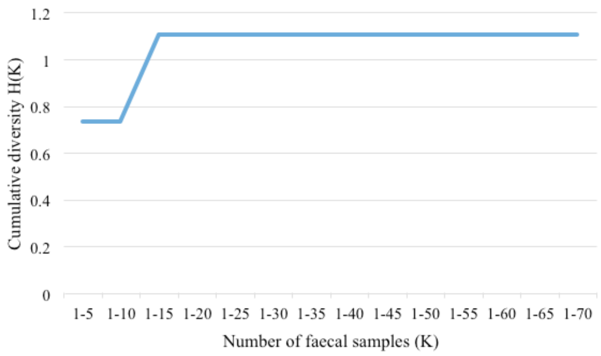

Figure 2. Cumulative diversity, H(k), of Tiger prey items with increased sample size (k).

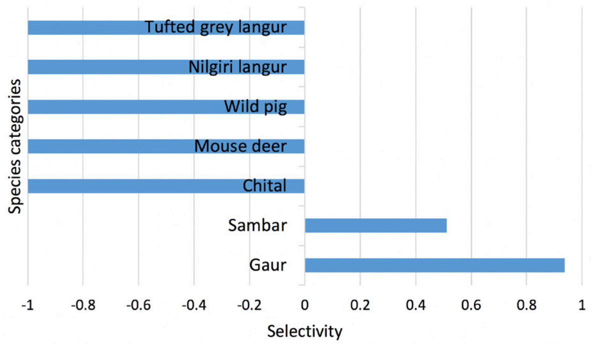

Figure 3. Prey selectivity index of Tiger in Kalakkad-Mundanthurai Tiger Reserve, as assessed by Jacob's index.

Table 2. Food habit of the Tiger in Kalakkad-Mundanthurai Tiger Reserve based on faecal analysis (n=66).

Prey species	Relative frequency of occurrence % (RFO)	Mean body weight (kg)	Biomass consumed/ faeces	Biomass consumed (kg)	Relative biomass consumed
Gaur	74.24	287 (Karanth & Sunquist 1995)	4.95	242.50	74.62
Sambar	16.67	212 (Karanth & Sunquist 1995)	4.94	54.35	16.73
Nilgiri Tahr	3.03	100 (Kumaraguru et al. 2011)	4.73	9.47	2.91
Sloth Bear	6.03	90 (Biswas & Sankar 2002)	4.66	18.65	5.74

DISCUSSION

Density and prey biomass

Comparative account of total ungulate densities estimated in the present study (Table 3) with that of other tropical forests in southern Asia revealed that KMTR harboured lower density of ungulates than most of them but higher than the Tiger reserves such as Bori-Satpura, Pakke, and Bhadra. The possible reason for the low density of ungulates might be the majority rocky outcrops and highly precipitous terrain. Mid-elevation forest is dry in most of the place coupled with contiguous tracts (c. 440km^2) of tropical rainforest in KMTR which is unfavourable for ungulates (Johnsingh 2001). Gaur was found to be most abundant species in the ISA and was comparable with other Tiger reserves of Western Ghats such as Mudumalai (Ramesh 2010) and Nagarahole (Karanth & Sunquist 1992). Nevertheless, most observation of Gaur were in grassland due to increased visibility compared to heavily vegetated habitat types in KMTR, therefore, we presume that this might have influenced the overall density of Gaur. Therefore, we speculated that true density of Gaur would be closer to the lower confidence limit of 3.08km^{-2} and it is similar to the previous study in KMTR by Ramesh et al. (2012b). Gaurs were mostly recorded in the morning within the wet grasslands of higher altitude, whilst they were observed in the dry thorn and teak forest during the dusk hours. The density of Wild Boar appears to be closely comparable to Ranthambore (Bagchi et al. 2003), Barida (Stoen & Wegge 1996), and Katka-Kochikahali of Sundarbans (Reza et al. 2002) but different from Anamalai Tiger Reserve (Kumaraguru et al. 2011). Estimated density of Sambar in the current study was comparable to tropical dry moist deciduous (Bori-Satpura, Badhra, Nagarahole) and tropical dry thorn, dry deciduous, and evergreen forest habitat of Mudumalai and Bandipur (Table 3). Sambar density, however, was quite low compared to Anamalai (Kumaraguru et al. 2011) and Pench (Acharya 2007).

The density of chital estimated (2.5 individuals km^2) was very low compared to other tropical forests in southern Asia. In ISA Chital distribution was restricted to 60km^2 of the Mundanthurai plateau (Sathyakumar 2000), which was covered with dry thorny and deciduous vegetation interspersed with the overgrown teak plantation. Plateau is dominated by unpalatable tall-grass species *Cymbopogon flexuosus* (Sankaran 2005) and invasive thickets, such as Lantana *Lantana camara* and Eupatorium *Eupatorium glandulosum* (Uma et al. 1999). Though cattle grazing has been prohibited in KMTR since 2000 (Venkatesh et al. 2017), there were substantial number of cattle grazing in the reservoir (Karaiyar and Manimuthar) and Mundanthurai Plateau.

Table 3. Comparison of ungulate densities and their biomass (Individuals km^{-2}) from different protected areas in southern Asia.

Study area	Chital	Gaur	Sambar	Wild Boar	Muntjac	Mouse Deer	Nilgiri Tahr	Total ungulate density	Total ungulate biomass	Source
Current Study	2.5	9.04	4.8	8.79	…	1.74	-	26.87	5115.20	
Mudumalai Tiger Reserve	25.4	9.4	4.8	1.3	1.2	…	NP	42.1	6133.8	Ramesh (2010)
Keoladeo National Park	52.37	NP	0.32	3.21	NP	…	NP	69.58	5069.39	Aakrithi et al. (2017)
Nagarahole National Park	50.6	9.6	5.5	4.2	4.2	…	NP	74.1	7657.8	Karanth & Sunquist (1992)
Anamalai Tiger Reserve	20.54	12.34	6.54	20.61	0.28	…	13.67	73.98	9181.08	Kumaraguru et al. (2011)
Bilgiri Rangasamy Tiger Reserve	13.96	5.08	6.01	5.33	3.7	…	NP	34.08	3995.72	Kumara et al. (2012)
Kalakkad-Mundanthurai Tiger Reserve	…	3.6	7.0	1.3	…	…	NP	11.9	2599.6	Ramesh et al. (2012b)
Bandipur Tiger Reserve	20.1	7	5.6	…	0.7	…	NP	33.4	4859.8	Karanth & Nichols (1998)
Bhadra Tiger Reserve	8.88	3.86	4.4	2.46	4.35	…	NP	23.95	2914.03	Gopalaswamy et al. (2012)
Pench National Park	115.6	0.4	12.2	20.3	-	…	NP	149.4	8059.6	Acharya (2007)
Kanha National Park	469.7	…	1.5	2.5	0.6	…	NP	57.3	3103.5	Karanth & Nichols (1998)
Bardia National Park	77.7	NP	…	8.8	1.7	NP	NP	99.2	4786.5	Stoen & Wegge (1996)
Bori-Satpura Tiger Reserve	5.4	…	4	1.8	0.8	NP	NP	13.6	1152.2	Edganokar (2008)
Ranthambore National Park	31	…	17.1	9.7	…	NP	NP	74.8	6228.4	Bagchi et al. (2003)
Gir National Park	50.8	NP	2	-	…	NP	NP	56.2	2819.22	Khan et al. (1996)
Sariska Tiger Reserve	33.88	NP	26.38	54.12	NP	NP	NP	157.1	14548.72	Mondal et al. (2011)
Chitwan National Park	61.8	…	20	3.6	…	NP	NP	85.4	5699.8	Sunquist (1981)
Kaziranga National Park	NP	…	…	2.6	…	NP	NP	58.1	4815.6	Karanth & Nichols (1998)
Rajaji National Park	49.9	NP	14.6	1.9	NP	NP	NP	68.8	4794.5	Harihar et al. (2009)
Pakke Tiger Reserve	NP	3.5	3.8	6.7	3.9	NP	NP	17.9	2380.5	Selvan et al. (2013a)
Sundarbans	70.4	NP	NP	7.9	NP	NP	NP	78.3	3561.6	Reza et al. (2002)

Notes: NP - The respective species was not found in the respective area; ... - Data were not reported

Thus, the cattle grazing and lack of suitable grassland might be a potential factor explaining the low density of Chital. Despite being nocturnal in nature, we sighted Mouse Deer on transect line, however, no further analysis could be done as it was a solitary sighting.

We compared the density of Bonnet Macaque with the estimates available from other tropical forests in India (Table 4). The density of Bonnet Macaque was available only for Mudumalai (Ramesh 2010), Nagarahole (Karanth & Sunquist 1992), Bilgiri Rangaswamy Tiger Reserve (Kumara et al. 2012), and Srisi-Honnavar (Babureddy et al. 2015). Bonnet Macaque density in KMTR was lower than that of the aforesaid parks. The specialist folivore Tufted Grey Langur was in low densities but their density was found to be comparable with Bilgiri Rangasamy Tiger Reserve. In terms of density amongst ungulates and primates, Nilgiri Langur was found in high density (38.05 individuals km^{-2}) in ISA. The present study has reported that the densities have increased as compared to a previous study (Ramesh et al. 2012b).

Prey composition and selection of tiger

In the current study, the Tiger preyed on three large ungulates, including Gaur, Sambar, and Nilgiri Tahr. We did not find multiple prey species in a single sample which is contrary to the prediction of Bekoff et al. (1984). Gaur accounted for 74.6% of the Tiger diet by biomass. Such selective predation towards large body mass was also reported in Anamalai Tiger Reserve (Kumaraguru et al. 2011), Nagarahole (Karanth & Sunquist 1995), Bandipur Tiger Reserve (Andheria et al. 2007), and Pakke Tiger Reserve (Selvan et al. 2013a). Carnivores tend to prefer the most abundant prey (Breuer 2005). Tiger's selective predation for Gaur in the present study area indicates

Table 4. Comparison of arboreal prey densities (individuals km^{-2}) and biomass from protected areas in Indian subcontinent.

Study area	Tufted Grey Langur (previously known as common langur)	Nilgiri Langur	Bonnet Macaque	Total primate density	Total primate biomass	Reference
KMTR (Present study)	6.14	38.05	1.7	45.89	404.51	
Mudumalai Tiger Reserve	35.4	…	1.9	37.3	340.6	Ramesh (2010)
Nagarahole National Park	23.8	…	5.5	29.3	236.2	Karanth & Sunquist (1992)
Bilgiri Rangasamy Tiger reserve	6.34	NP	6.56	12.9	83.3	Kumara et al. (2012)
Kalakkad–Mundanthurai Tiger Reserve	…	9.9	…	9.9	89.1	Ramesh et al. (2012)
Sirsi-Honnavar	25.06	NP	12.4	37.46	275.14	Babureddy et al. (2015)
Badhra Tiger Reserve	22.6	NP	…	22.6	203.4	Jathanna et al. (2003)
Pench Tiger Reserve	65.8	NP	…	65.8	592.2	Acharya (2007)
Bori – Satpura	28.3	NP	NP	28.3	254.7	Edganokar (2008)
Melghat	42.92	NP	NP	42.92	386.28	Narasimmarajan et al. (2014)
Bardia National Park	2.3	NP	NP	2.3	20.7	Stoen & Wegge (1996)
Ranthambore National Park	21.75	NP	NP	21.75	195.75	Bagchi et al. (2004)
Sariska Tiger Reserve	50.67	NP	NP	50.67	456.03	Mondal et al. (2011)
Chitawan National Park	3.6	NP	NP	3.6	32.4	Sunquist (1981)
Chilla range of Rajaji National Park	14.1	NP	NP	14.1	126.9	Harihar et al. (2009)

Notes: NP - The respective species was not found in the respective area; ... - Data were not reported

selection for a large ungulate. Thus, in ISA of KMTR, Gaur occurred in higher densities (9.04km^{-2}) at wet grassland in high altitudes interspersed with reed brakes (*Ochlandra* sp.), majority of collected faecal samples were found from such habitat, which suggests that the Tiger prefers habitat where Gaur occur more commonly. Such spatial correlation might have increased their encounter with the predator. Crepuscular and poor eyesight of Gaur could have enabled the Tiger to stalk Gaur easily (Karanth 1993). On the other hand, this selective predation could also be related to optimal foraging theory (Stephens & Krebs 1987), which suggests that the selected prey could provide higher benefits in terms of net biomass intake whilst reduce the cost of handling (stalking, subduing, and disemboweling prey) and injury risks (Scheel 1993). Hence, the predator must shift to profitable species, which may be either medium-size or high density that make them easier to be captured (Lamichhane & Jha 2015).

In the current study, Sambar biomass constituted relatively lesser (16.73%) proportion in the Tiger diet than other tropical forests of India such as Nagarhole (Karanth & Sunquist 1992), Sariska (Sankar & Johnsingh 2002), Ranthambhore (Bagchi et al. 2003), Bandipur (Andheria et al. 2007), Satpura (Edgaongar 2008), and Mudumalai (Ramesh 2010). This may be due to spatial distance from the Tiger, as Sambar mostly forage around tea plantation (personal observations), near human habitation, and dry deciduous and thorn forest of low elevation. Such spatial segregation between them might have strengthened the predation on Gaur. Chital, being a common prey for the Tiger in other protected areas (McDougal 1977; Sunquist 1981; Johnsingh 1983; Karanth & Sunquist 1995; Stoen & Wegge 1996; Biswas & Sankar 2002) was absent in the faecal samples of Tigers in KMTR. This is due to scarce and restricted distribution of Chital in Mundanthurai Plateau with low density (Selvan et al. 2013b). This spatial segregation has compelled the Tiger to depend on Gaur. During the current study, we did not see any sign of Tigers in Mundanthurai Plateau, which also corroborates a previous study by Uma et al. (1999).

Presence of Sloth Bear remains in the Tiger's faeces reflected the occasional predation on this species. Predation on bear is not a new phenomenon, as other investigators also reported the same (Biswas & Sankar 2002; Swaminathan et al. 2002; Harsha et al. 2004; Andheria et al. 2007). Though the bear remains a relatively minor component of the Tiger diet relative to Gaur and Sambar, this was more than Nilgiri Tahr in the current study. One possible explanation is the density of Sloth Bear and Nilgiri Tahr in the study area. In addition, Nilgiri Tahr occur only in restricted cliffs in the present study area (Hopeland et al. 2016). Conversely, bears are spread across the study area and are mostly nocturnal and crepuscular (Chauhan et al. 2004; Yoganand et al. 2005). Such spatial segregation between the Tiger and the Nilgiri Tahr, while spatial and temporal overlap between the Tiger and the Sloth Bear, could have increased encounter rate and led to high predation on Sloth Bear compared to Nigliri Tahr in our study area. Unfortunately, we could not determine density of Sloth Bear, Nilgiri Tahr, and their activity pattern on our study site; therefore, future research is needed to confirm the relationships among density, prey selection, spatial, and temporal overlap.

The present study revealed that the moderate prey availability is enough to preserve the Tiger in the long run in this landscape. Management of relatively few ungulates, primarily Gaur may be critical for Tiger conservation in this region.

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Appendix 1. Average estimated unit weight of prey species in Kalakkad-Mundanthurai Tiger Reserve.

Species	Weight (kg)	Source
Bonnet Macaque	4	Karanth & Sunquist (1992)
Tufted Grey Langur	9	Karanth & Sunquist (1992)
Nilgiri Langur	9	Karanth & Sunquist (1992)
Chital	47	Karanth & Sunquist (1992)
Sambar	134	Karanth & Sunquist (1992)
Mouse Deer	5	Karanth & Sunquist (1995)
Gaur	450	Karanth & Sunquist (1992)
Wild Boar	32	Karanth & Sunquist (1992)

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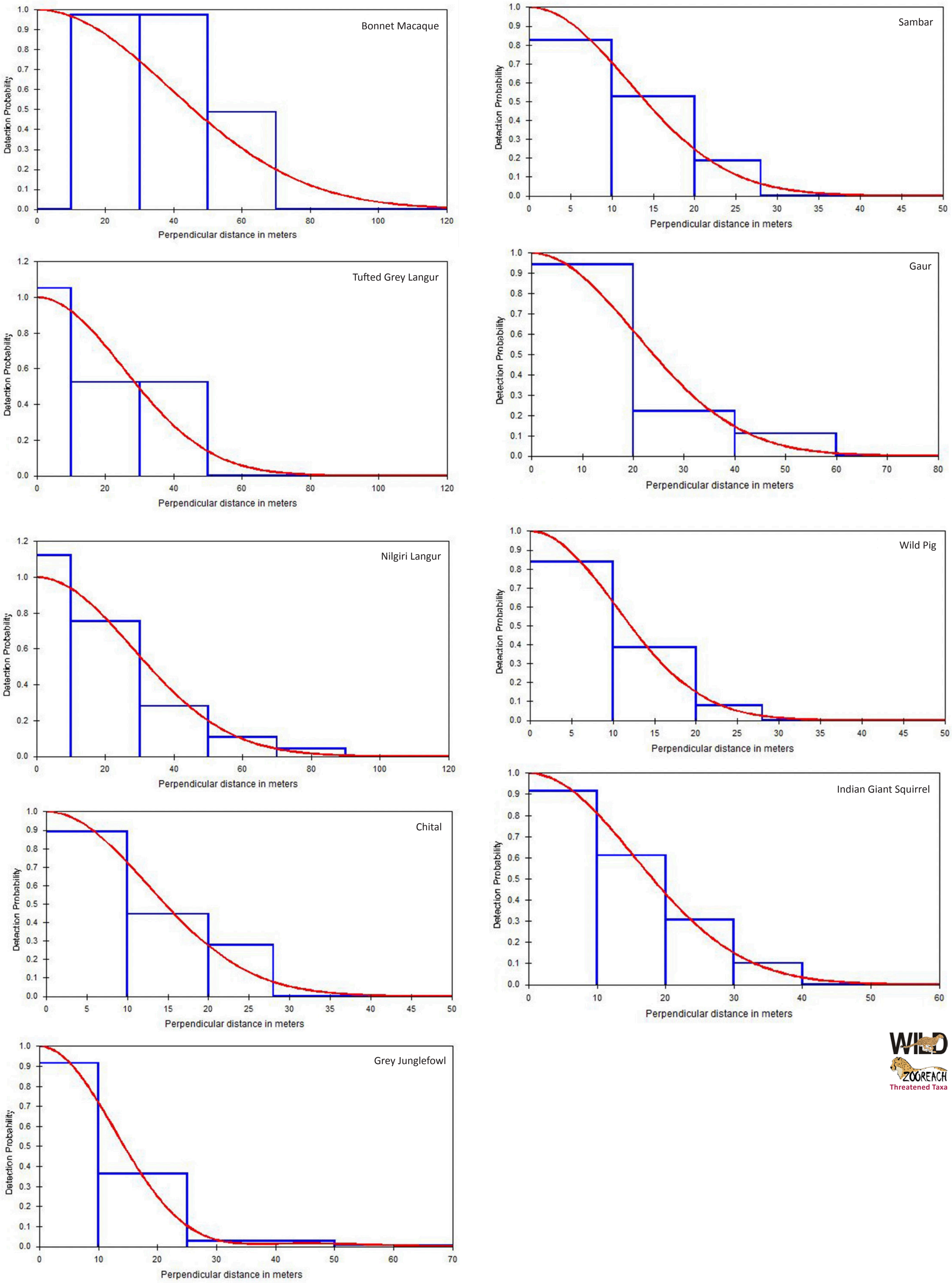
Appendix 2. Detection distances for primates and ungulates in Kalakkad-Mundanthurai Tiger Reserve.



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