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Investigating resource selection of the Indian leopard *Panthera pardus fusca* (Meyer, 1794) in a tropical dry deciduous forest

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Abstract

In order to understand the generalist nature of leopards and whether they have any degree of specialization, a study on resource selection of the Indian Leopard (*Panthera pardus fusca*) was carried out in a tropical dry deciduous forest in Sariska Tiger Reserve, Western India from January 2007 to May 2011 with the use of camera trapping under the mark-recapture framework. Camera trapping was done in an intensive study area (230 km^2) encompassing 200 camera locations on 85–130 occasions each year. In total, 40 Indian leopards were identified in the study area, of which seven individual leopards were selected for resource selection analysis. Resource selection by Indian leopards was investigated at two scales. First, habitat selection was studied using compositional analysis comparing habitat availability in the geographic range of all seven Indian leopards and utilization by the individual animals within it. The results showed that habitat selection was non-random ($P< 0.001$). The leopard's preference of habitat selection was in the following order: *Boswellia* forest> *Anogeissus* forest> *Acacia* forest> *Butea* forest> *Zizyphus* forest> Barren land> Scrubland. Second, resource selection was studied through a generalized linear mixed-effect model (GLMM) comparing the resource availability and utilization in each leopard's range. The results showed that leopards preferred *Anogeissus* dominated forest followed by *Zizyphus* mixed forest and scrubland. In addition, leopards preferred habitat with a higher encounter rate of sambar (*Rusa unicolor*) and chital (*Axis axis*) and to a lesser degree of use, habitat with a higher livestock encounter rate. The results revealed that Indian leopards showed a significant degree of preference for moderate to thick vegetation cover and wild prey species rather than areas with open forest types and domestic prey species.

Key words: Compositional analysis, generalized linear mixed effect model, mark-recapture, utilization distribution

Introduction

The Indian leopard *Panthera pardus fusca* (Meyer, 1794) is a wide-ranging large carnivore that is less susceptible to disturbance than other large cats (Sunquist and Sunquist, 2002). The leopard can be termed a 'generalist' as it can survive on a wide range of prey species and in various habitat types (Sunquist and Sunquist, 2002). The Indian leopard is distributed throughout the Indian subcontinent, ranging from the high Himalayas to dry deciduous forests (Mondal, 2011).

However, Indian leopard populations are vulnerable to habitat loss, habitat fragmentation, and direct conflict with humans in many parts of their range which leads to poaching and retaliatory killing (Mondal, 2011). Past studies have reported that the Bengal tiger *Panthera tigris tigris* (Linnaeus, 1758) (hereafter also referred to as 'tiger') survives on a high biomass of large-sized prey (Karanth and Sunquist, 1995), whereas the Indian leopard is known to survive on domestic animals and rodents in the absence of wild prey populations (Edgaonkar and Chellam, 2002).

Considering the Indian leopard's elusive nature and its occurrence in low densities, it is difficult to gather information on its use of resources in forested areas. In the recent past, camera trapping technique under the mark-recapture framework has gained momentum for long-term monitoring of Indian leopard populations (Mondal et al., 2012a) and understanding their resource selection patterns (Mondal, 2011).

Resource selection is a hierarchical process of behavioral responses of an animal to varying aspects of its immediate environment (Vanak and Gompper, 2010) and it cannot be assessed directly (Horne et al., 2008). Different ecological factors at different scales (spatial and temporal) affect the movement of an animal within its established home range in a landscape (Vanak and Gompper, 2010). Hence, studying animal-landscape relationships at different scales is vital for understating resource selection of a species inhabiting human-dominated or fragmented landscapes (Johnson, 1980; Anderson et al., 2005; Boyce, 2006; Vanak and Gompper, 2010). Lack of information on such animal-landscape dynamics can affect the conservation and management of a species in a particular habitat. The Indian leopard, although one of the subcontinent's top predators, represents an example of such an information deficiency.

The Sariska Tiger Reserve (Sariska TR), a tropical dry deciduous forest in Western India and the westernmost distribution of the Bengal tiger, lost all its tigers in 2004 due to poaching (Sankar et al., 2009). A subsequent ecological study was conducted (in 2005–2006) in the Sariska TR to evaluate the potential of the habitat and to ultimately determine whether it is capable of tiger re-introduction and holding a viable tiger population (Sankar et al., 2009). It was found that in absence of tiger in the Sariska TR, the Indian leopard took over the entire tiger habitat and became the top predator. Furthermore, the prey base in Sariska TR was found to be one of the highest in the country and capable of supporting a large number of large carnivore populations (Mondal, 2011). However, after the re-introduction of tigers in the Sariska TR during 2008–2010, an investigation revealed that the leopard population declined by 18% and considerable spatial and temporal segregation between leopard and tiger was also noted (Mondal et al., 2012b).

The authors of the present study continued the investigations of leopard and tiger throughout 2007–2011 based on radio-telemetry and camera-trap exercises and found that leopard population initially declined immediately after the tiger reintroduction; and then again increased after the settlement of home ranges by re-introduced tigers (Sankar et al., 2010; Mondal et al., 2012a). It was assumed that the leopard population in Sariska TR was stable and there must be some favoring factors that were contributing towards sustaining the leopard population, despite the existence of a rival species such as the tiger.

As a result, further investigation was required in order to evaluate the influence of various habitat factors (including prey species, vegetation types, terrain and the presence of tigers) on the habitat selection of the leopard in India. Moreover, it is widely expected that a conservation plan focused on large carnivores in a protected area consequently protects most other species present in that area as well (Foreman, 1992). The leopard, being one of the top predators in Sariska TR, acts as the "umbrella species" (Soule, 1985) for all other species associated with the ecosystem. Hence, there was a necessity to understand the habitat requirements and the pattern of habitat use by the leopard population in the study area.

In the present study, leopard resource selection was examined by comparing different vegetation types, elevation, prey species, and livestock encounter rate, as well as presence of tiger in Sariska Tiger Reserve, Western India.

Material and Methods

Study area

The present study was carried out in the Sariska Tiger Reserve (Sariska TR) from January 2007 to June 2011. Sariska TR lies in the Aravalli landscape in the state of Rajasthan, Western India (27°05'N to 27°45'N and 76°15'E to 76°35'E) (Fig. 1). The vegetation of this region includes tropical dry deciduous forest (~70%) and tropical thorn forest (~30%) (Champion and Seth, 1968). The total area of the reserve is 881 km^2, of which 273.8 km^2 is a designated national park (Core Zone). The climate in the Sariska TR is subtropical and characterized by a distinct summer (March–June), monsoon (July–August), post-monsoon (September–October) and winter (November–February). The average annual rainfall is 700 mm (Mondal, 2011).

Apart from the Indian leopard and tiger, other carnivores present in the Sariska TR are: Striped hyena *Hyaena hyaena* (Linnaeus, 1758), Golden jackal *Canis aureus* Linnaeus, 1758, Jungle cat *Felis chaus* Schreber, 1777, Wild cat *Felis silvestris ornate* Gray, 1832, Ratel *Mellivora capensis inaurita* (Hodgson, 1836), Common mongoose *Urva edwardsii* (É. Geoffroy Saint-Hilaire, 1818), Small Indian mongoose *Urva auropunctata* (Hodgson, 1836), Asian palm civet *Paradoxurus hermaphroditus* (Pallas, 1777), and Small Indian civet *Viverricula indica* É. Geoffroy Saint-Hilaire, 1803. The wild ungulates found in Sariska TR are: the Sambar *Rusa unicolor* (Kerr, 1792), Chital *Axis axis* (Erxleben, 1777), Nilgai *Boselaphus tragocamelus* (Pallas, 1766), and Wild pig *Sus scorfa* Linnaeus, 1758. The Northern plains gray langur *Semnopithecus entellus* (Dufresne, 1797) and Rhesus monkey *Macaca mulatta* (Zimmermann, 1780) represent the two primates that occur at the area. The Indian crested porcupine *Hystrix indica* Kerr, 1792 and Rufous tailed hare *Lepus nigricollis ruficaudatus* Geoffroy, 1826 are also present in the Sariska TR (Mondal, 2011).

Thirty-one villages were situated within the boundaries of the Sariska TR Tiger Reserve and ten of these were located inside the Sariska National Park area during the study period. The human population was over 1650 individuals in the villages of the National Park along with a population of ~10,000 livestock including the Buffalo *Bubalus bubalis* (Linnaeus, 1758), cow *Bos indicus* (Linnaeus, 1758), goat *Capra hircus* (Linnaeus, 1758), and sheep *Ovis aries* (Linnaeus, 1758). In the entire Sariska Tiger Reserve, the human population was around 6000 and the livestock population was more than 20,000 (Sankar et al., 2009).

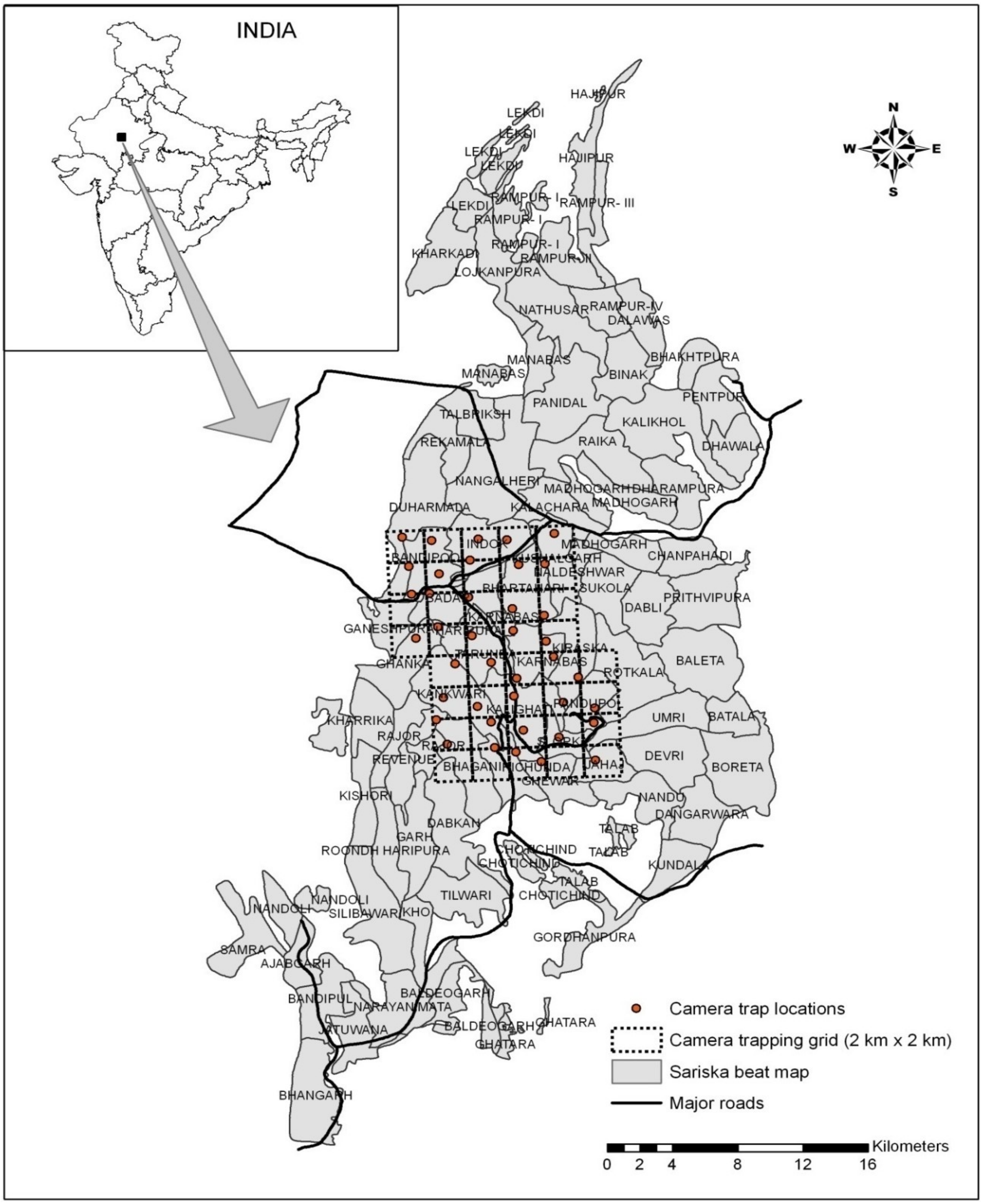


Figure 1: Location of the Sariska Tiger Reserve, Western India along with camera trapping grids and locations (Projection–WGS84).

Determination of sample size

Leopard presence data for resource use was collected using camera traps between January 2007 and June 2011. The authors used the presence data of individual leopards that were repeatedly recaptured in the camera trap locations. The number of locations of each individual was determined by the photo-capture locations of that particular individual obtained from the camera traps. Although, for any method, what matters is the stability of the home range with an increasing number of locations (Aebischer et al., 1993), and the number of locations necessary to achieve stability may be assessed by plotting the home range area against the number of locations (Kenward, 1982; 1987; Parish and Kruuk, 1982; Harris et al., 1990; Aebischer et al., 1993). Since, the authors could not use radio telemetry to determine the home range of resident leopards in the study area, the ‘range’ of each individual was inferred by the minimum home range of each individual studied through photo capture locations.

In this study, it was found that after recording 19–28 capture locations, the ‘range’ of each leopard reached asymptote (Mondal, 2011). Thus, considering the above-mentioned assumptions (Neu et al., 1974; Aebischer et al., 1993), seven individual leopards that were photo-captured in more than 30 locations were selected for studying resource selection in the study area.

Use of camera traps

The intensive study area of 160 km^2 (inside the notified National Park area) was divided into two blocks of 80 km^2 and each of those blocks was sub-divided into 20 grid-cells of 4 km^2 (2 km x 2 km). One pair of cameras was deployed in each 4 km^2 grid-cell (Fig. 1) selected on the basis of present leopard evidence (direct sightings, scratches, urine scents, scats and pugmarks) on the forest trails. Forty units of analog (Stealth Cam, GSM, Stealth Cam LLC and Deer-Cam, Hunting Network, LLC) and digital cameras (Spypoint, GG Telecom) were deployed, which worked on passive infrared motion sensors. The cameras were equipped with a 35 mm lens and recorded the date and time of each photograph. The cameras were placed 18–24 inches (45–60 cm) above the ground and facing the center of the trails. Forty locations were selected in 40 grid-cells for the placement of permanent camera traps for the entire study duration. The number of consecutive nights in which those cameras were operated each year were: 90 nights in 2007, 117 in 2008, 130 in 2009, 85 in 2010, and 110 in 2011, covering both summer and winter in each year.

In addition, the same study area was subdivided into 1 x 1 km^2 grid-cells for intensive camera trapping of leopards and other co-predators (Gupta, 2011). To record more leopard capture locations, twenty pairs of camera traps were placed in rotation in 1 x 1 km^2 grid-cells covering each vegetation and terrain type and were run for 25 nights in 2008 and 2009. Hence, in total, there were 200 camera trap locations (40 permanent locations and 160 temporary locations for intensive trapping) in the study area.

From January 2007 to June 2011, during camera trapping, 40 individual leopards were identified in the study area by a combination of distinguishing characteristics such as the shape and position of rosettes on limbs, flanks, and forequarter (Mondal, 2011). Each photo-captured leopard was given a unique identification code (e.g. L1, L2, L3, L4, etc.) (Fig. 3). Out of those 40 individual leopards, seven that were captured repeatedly in more than 30 locations were selected for resource selection analysis. The approximate age and sex of these seven leopards were determined from the camera trap photographs and direct sightings in the study area. The details of each leopard and the numbers of locations used for resource selection analysis are given in Table 1.

Data collection for habitat features

Data on different habitat features (available habitat for leopards in the study area), were recorded in four categories: a) vegetation types, b) terrain types, c) prey species and d) the presence of tiger. Since the minimum leopard home range of leopard has been previously recorded as 8–10 km^2 (Muckenhirn and Eisenberg, 1971; Eisenberg and Lockhart, 1972), all data on different habitat features were recorded and later extracted in 4 km^2 grid-cells to maintain uniformity in the analysis. The percentage area of different vegetation types in each 4 km^2 grid-cell (such as *Anogeissus* dominated forest, *Boswellia* dominated forest, *Butea* dominated forest, *Acacia* dominated forest, *Zizyphus* mixed forest, scrubland, and barren land), were extracted from land use/land cover maps of the Sariska TR (Sankar et al., 2009). A multi-spectral (Landsat 7 ETM+), high resolution (~30 m) satellite imagery from the Global Land Cover Facility (NASA) was used to generate a landuse/ landcover map of the study area (Fig. 2).

Information on the terrain types (mean and variance of elevation in each grid-cell) was extracted from SRTM (Shuttle Radar Topography Mission) maps of the Sariska TR (Mondal, 2011). The encounter rate of different prey species in the study area was estimated using line transects under the distance sampling technique. In total, 32 line transects varying in length from 1.6 km to 2 km were laid across 40 grids (160 km^2) in the study area. The total transects length of 60.4 km was walked three times (between December and June each year from 2007–2011) in early morning hours (06:00 AM to 08:00 AM) resulting in a total effort of 181.2 km (Mondal et al., 2011). The encounter rates of different prey species (wild prey and livestock) in each grid-cell were obtained from line transects. Camera trap data was used to obtain a photo-encounter rate for tigers in each grid-cell in the study area. Hence, information on encounter rate of prey species, vegetation types, elevation, and presence of tiger were obtained in each grid-cell (4 km^2).

Table 1: Details of individual Indian leopards, *Panthera pardus fusca* with number of locations collected for resource selection analysis, 2007–2011.

Individual leopard and sampling period	Sex	Number of locations collected
L2 (January 2007–June 2010)	Male	61
L4 (January 2007–April 2011)	Female + 3 cubs	44
L6 (February 2007–February 2011)	Old male	65
L8 (February 2007–April 2011)	Young male	54
L14 (January 2007–June 2007)	Old female + 3 cubs	48
L17 (January 2008–May 2010)	Young female	31
L26 (February 2009–June 2011)	Young female	39

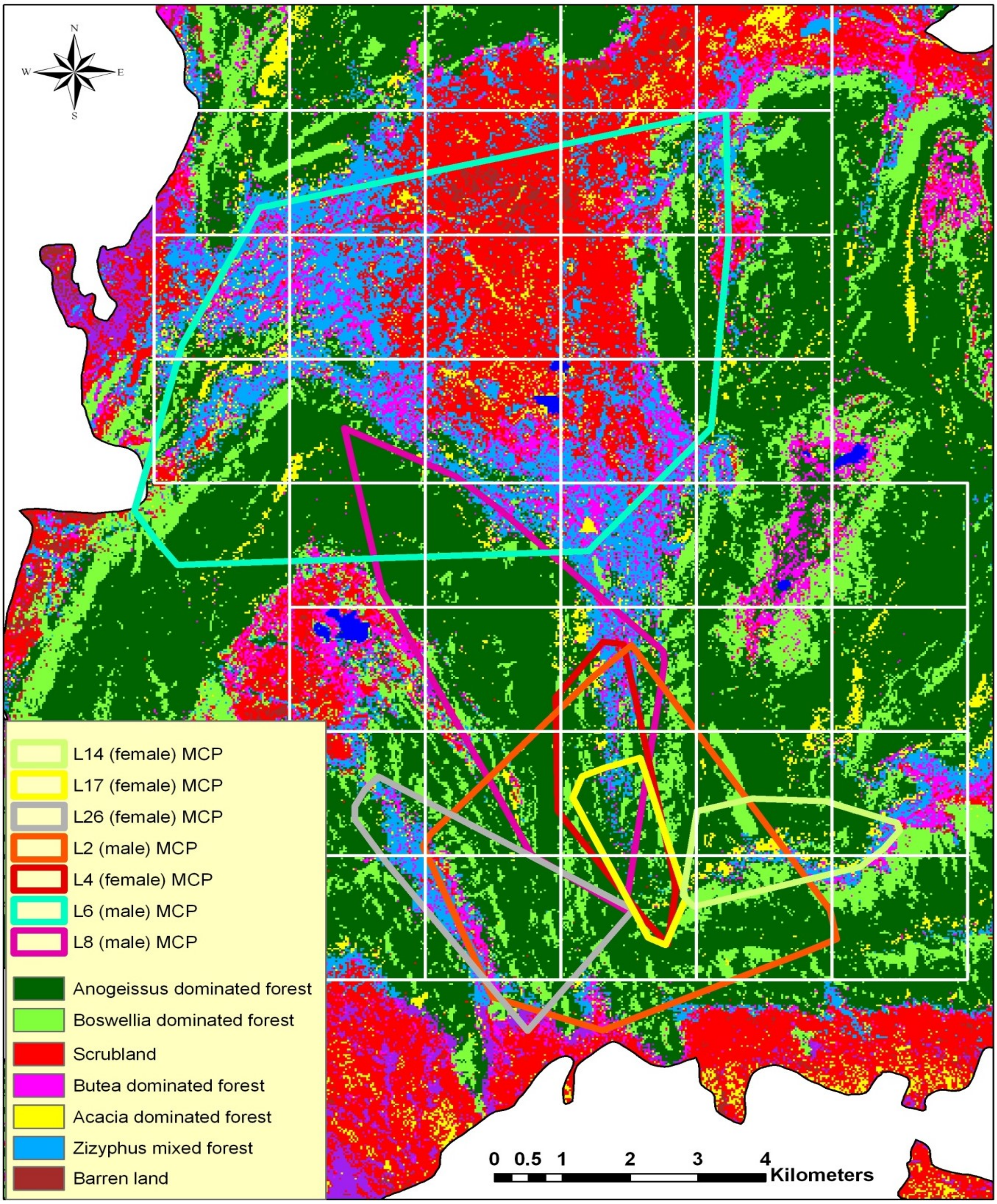
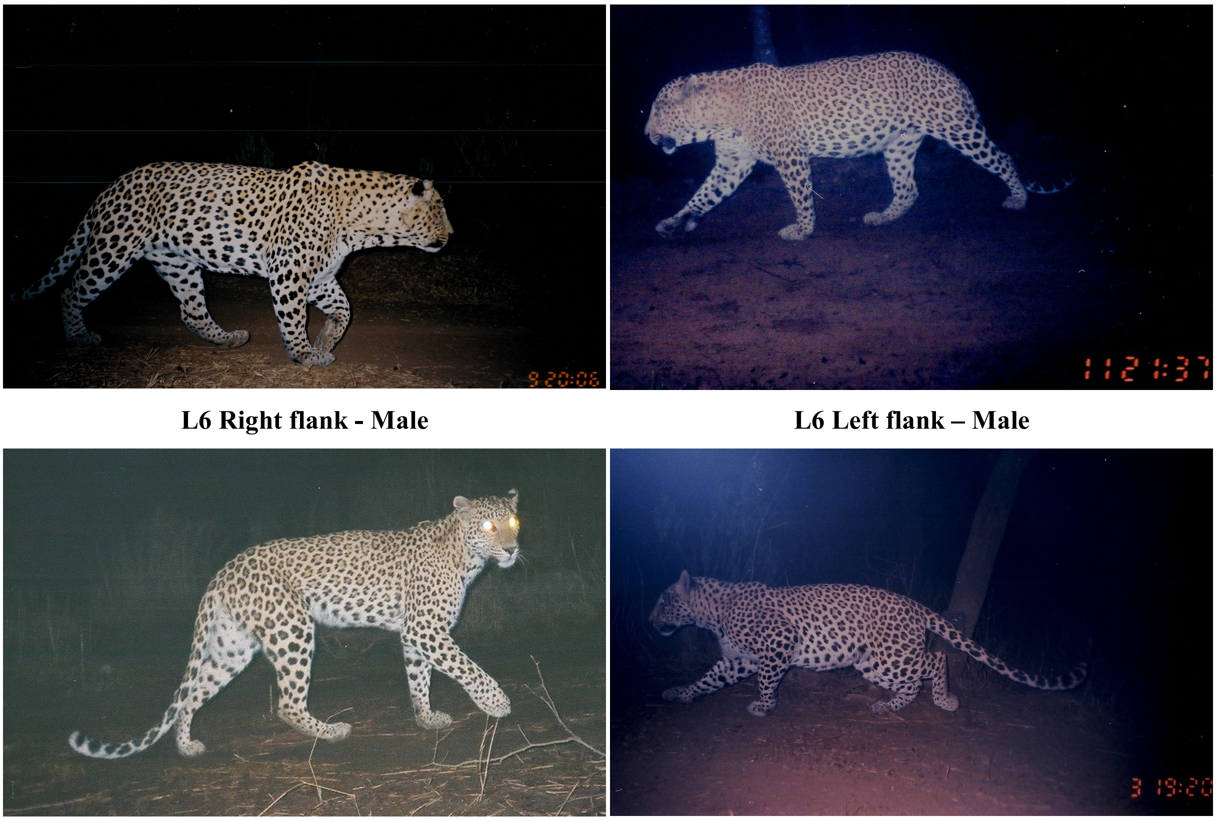


Figure 2: Ranges of seven Indian leopards (*Panthera pardus fusca*) as determined from camera traps on a land cover map of the Sariska Tiger Reserve, 2007–2011.



L6 Right flank - Male

L6 Left flank – Male

L17 Right flank - Female

L17 Left flank - Female

Figure 3: Camera trap photographs of Indian leopards (*Panthera pardus fusca*) at the Sariska Tiger Reserve, 2007–2011.

Based on this data, resource selection for leopards was assessed at two scales, i.e. second and third-order resource selection, under the rank-based method developed by Johnson (1980). According to Johnson (1980), second-order resource selection can be defined as "the selection of range [minimum home range obtained from camera trap photographs as studied in the present study] within a geographic range" and third-order resource selection is defined as "the selection of habitats within that range". In the second order, habitat use was estimated by a set of proportions describing habitat composition in an individual leopard's 'range' and habitat availability was determined by the proportion of habitat composition of a global area summing the minimum convex polygons (MCPs) of all the leopards. At the third order, resource use was estimated by the usage of various resource components within the utilized habitat range.

Second-order resource selection

Second-order habitat selection (Johnson, 1980) was evaluated in order to understand habitat selection by a leopard within its geographic range within the study area. The extent of the geographic range (81.36 km^2) was defined by calculating MCPs around the collective ranges of all of the study animals (Fig. 2). The percentage area of each vegetation type within that geographic range, which was the available habitat for each leopard, is given in Table 2. Based on the locations where an individual of leopard was photographed, the utilization distribution (UD) based kernel range of each leopard was calculated using HRT tools in ArcGIS 9.2 (Environmental Systems Research Institute, Redlands, CA, USA). The UD values were then extracted in 4 km^2 grids and the percentage area of each vegetation type in each grid-cell was multiplied by the UD value of that grid-cell to obtain the proportional use of different vegetation types by each leopard in each grid-cell. In this process, different vegetation types in each grid will reflect their appropriate importance based on the UD value of that grid (actual use) with respect to their area. If an individual leopard uses an area around a camera trap more frequently, then the UD value of that grid will be correspondingly high, and eventually, the habitat in that grid-cell will show higher preference and *vice versa* (Mondal, 2011).

Compositional analysis (Aebischer et al., 1993) was used to determine leopard resource selection in the study area, but with a modification that assigns values based on the UD of each animal in the study area (Millspaugh et al., 2006; Vanak and Gompper, 2010). Compositional analysis requires the percentage area of different habitat types, which are available to an individual animal and their extent of use, but this method does not calculate the intensity or weight of use of different habitat types.

Since the kernel 'range' provides a UD value based on the density distribution of locations of an animal, in the present study, the weight of use of a vegetation/habitat type was determined by a leopard's kernel 'range' (Vanak and Gompper, 2010; Mondal, 2011).

In that way, an individual leopard's use of a habitat is calculated by the proportion of UD volume in each vegetation/habitat type and its area within the 'overall geographic range' combining the 'ranges' of all study animals (Millspaugh et al., 2006). The program Resource Selection for Windows (RSW) was used to conduct the compositional analysis (Leban, 1999).

The available (total geographic range joining all MCPs of all study animals) and utilized (kernel utilization distribution of each animal) habitat components were transformed to log-ratios y_0 and y, respectively, using the proportion of *Boswellia* dominated forest as the denominator and then the difference ($d= y - y_0$) was calculated (Aebischer et al., 1993). The residual matrix R_2 was calculated by the raw sums of squares and cross products calculated from d. R_1 was calculated by the mean corrected sums of squares and cross-products calculated from d using the program Resource Selection for Windows (RSW) (Aebischer et al., 1993).

Third-order resource selection

Third-order resource selection (Johnson, 1980) was evaluated in order to understand the resource selection of an individual leopard within its 'range'. Leopard third-order resource selection was studied through the Generalized Linear Mixed Effect Model (GLMM) (Mondal et al., 2013). In the present study, the 'range' of each individual leopard was extracted into 4 km^2 grids-cells along with information on the encounter rate of prey species, vegetation types, elevation, and presence of tigers. It was assumed that the resource selection of leopards in the study area is a function of habitat (mean of elevation and percentage area of vegetation types in each grid), available food (encounter rate of prey species in each grid), and presence of competitor species (encounter rate of tiger in each grid) (Mondal et al., 2012b). Hence, all resource parameters (including food, habitat, and competition) were picked as fixed effects and individual leopards were selected as the random effect for GLMM models (Mondal et al., 2013). The data was analyzed in the R environment (R Development Core Team (2008) using lme4 (Bates et al., 2011) and MuMin (Barton, 2011) packages.

Results

Second-order habitat selection

The log-transformed ratios of utilized habitat types by leopards (y) are given in Appendix Table 1. The differential log-transformed ratios of available and utilized habitat ($d= y - y_0$) by leopards are given in Appendix Table 2. Ratios of residual matrices between R_2 (raw sums of squares and cross products calculated from d) and R_1 (f mean corrected sums of squares and cross-products calculated from d) are given in Appendix Table 3. The ratio of R_1 and R_2 matrices yielded λ ($\lambda= [R_1]/ [R_2] = (0.0798/ 0.7084) = 0.1127$) and resulted significantly ($P< 0.001$) when compared to X^2 (15.2807, $P< 0.05$) with six degrees of freedom (Aebischer et al., 1993). Inspection of d showed (Appendix Table 2) that its distribution is not multivariate normal; however, the level of significance obtained by randomization was $P< 0.001$. This showed that habitat use by leopards in the study area was non-random (Aebischer et al., 1993). To rank the habitat/ vegetation types in order of use by leopards in the Sariska TR, a matrix of the mean and standard error of all of the habitats was calculated overall for all of the study animals (Appendix Table 4). The final outcome was obtained when the mean values were replaced by its sign in a simplified manner as given in Table 3.

The final simplified matrix (Table 3) ranked leopard habitat use in the following order: *Boswellia* dominated forest> *Anogeissus* dominated forest> *Acacia* mixed forest> *Butea* dominated forest> *Zizyphus* mixed forest> Barren land> Scrubland. Although each habitat type ranked in order from greatest to least use, there were no significant differences observed (p> 0.05) between the selection of *Anogeissus* dominated forest and *Boswellia* dominated forest, or amongst *Acacia* mixed forest, *Butea* dominated forest and *Zizyphus* mixed forest.

Third-order resource selection

To understand third order resource selection of leopards, 16 models were analyzed in combination with different parameters including encounter rates of the wild prey species and livestock, different habitat types, elevation, and tiger encounter rate. A correlation test was done amongst all variables, and *Butea* dominated forest and barren land were found to be significantly correlated (P< 0.5) with *Zizyphus* mixed forest and scrubland, respectively, hence excluded from the aforesaid models. The model with habitat variables (excluding *Boswellia* dominated forest), wild prey species (excluding nilgai, wild pig, and peafowl *Pavo cristatus* Linnaeus, 1758) and livestock was top-ranked based on the lowest AIC value (Akaike Information Criterion) (Table 4), but no single model could best explain the patterns of leopard resource use in the study area. Since the differences between AIC values were less than four for the top five models, model averaging was done to obtain the best explained estimates (Table 4). The model-averaged importance value for each parameter is given in Table 5.

Amongst the habitat parameters, *Zizyphus* mixed forest was the most positive influence in explaining the leopard's presence, followed by *Anogeissus* dominated forest and scrubland. For instance, leopard utilization of an area was increased by a factor of 1.05 and 1.04 (log-transformed estimates) with unit increase of *Zizyphus* mixed forest and *Anogeissus* dominated forest, respectively (Table 5). Although it was not found to be significant, the *Acacia* mixed forest had a negative influence in explaining leopard resource utilization.

Amongst the prey species, leopard significantly used more habitats with a higher encounter rate of sambar and chital, and used less habitats with a higher encounter rate of livestock and Bengal hanuman langur. Use of an area by a leopard in the study area increased by a factor of 1.09 and 1.10 with unit increase in encounter rate of chital and sambar respectively. Similarly, the use of an area by a leopard decreased by a factor of 0.99 with unit increase in livestock encounter rate in that area. Although, the tiger encounter rate influenced positively and elevation influenced negatively in explaining the selection of an area by leopards, these were not found to be significant.

Table 2: Vegetation and land cover classes in the available geographic range of Indian leopards *Panthera pardus fusca* in the Sariska Tiger Reserve.

Vegetation/Landcover type	Area (km^2)	Percentage
Anogeissus dominated forest (Ano dom)	36.37	44.70
Boswellia dominated forest (Bos dom)	8.25	10.14
Butea dominated forest (But dom)	6.25	7.68
Zizyphus mixed forest (Ziz mix)	12.85	15.79
Acacia mixed forest (Aca mix)	3.51	4.32
Scrubland (Scrblnd)	13.24	16.27
Barrenland/ Agriculture (Barlnd)	0.89	1.09
Total	81.36	100.00

Table 3: Simplified ranking matrix comparing the utilization of each habitat type by the seven studied leopards (*Panthera pardus fusca*) with the proportion of total available habitat types, 2007–2011.

Resource	Bar lnd	Ziz mix	Scrblnd	But dom	Aca mix	Ano dom	Bos dom	Rank
Bar lnd		-1	3	-1	-1	-1	-1	**6**
Ziz mix	1		3	-1	-1	-3	-3	**5**
Scrblnd	-3	-3		-3	-3	-3	-3	**7**
But dom	1	1	3		-1	-3	-3	**4**
Aca mix	1	1	3	1		-3	-3	**3**
Ano dom	1	3	3	3	3		-1	**2**
Bos dom	1	3	3	3	3	1		**1**

Note: Each mean element in the matrix was replaced by its sign. A '-3' represents significant deviation from random (at $P< 0.05$). Bar lnd: barren land; Ziz mix: *Zizyphus* mixed forest; Scrblnd: scrubland; But dom: *Butea* dominated forest; Aca mix: *Acacia* mixed forest; Ano dom: *Anogeissus* dominated forest; Bos dom: *Boswellia* dominated forest.

Table 4: Model selection statistics of the Generalized Linear Mixed Model analysis for resource selection (3rd order) of the Indian leopard (*Panthera pardus fusca*) in the Sariska Tiger Reserve, 2007–2011.

Models in GLMM	K	AIC	ΔAIC
(la+sa+ch+livs+ziz+scrb+aca+ano)	8	396.1	0.000
(la+sa+ch+livs+ziz+scrb+aca+ano+demcv)	9	397.0	0.881
(la+sa+ch+livs+ziz+scrb+aca+ano+tiger)	9	397.4	1.266
(la+sa+ch+livs+ziz+scrb+aca+ano+tiger+demcv)	10	397.8	1.707
(la+wp+sa+ch+livs+ziz+scrb+aca+ano)	9	397.9	1.809
(la+ni+wp+sa+ch+livs+ziz+scrb+aca+ano)	10	399.9	3.743
(pe+la+ni+wp+sa+ch+livs+ziz+scrb+aca+ano)	11	400.3	4.187
(pe+la+ni+wp+sa+ch+livs+ziz+scrb+ano)	10	400.6	4.505
(pe+la+ni+wp+sa+ch+livs+ziz+scrb+aca+ano+bos)	12	401.1	4.923
(pe+la+ni+wp+sa+ch+livs+ziz+scrb+aca+ano+bos+demcv)	13	401.5	5.390
(pe+la+ni+wp+sa+ch+livs+ziz+scrb+aca+ano+bos+demcv+tiger)	14	402.3	6.200
(pe+ni+wp+sa+ch+livs+ziz+scrb+aca+ano+bos)	11	403.1	6.973
(pe+la+ni+wp+sa+ch+ziz+scrb+aca+ano+bos)	11	406.3	10.200
(ziz+scrb+aca+ano+bos)	5	437.2	41.034
(tiger)	1	472.5	76.359
(demcv)	1	510.3	114.161

K= Number of parameters; pe= peafowl, ni= nilgai, la= common langur, wp= wild pig, sa= sambar, ch= chital, livs= livestock, ziz= *Zizyphus* mixed forest, scrb= scrubland, aca= *Acacia* mixed forest, ano= *Anogeissus* dominated forest, bos= *Boswellia* dominated forest, demcv= elevation, tiger= tiger encounter rate.

Table 5: Most influential model-averaged parameter estimates from top models explaining resource selection (3rd order) of the Indian leopard (*Panthera pardus fusca*) in the Sariska Tiger Reserve, 2007–2011.

Parameters (Fixed effects)	Estimate	Log-transformed Estimate	Z value	Significance
Acacia mixed forest	-0.03929	0.961472	-1.620	Not significant
Anogeissus dominated forest	0.03761	1.038326	5.895	$P< 0.001$
Zizyphus mixed forest	0.04746	1.048604	5.534	$P< 0.001$
Scrubland	0.02693	1.027296	3.559	$P< 0.001$
Chital	0.08187	1.085315	2.271	$P< 0.05$
Sambar	0.09098	1.095247	4.563	$P< 0.001$
Wild pig	0.00159	1.001591	0.442	Not significant
Common langur	-0.03913	0.961626	-2.459	$P< 0.05$
Livestock	-0.00837	0.991665	-2.306	$P< 0.05$
Elevation	-1.47748	0.228212	-1.058	Not significant
Tiger	0.02602	1.026361	0.859	Not significant

Discussion

At the geographic scale (second order resource selection), *Boswellia* dominated forest was found to be the habitat most preferred by leopards, followed by *Anogeissus* dominated forest, *Acacia* mixed forest, *Butea* dominated forest, *Zizyphus* mixed forest, Barren land, and Scrubland, respectively. Compositional analysis is a comparison of used habitat types against available habitats (Johnson, 1980). The area of *Boswellia* dominated forest is only about 10% of the total available habitat in the study area but considering leopard kernel utilization distribution, *Boswellia* dominated forest was used by leopards more than its availability, thereby giving its rank as the most preferred habitat by leopards. Although the latter scored higher in the analysis, there was no significant difference in the uses of *Anogeissus* dominated forest and *Boswellia* dominated forest. Ecologically, *Boswellia* dominated forest and *Anogeissus* dominated forest play a key role in the ecosystem of tropical dry deciduous forest in the Aravalli landscape (Sankar et al., 2009; Mondal, 2011). *Boswellia* patches are generally distributed on table-top plateaus or high steep slopes and *Anogeissus* patches are generally distributed along gentle slopes of the Aravalli Mountain and comprise 45% of the total forest cover of Sariska TR (Sankar et al., 2009). Indian leopards are largely known to inhabit hilly terrain (Schallar, 1967; Seidensticker, 1976; Edgaonkar, 2008; Sankar et al., 2009), which is again attributed to the greater preference of *Boswellia* dominated forests and *Anogeissus* dominated forests. The other forest types, *i.e.*, *Acacia* mixed forest, *Butea* dominated forest, and *Zizyphus* mixed forest, were used by leopards roughly according to their availability and no significant difference was observed between them. Leopards have used barren land and scrubland significantly less ($P < 0.05$), as these forests are low in terms of production of prey biomass and provide less cover for large carnivores (Sankar et al., 2009; Gupta, 2011).

The importance of *Anogeissus* dominated forest was further supported at the third order resource selection (at individual scale), as *Anogeissus* dominated forest, in conjunction with *Zizyphus* mixed forest and scrubland, were the main predictors of leopard resource selection in the GLMM models. Although, *Boswellia* dominated forest was the most selected habitat type at the second order compared to its availability, at the third order it could not explain the resource use within the utilized range. Scrubland was less used by leopards at the second-order of habitat selection because of its comparatively high availability (16.3%) in the total geographic area, but at the third-order scrubland positively explained ($P < 0.001$) leopard habitat selection. In other words, leopards preferred some proportion of scrubland within the home 'range' level, but not at the geographic scale.

A number of studies have reported that leopards, as generalist predators, take a much wider range of prey, in terms of type and size, than most other large cats (Bothma and Le Riche, 1986; Schaller, 1972; Bailey, 1993). Indian leopards are capable of surviving on small-sized prey, which allows them to exist in places where large prey are very low in number or have been exterminated. It has also been reported that in areas where leopards live in closer proximity to human-modified landscapes their diet is often supplemented by dogs, cats, and domestic livestock (cow, buffalo, pig, goat, and sheep) (Edgaonkar and Chellum, 2002; Chauhan et al., 2005; Odden, 2014). Instances of 'surplus killing' of livestock sometimes occur when large numbers of domestic prey might be killed in some circumstances but only a few are eaten (Turnbull-Kemp, 1967). On the contrary, the present study showed that leopards significantly selected the habitat with higher encounter rates of chital and sambar rather than the habitat with a higher encounter rate of livestock (Table 5). A previous study also showed that chital and sambar constituted more than 60% of the leopard diet in the study area, where the contribution of livestock was less than 5% (Mondal et al., 2011). Since the abundance of wild prey species in the study area was considerably high (chital: 33.8 individuals/ km^2, sambar: 26.4 individuals/ km^2, and wild pig: 54.1 individuals/ km^2), leopards tended not to utilize domestic prey species for survival despite the presence of ~2000 livestock in that area (Mondal et al., 2011). A few studies have reported incidences of dog and livestock predation by leopards from villages along the forest periphery where wild prey species are less abundant (Edgaonkar and Chellum, 2002; Athreya et al., 2004; Chauhan et al., 2005). Those leopards, in a sense, could be considered as urban leopards due to extensive habitat degradation and prey base depletion. It was reported that in human-dominated landscapes, human-felid conflict is raised due to active livestock herding and forest resource consumption from the nearby forest in the protected area (Fitzmaurice et al., 2021). In contrast, cases of human-leopard conflict are comparatively less in the Sariska landscape than the other protected areas (Kafle et al., 2020). Although there are ten villages inside the study area, there were no human fatalities and only a few incidences of livestock predation (n= 6) recorded during the five-year study period (Mondal, 2011).

At the individual scale (third order resource selection), tiger encounter rate did not show any significant role in explaining leopard resource selection in the study area. Unlike the studies of Arivazhagan et al. (2007) and Seidensticker and Lumpkin (1991), where leopards ventured through open terrain and raided villages for domestic prey, in the Sariska TR leopards selected medium to thick habitat types and largely preferred wild ungulate species.

Although leopards are absent from true deserts and alpine terrains above the timberline, they do live in almost every type of habitat and even in fringe areas (Bailey, 1993). It is important to understand which factors may limit this cat's distribution in an area. Limitations in cover, food, and water are usually the major factors affecting an animal's distribution (Stuart, 1981), but for an individual leopard, the definition of these basic requisites is extremely broad. Based on previous studies, leopards were found to consume a number of diverse species from beetles to large ungulates like adult chital and sambar (Hayward et al., 2006). Leopards even can survive in only a few scattered shrubs and trees or in dense, moist, tropical evergreen forest (Bothma and Le Riche, 1986). Leopards are found in a range of forests, from woodlands to Acacia savannas, exotic pine plantations, scrub forests, rocky hills, and mountain terrains from sea level to elevations of 5000 m (Harrison and Bates, 1991). Leopards can live in areas where annual rainfall is 2000 mm like the West Africa and Tropical Asia, as well as areas of almost no rainfall areas (50 mm per year) (Mondal, 2011). So, it can be concluded that the factors that limit leopard distribution are very site-specific and leopards do have an adaptive capability for coping with these different factors for survival.

The Indian leopard is distributed throughout the Aravalli landscape, but right after tiger reintroduction during the present study, the leopard was confined due to some degree of preference of major habitat factors. The observed preferences of moderate to thick vegetation cover and wild prey species rather than open forest types and domestic prey species cannot be extrapolated to other study sites, even those only outside the Sariska TR. There is a conventional assumption that leopards can cope in human-dominated landscapes and persevere despite pressures such as habitat fragmentation due to their great nature of adaptability (Edgaonkar, 2008). However, conservationists agree that leopards may be more prone/vulnerable to population decline as well as extinction than once previously thought (Gopal, 2011). On either side of the argument, very little research (based on conservation priority) has been done that can direct easy and successful conservation strategies for leopards. However, long-term research on resource selection of leopards in different landscapes can lead to a broader understanding of the ecology and adaptation strategy of this species.

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Conflict of interest

The authors declare that there are no conflicting issues related to this research article.

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Appendix

Appendix Table 1: The residual matrix R_2 is the matrix of raw sums of squares and cross products calculated from *d* (differential log-ratios of utilized habitats); R_1 is the matrix of mean corrected sums of squares and cross-products calculated from *d*.

	19.0789	8.832	20.9563	9.3283	5.2438	1.4275
	8.832	6.0106	11.4332	5.9661	3.0272	0.8077
R_1=	20.9563	11.4332	26.0542	11.5139	5.4215	1.5157
	9.3283	5.9661	11.5139	6.05	3.3028	0.9298
	5.2438	3.0272	5.4215	3.3028	3.208	0.6995
	1.4275	0.8077	1.5157	0.9298	0.6995	0.3202
	32.8929	20.5882	48.147	20.3852	13.0129	2.7036
	20.5882	16.0155	34.5734	15.3759	9.639	1.8937
R_2=	48.147	34.5734	79.5749	33.2777	20.7137	4.0275
	20.3852	15.3759	33.2777	14.9001	9.5213	1.9512
	13.0129	9.639	20.7137	9.5213	7.5774	1.4172
	2.7036	1.8937	4.0275	1.9512	1.4172	0.4381

Appendix Table 2: Log ratios of utilized habitats by each individual Indian leopard (*Panthera pardus fusca*) in the Sariska Tiger Reserve, 2007–2011.

Individual	Log-ratios of utilized habitat (y)					
	Bar-lnd/ Bosdom	Zizy-mix/ Bosdom	scrblnd/ Bosdom	But-dom/ Bosdom	Aca-mix/ Bosdom	Anodom/ Bosdom
1	-3.3003	-1.3564	-1.9345	-1.9625	-2.0789	1.1872
2	-5.9103	-1.266	-4.5666	-2.0461	-2.234	1.0944
3	-1.0894	1.0209	1.0318	0.2949	-0.4261	1.4536
4	-3.3098	-0.1458	-1.4235	-0.6949	-1.2394	1.7518
5	-4.0295	-1.6018	-4.1726	-2.0146	-1.0974	1.4412
6	-5.7612	-1.6885	-4.1235	-2.5309	-2.4087	1.139
7	-2.0451	-0.231	-0.8569	-0.8619	-2.0184	1.4088

Appendix Table 3: Difference in log-ratios of utilized habitats by each individual of the Leopard in (*Panthera pardus fusca*) the Sariska Tiger Reserve, 2007–2011.

Individual	Difference in log-ratios ($d = y - y_0$)					
	Bar lnd/ Bosdom	Zizy-mix/ Bosdom	scrblnd/ Bosdom	But-dom/ Bosdom	Aca-mix/ Bosdom	Anodom/ Bosdom
1	-1.07	-1.7992	-2.4074	-1.6846	-1.2257	-0.2962
2	-3.68	-1.7088	-5.0394	-1.7682	-1.3808	-0.3891
3	1.1409	0.578	0.5589	0.5728	0.4271	-0.0299
4	-1.0795	-0.5887	-1.8963	-0.417	-0.3861	0.2684
5	-1.7992	-2.0447	-4.6454	-1.7367	-0.2442	-0.0423
6	-3.5308	-2.1314	-4.5964	-2.253	-1.5555	-0.3445
7	0.1852	-0.6739	-1.3297	-0.584	-1.1652	-0.0747

Appendix Table 4: Ranking matrix of mean and standard error obtained by averaging each habitat for all for seven Indian leopards (*Panthera pardus fusca*) in the Sariska Tiger Reserve.

Resource	Bar lnd	Ziz mix	Scrblnd	But dom	Aca mix	Anodom	Bosdom
Bar lnd		-0.2093	1.3603	-0.2804	-0.6147	-1.275	-1.4048
SE		0.4205	0.2769	0.3926	0.53	0.6276	0.674
Ziz mix	0.2093		1.5696	-0.0711	-0.4055	-1.0658	-1.1955
SE	0.4205		0.468	0.0553	0.2745	0.3351	0.3783
Scrblnd	-1.3603	-1.5696		-1.6407	-1.975	-2.6353	-2.7651
SE	0.2769	0.468		0.4649	0.6622	0.7455	0.7876
But dom	0.2804	0.0711	1.6407		-0.3343	-0.9946	-1.1244
SE	0.3926	0.0553	0.4649		0.2513	0.3277	0.3795
Aca mix	0.6147	0.4055	1.975	0.3343		-0.6603	-0.7901
SE	0.53	0.2745	0.6622	0.2513		0.2252	0.2764
Anodom	1.275	1.0658	2.6353	0.9946	0.6603		-0.1298
SE	0.6276	0.3351	0.7455	0.3277	0.2252		0.0873
Bosdom	1.4048	1.1955	2.7651	1.1244	0.7901	0.1298	
SE	0.674	0.3783	0.7876	0.3795	0.2764	0.0873	