EVALUATING THE USE OF CAMERA-TRAPS FOR POPULATION ESTIMATION OF UNMARKED INDIVIDUALS USING SPATIALLY EXPLICIT MODELS IN TADOBA-ANDHARI TIGER RESERVE, MAHARASHTRA, INDIA

A THESIS
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Under the guidance of

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Declaration by the Candidate

I declare that the thesis entitled "**Evaluating the use of camera-traps for population estimation of unmarked individuals using spatially explicit models in Tadoba-Andhari Tiger Reserve, Maharashtra, India"** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2017 to 2021** Under the guidance of **Bilal Habib** and has not formed the basis for the award of any degree, diploma, associate ship, fellowship, titles in this or any other University or other institution of higher learning. I further declare that the material obtained from other sources has been duly acknowledged in the thesis. I shall be solely responsible for any plagiarism or other irregularities if noticed in the thesis.

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Place: Dehradun Date:

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Summary

Wildlife monitoring is of fundamental importance to establish baseline information, measure population changes and extinction risk. Motion-triggered camera traps are an increasingly popular tool for monitoring terrestrial species over large landscapes. Over the years, the application of camera traps has increased exponentially but studies aiming at fundamental information about sampling design and protocols are still limited to simulation studies. In this dissertation, we have used occupancy as an indicator of effective species monitoring. Occupancy has become a robust and unbiased state variable to monitor species worldwide. However, the optimal sampling design required for robust estimations of occupancy is lacking for many species. In the first technical chapter (Chapter 3), we estimated the optimum sampling design by varying the number of sites (50–400) and sampling days (10–25) for a range of mammal species using camera-trap survey data from central India. We used power analysis and mean-squared error and evaluated results in the context of species' body size, social status, diet and the detectability of the species. We found that mean-squared error changed significantly with the number of sites for rare species, whereas for species with moderate and high detection probability, the mean-squared error changed significantly with the number of sampling occasions. Power increased with an increase in the number of sampling sites and occasions for all species, although the change was not significant for species with higher occupancies or detection probabilities. We found that body size was positively related to occupancy but did not influence detection probability significantly. No relationship was detected with social status or diet on occupancy or detection probability. Our results suggest a minimum of 50 sites for 15-20 days for common species and 100 sites for 20-30 days for rare, elusive species. Our results provide guidelines to managers and practitioners for effective allocation of cost and sampling effort for a wide variety of terrestrial mammals in camera trap surveys.

In the second technical chapter (Chapter 4), we estimated the abundance of two small cats and one Mustelidae, the jungle cat (*Felis chaus*), and the rusty-spotted cat (*Prionailurus rubiginosus*) and the honey badger (*Mellivora capensis*). We used an extension of the spatial count model in a Bayesian framework approach to estimate the population density of jungle cat, rusty-spotted cat and honey badger. Densities of the rusty-spotted cat, jungle cat and honey badger were estimated as 6.67 (95% CI 4.07-10.74) and 4.01 (95% CI 2.65- 6.12) and 14 (95% CI 10-22.25) individuals/100 km^2 respectively. Our estimates highlight the widespread applicability of this model for density estimation of species with no individual identification. Moreover, the study outcomes can aid in targeted management decisions and serve as the baseline for species conservation as these models allow robust population estimation of elusive species along with predicting their habitat preferences.

For the third technical chapter (Chapter 5), we here tried to develop a model to estimate the population of a social animal, Dhole (*Cuon alpinus*) from camera trap captures. We used hierarchical clustering on the capture locations with the highest number of individuals captured as weight, to estimate the number of packs. Once we have the number of packs, the pack size is estimated from the probability of missing an individual from the captures. To test the effect of the number of photographs on detection probability and pack size, we tested in different simulated scenarios with a varying number of photographs. Using a further simulation, we tried to evaluate the efficiency of our model by varying the radius of the pack-operating area with the distance between the home-range centres. Using photo-captures from multiple years (2014-18), we found 7-9 packs operating in the study area. The population density was estimated to be around 4.7-8.25 individual per 100 sq. km. Simulation study showed our model performs well till the ratio of the radii of the pack operating areas and pack home-range centre is less than 0.8.

The last technical chapter (Chapter 6) was majorly aimed at the comparison of population estimates using different sampling techniques. We compared the density estimate of one group living (chital) and one solitary (Indian muntjac) using Line-transect based distance sampling and distance sampling using camera traps. We estimated the density estimates from camera-trap distance sampling using different photo-capture interval (0-30 min). We found distance sampling estimates from camera traps were comparable with line-transect based density estimates when we used a time-interval of 20 minutes as the independent time between two groups. These findings can be extended to other species and replicated for other landscapes with proper caution. Moreover, the concurrence of the outcomes with line-transect distance sampling reflects simultaneous population estimation of multiple species.

The work reflected the use of occupancy as an effective indicator to monitor long-term changes in species abundance. Also, we estimated the population density of several uniquely unidentifiable species. This was the first density estimate of Jungle cat, Rusty-spotted cat, and first density estimate of Dhole from India. With proper caution, these methods can also be extended to other species lacking unique marks.

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Chapter 1

Introduction

Assessing the status of species is imperative for management and conservation. It requires an understanding of basic ecological processes affecting population dynamics and the impacts of ongoing climate and environmental changes. A large spectrum of biotic and abiotic forces drive species distributions and abundances across large spatial and temporal scales. Traditional ecological tools can often appear inadequate to understand the interplay of forces due to their multi-scale effects. Evaluating the relative effects of these forces on population dynamics is often difficult because data for most of the species are insufficient and/or comprised of disparate types as they are cryptic, elusive and exist at low densities. A fundamental challenge of population ecology is to detect species trends, extrapolate inference across spatio-temporal scales, and create credible projections of dynamics and viability. Modeling approaches that incorporate multiple, interacting processes using dissimilar data types are thus needed, and indeed the development of such models is a rapidly growing area of research within ecology.

Camera traps, with widespread use in various wildlife ecological studies in this era, proved to be a solution for the drawbacks with data collection of rare and elusive species. Though the tool has immense potential, it has not been used to its maximum limits due to methodological constraints regarding designing and sampling errors. Species occupancy is of the fundamental interest in ecology and conservation biology. The proportion of sites occupied by a species in a given area is defined as the occupancy of the species (Mackenzie et al. 2002). It is used to gain insight about conservation efforts, trends and status of species and other important parameters which are indispensable for conservation under the present scenario. Modelling species occupancy requires insights about the detection probability of a species. That is difficult to achieve without bias due to improper detection.

Earlier applications of camera traps were restricted to estimating the density of uniquely identifiable species, e.g. tiger *Panthera tigris* (Karanth and Nichols 1998), jaguar *Panthera onca* (Silver et al. 2004), ocelot *Leopardus pardalis* (Maffei et al. 2005), Leopard *Panthera pardus* (Chauhan et al. 2005), snow leopard *Panthera uncia* (Jackson et al. 2006), striped hyena *Hyaena hyaena* (Singh 2008). The application experienced a steep growth over years with the advent the capture-recapture framework which incorporated spatial modelling of the distribution of the species in the landscape, popularly known as spatially-explicit capture-recapture (SECR) (Borchers & Efford 2008, Royle et al. 2014). As in most of the animals, individuals cannot be easily identified, focus of the camera-trap studies shifted more towards surveying other animals that are not uniquely identifiable and hence studying entire guilds and communities (Tobler et al. 2008, Ahumada et al. 2013, Rovero et al. 2013, Meek et al. 2014) with broad-scale surveys. This has led to widespread application of camera-traps and initiated alternative approach for the analysis of 'unmarked' species. The assumption of constant detection probability for the unidentifiable animal has been critiqued (Jennelle et al. 2002, Sollmann et al. 2013) and as a result the inferences with the unmarked individuals are not robust and the results are often debatable (Foster and Harmsen 2012). Unbiased density estimation is difficult to attain as the number of individuals captured is an unknown proportion of the total population (Chandler and Royle 2013). Also, detection probability varies with season, species and time. Hence, with varied detection rates across different species in a community, the survey effort and time has to be considered keeping in mind about the less detectable species in community studies. Designing studies for an entire community is an arduous job as a lot of factors have to be taken into account. The relation between detectability and effort is a crucial factor for designing camera trap studies for any terrestrial species. With a lot of theoretical advances using rigorous models, reliable densities of unmarked individuals can be achieved (Royle and Nichols 2003, Chandler and Royle 2013). The spatial correlation earlier thought as an obstacle for inference, is now used to gather information on animal activity centre and correlate density with population size. Utilizing the spatial information effectively in the captures, the application of spatially explicit methods (Borchers and Efford 2008) for estimating the density of an unmarked animal can be a novel approach for monitoring wildlife. Also, there is a need to bridge the gap between different sampling methods by a calibration technique that can also be used for missing and improper detections of species (Mackenzie et al. 2003, Guillera-Arroita et al. 2010).

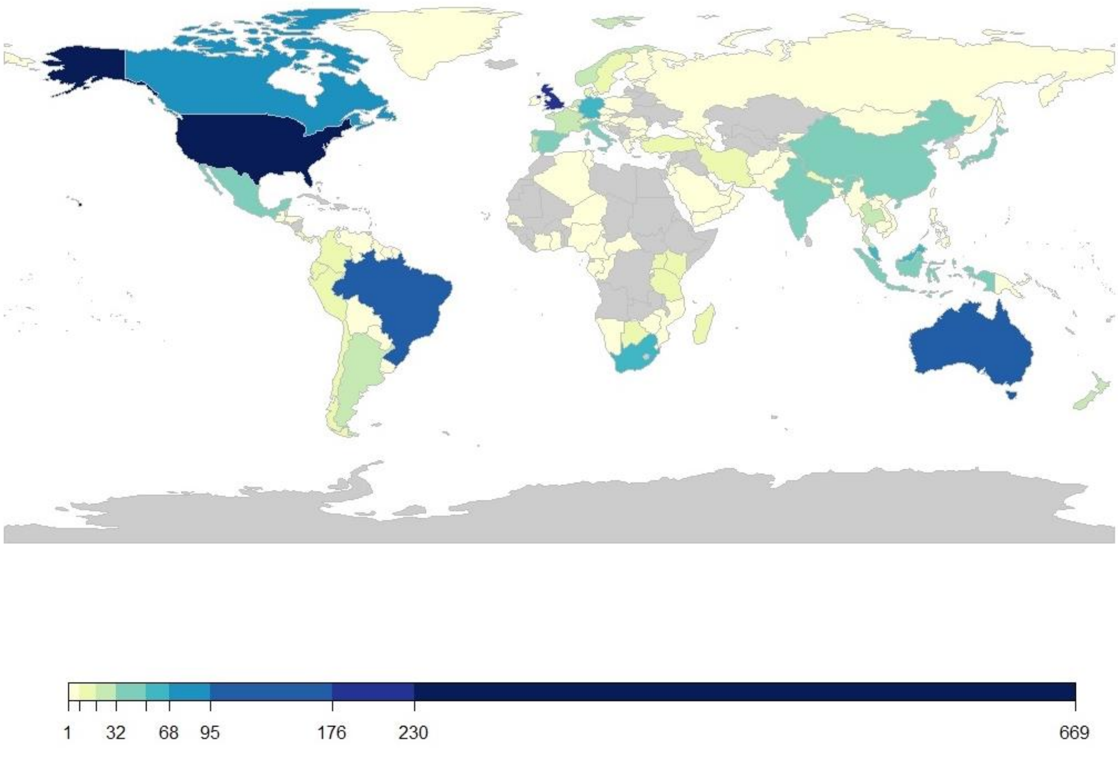

Figure 1: Number of camera-trap studies published (N=1520) country-wise from the year 1990-2019 (Aug). Records were obtained from Web-Of Science using the queries “camera-trap”, “trail camera”, “remote camera”, “automated camera trap”.

Standardizing the different sampling techniques will help us design studies targeted for different animals. We want to estimate optimum trapping effort to sample a terrestrial community focusing on different survey length and number of camera trap sites. With the help of the outcomes planning large-scale camera trap studies will be easier. Also, the usage of camera traps can offer more cost-effective wildlife surveys if the sampling error can be standardized for different species. Wide-ranging adaptations of these methods with explicit assumptions can provide stronger inferences for the elusive animals.

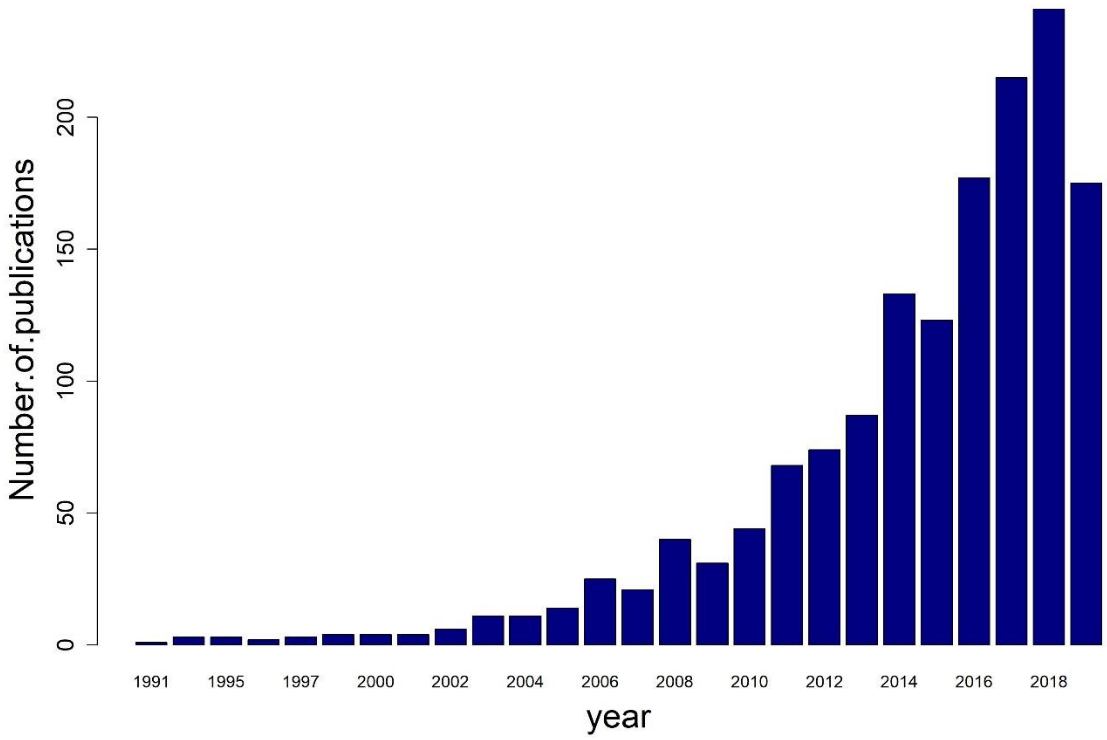

Figure 2: The number of camera trap papers published per year (1990-Sep 2019) according to the Web of Science's categories ecology, biology, zoology and veterinary sciences queried for terms "camera trap", "infrared triggered camera", "trail camera", "automatic camera", "photo trap", "remotely triggered camera", "remote camera".

Despite a large number of camera trap studies available till date, there is no clear indication about the sampling length, camera spacing and effects of other factors on the studies focusing on occupancy and density of target species or communities. A better understanding of these factors and associated trade-offs will help researchers and managers to design a study more effectively and maximize the outcomes. There is a lack of focus to compare the cost and labour for different sampling methods as most studies focus only on the density estimates, relative abundance or presence-absence of species. If the relation between different methods can be established, it will also help us to compare and optimize for different species. In order to compare results across different camera-trap studies more thorough and consistent reporting of detailed information is required. Also, there is a lack in linking the detectability of the camera and ecology of the target species (e.g. solitary/group living, body size, movement speed). These improvements can be utilized to address the problem of imperfect detection, equal detectability for all species. Empirical and simulation testing of new methods for density estimation of unmarked species is also much-required advancement of camera-trap methodology. If the basic methodological inconsistencies can be overcome, camera-trap can be used to its full potential for broad-scale ecological questions and global biodiversity monitoring. In this study, I will try to fill in the research gaps mentioned above focusing on more widespread application of camera-trap surveys. This will lead to stronger inferences and aid in enhanced ecological understanding for better wildlife conservation.

1.1 Objectives and Research questions:

a) Estimating the minimum survey effort requirement for detecting different species in camera traps.

- How detection probability and animal density influences the minimum trapping effort in camera trap surveys?
- How sampling effort and camera spacing affects the estimates of camera trap surveys?

b) Population estimate of unidentifiable or unmarked animal from camera traps.

- How the population density can be estimated for unidentifiable species from camera trap?

c) Comparing density estimates of animals captured in camera traps and from distance sampling using line-transect.

- Which is the most precise, cost-effective and less labour intensive method for estimating animal density?

Chapter 2

Study Area

The Tadoba-Andhari Tiger Reserve (TATR) is situated in the Chandrapur district in the the Vidharbha Landscape of Maharashtra state, between 20°4’53” to 20°25’51’’ N and 79°13’13” to 79° 33’34” E (Figure 6). The TATR is distributed over an area of 1700 sq. km which consists of Tadoba national park and Andhari wildlife sanctuary. The core area of the tiger reserve extends over 625 sq. km with a buffer area of 1100 sq. km. The tiger reserve covers a landscape that is an interspersion of grasslands, water bodies and dry tropical deciduous forests along with patches of riparian forest alongside streams. Two main rivers flow through the region, with the Erai river in the west and the Andhari river in the east. The northern and south-eastern part of the reserve is mostly undulating in topography, with the foothills of the Chimur range gradually giving way to the plains as one moves south. The Tadoba and Kolsa lakes constitute the largest water bodies in the TATR (Fig. 2). Most of the annual rainfall (1175 mm) is received between the months of June to September (Figure 4), with a minimum temperature of about 3°C in December, rising to a maximum of about 44°C in May. The tiger reserve is highly biodiverse with a rich variety of animal species inhabiting this region, including 41 species of mammals, 195 species of birds, 74 species of butterflies and 30 species of reptiles (Khawarey & Karnat, 1997; Marathe et al. 2002). The reserve has corridor connectivity through the forested landscape of Brahmapuri forest Division to Umred-Karandla Wildlife Sanctuary, Bor Tiger Reserve which extends further up to Nagzira-Navegaon Tiger Reserve and Melghat Tiger Reserve. Regular tiger dispersal has been reported from the corridor that makes the tiger reserve more significant in order to maintain the long-term survival of the predator and prey population in the landscape.

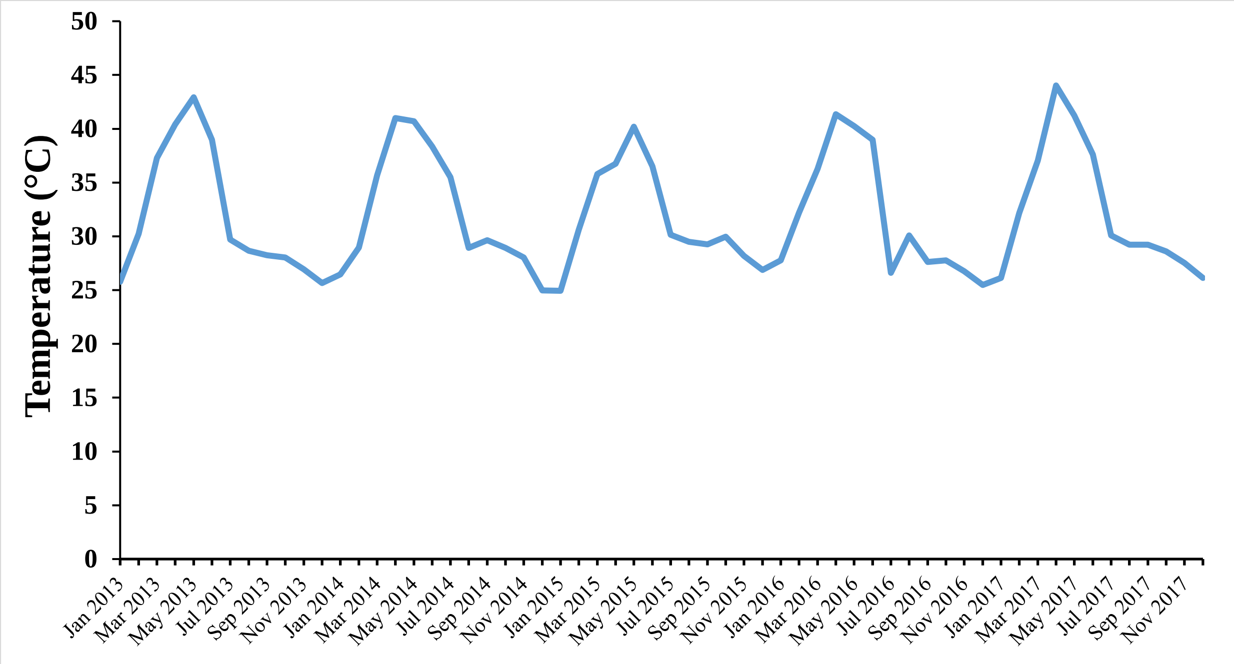

Figure 3: Land surface temperature of Tadoba-Andhari Tiger Reserve from year 2013-2017 was calculated using MODIS 8-day composite land-surface temperature satellite data

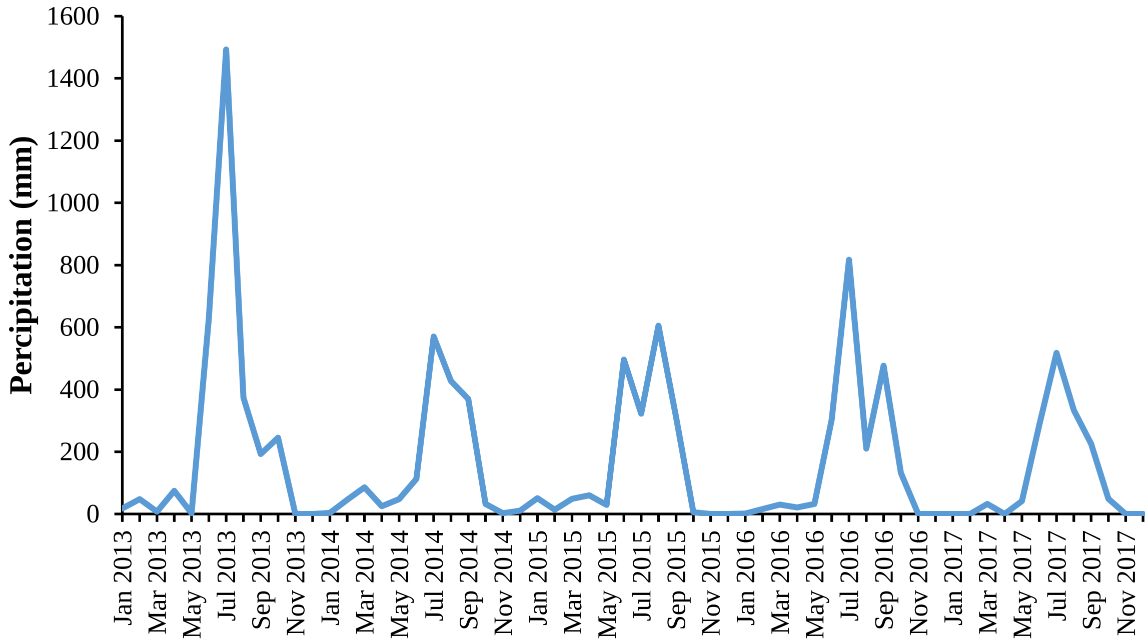

Figure 4: Precipitation of study area of Tadoba-Andhari Tiger Reserve was calculated using WorldClim dataset from the year 2013-2017

2.1 Flora:

The vegetation type is southern tropical dry deciduous forest (Champion and Seth 1968), dominated by bamboo *(Dendrocalamus strictus)*, teak (*Tectona grandis)*, along with ain *(Terminalia tomentosa)*, tendu *(Diospyros melanoxylon)*, moha (*Madhuca indica)*, bel *(Terminalia bellerica)*. Riparian vegetation mostly around the large water bodies includes species such as jamun (*Syzygium cumini)*, Arjun (*Terminalia arjuna*) and mango *(Mangifera indica)*. Bamboo forms an extensive understory through the tiger reserve.

Figure 5: A photograph showing the landscape of dry-deciduous forest of Tadoba-Andhari Tiger Reserve from above

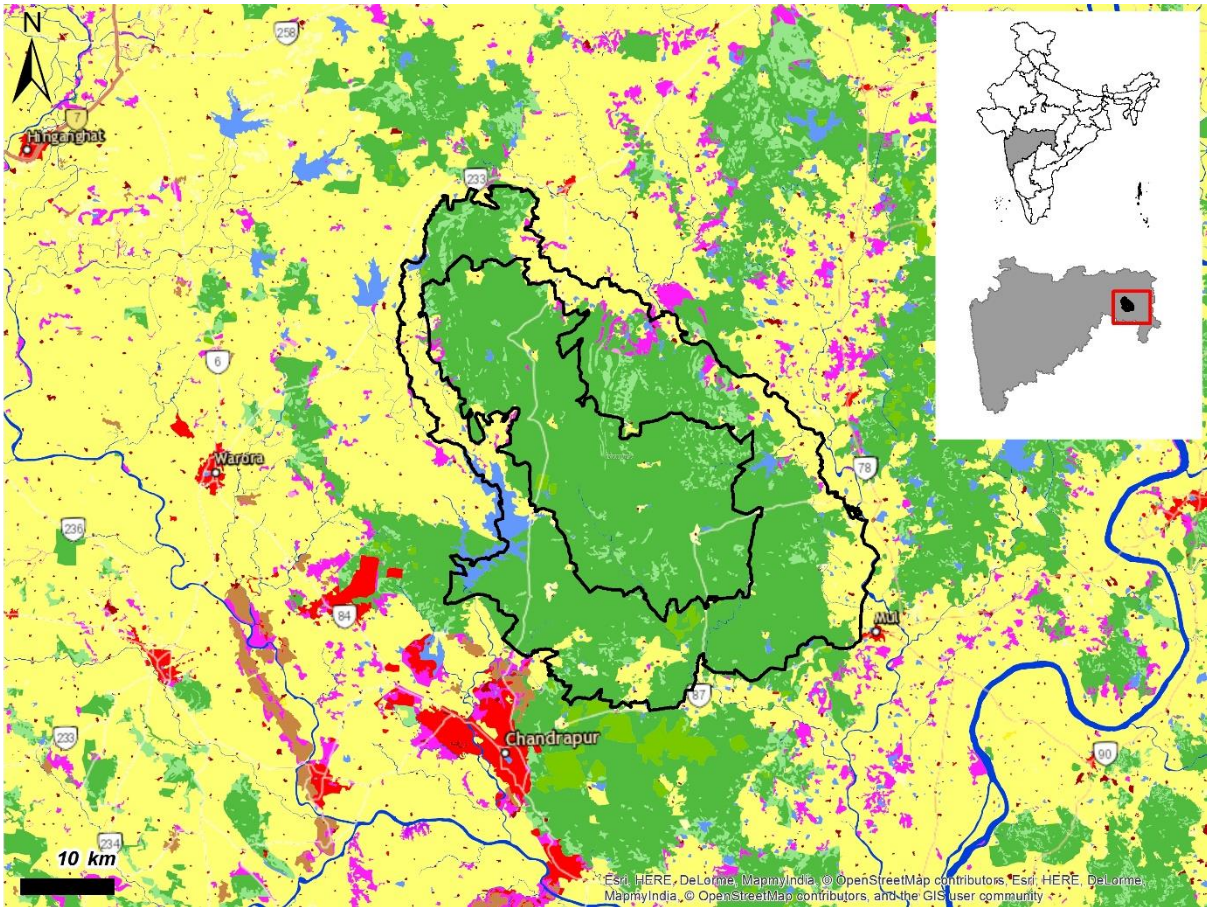

Figure 6: The Study area Tadoba-Andhari Tiger Reserve (TATR) is marked in black. The Green colour shows the extant deciduous forest in the study area. Inset: Map of India and State of Maharashtra with the red square showing the location of TATR in the state

2.2 Fauna:

The large carnivores in the reserve are tiger (*Panthera tigris)*, leopard *(Panthera pardus)*, dhole (*Cuon alpinus*), and sloth bear (*Melursus ursinus*), with jungle cat *(Felis chaus)*, rusty-spotted cat *(Prionailurus rubiginosus)*, small Indian civet (*Viverricula indica*), the common palm civet *(Paradoxurus hermaphrodites*), grey mongoose *(Herpestes edwardsi)*, ruddy mongoose *(H. smithii)*, jackal *(Canis aureus)* and honey-badger (*Mellivora capensis)* representing the small-carnivore guild.

The herbivore assemblage is typical of peninsular deciduous forests, comprised of gaur (*Bos gaurus*), sambar (*Rusa unicolor*), chital (*Axis axis*), wild boar (*Sus scrofa*), barking deer (*Muntiacus muntjac*), Chowsingha (*Tetracerus quadricornis*), nilgai (*Boselaphus tragocamelus*). The larger arboreal mammal includes grey langur (*Semnopithecus sp*.)

The reserve has 30 recorded species of reptiles, 5 species of amphibians and over 195 species of birds.

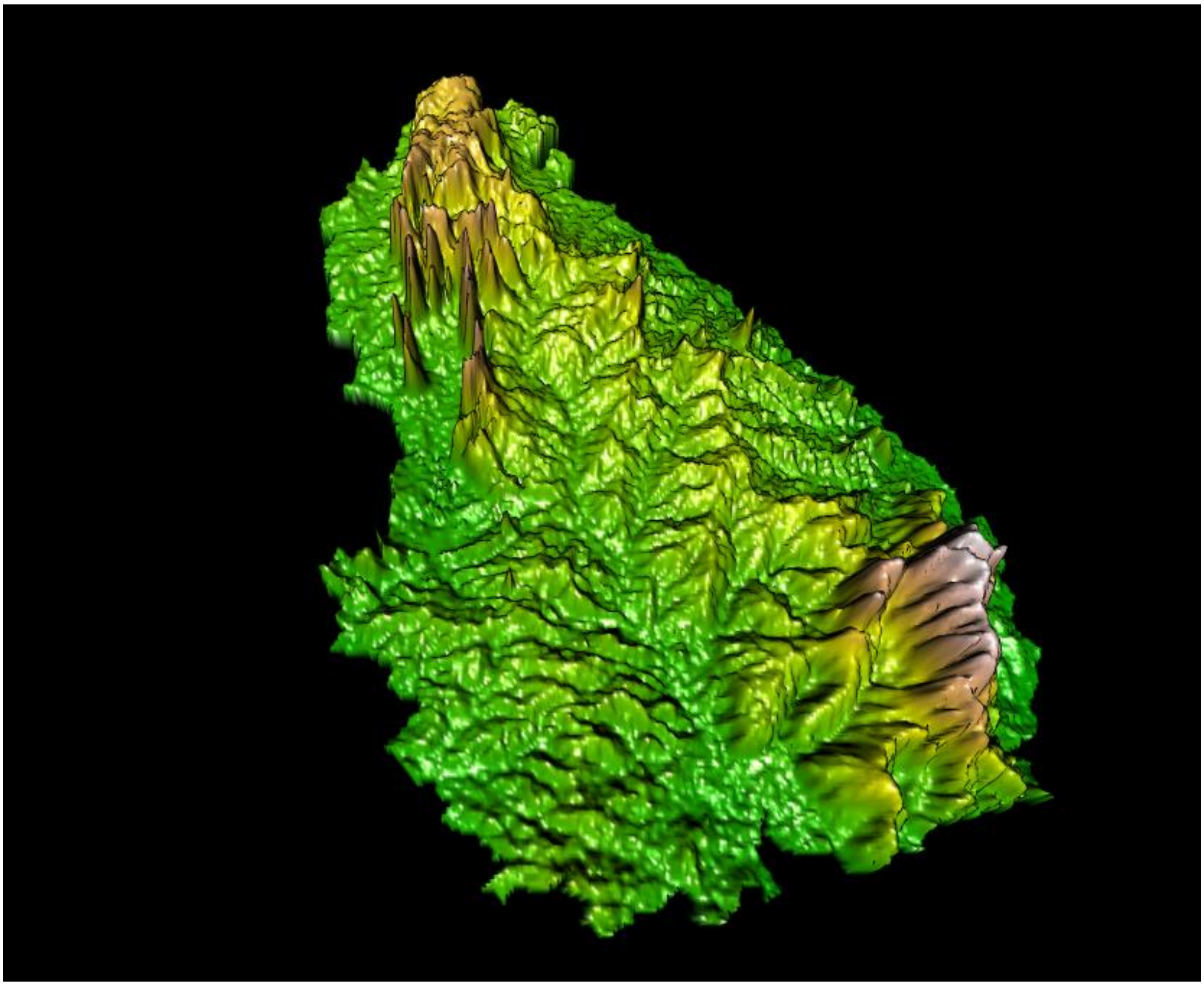

Figure 5: 3-D Elevation map of Tadoba-Andhari Tiger Reserve. The highlands on the south-eastern side and the north-western side can be visualized in the elevation map.

The Management Plan for Tadoba-Andhari Tiger Reserve for the period 1997-98 to 2006-2007 has been approved by the Chief Conservator of Forests (Wildlife). Management inputs as prescribed in the plan have been initiated since 1997-98. Protection is the most important management input in TATR. STPF forces have been prepared from the local villagers to carry out patrolling the fringes of the reserve to control poaching and other illegal activities. The effective protection measures have led to an increase in prey and predator density across the study period. Along with protection, the reserve has a long history of village relocation also. The first village relocation was carried out during the year 1975 (Khatoda and Pandherpouni), followed by Botezari (2007), Navegaon (2012) and Jamni (2014).

2.3 Review of literature on Tadoba-Andhari Tiger Reserve

Few research studies have been carried out in TATR. The First attempt to study plants of Tadoba National Park was initiated by Haines (1916). Malhotra and Moorthy (1992) gave the floristic account of Tadoba National Park and its surroundings. Mathur (1991) studied the ecological interaction between habitat composition, habitat quality and abundance of some wild ungulates in Tadoba National Park. A computerized wildlife database was established for conservation, monitoring and evaluation in Tadoba-Andhari Tiger Reserve (Dubey and Mathur 1999, Dubey 1999, Dubey & Mathur 2000). A study on the vegetation ecology of Tadoba National Park was carried out by Kunhikannan (1999). TATR was surveyed as a part of a study carried out by the Forest Survey of India (2006) to estimate the status and changes in forest cover in all the tiger reserves of the country. Paliwal & Mathur (2007) carried out a study in TATR on spatial analysis of landscape patterns and their relevance for large mammal conservation. TATR had also been studied as a part of the countrywide study conducted by Jhala *et al.*, (2008,2010, 2015) in all the tiger reserves to describe the status of tigers, co-predators and prey. Since 2013, the Wildlife Institute of India is working on a project on "**Long term monitoring of Tigers, co-predators and prey species in Tadoba-Andhari Tiger Reserve and adjoining areas in Maharashtra**" under the supervision of Dr Bilal Habib. The project aimed at data-collection on prey-predator dynamics in long-term and radio-telemetry of large predators and evaluating the changes at a very fine scale over the years.

Chapter 3

Sampling design trade-offs for terrestrial mammals using motion-triggered cameras

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3.1 Introduction:

Effective species conservation at broad scales requires comprehensive ecological knowledge of the distribution pattern and the habitat requirements of targeted species or community. Long-term monitoring enables/facilitates robust assessments of population trends and biodiversity management by providing baseline information to evaluate extinction risk and changes in population trends. Motion-triggered camera traps are increasingly used by scientists globally for surveying terrestrial mammals over large spatial scales (McCallum 2013), which have remained traditionally challenging to sample using other non-invasive methods. Data from camera traps can be used simultaneously for species richness (Tobler et al. 2015), community structure (Jimenez et al. 2017), population estimates (Karanth and Nichols, 1998), behaviour and activity patterns (Ridout and Linkie 2009), and occupancy modelling (Thorn et al. 2009).

Occupancy, defined as the proportion of sites occupied by a species, is popularly being used in wildlife monitoring programmes throughout the world for many species across diverse taxonomic groups (Guillera-Arroita 2012). Occupancy can be used as a surrogate for abundance (MacKenzie and Royle 2005, Kery and Schmidt 2008) and has the potential to reflect changes in populations unbiasedly (Ahumada et al. 2013). Occupancy surveys aid in understanding species distributions, habitat use (Long et al. 2011), and population dynamics parameters (MacKenzie et al. 2012). Using camera traps, data required for occupancy modelling can be collected for a diverse range of species cost-effectively over broad temporal and spatial scales.

Earlier research using occupancy modelling from camera traps has been limited by small study areas, standard monitoring protocol (Bailey et al. 2007, Guillera-Arroita et al. 2010, Shannon et al. 2014). Moreover, logistical and financial constraints have also posed a major challenge to meet the requirement of a larger sample size for robust, large-scale monitoring assessments. Additionally, a majority of camera-trap studies have focused on population estimations, relative abundance, and species inventories (Burton et al. 2015). Only ~15% of published camera-trap studies used occupancy models across different taxa (Burton et al. 2015). Moreover, inadequate reporting and the absence of a comprehensive protocol, have made it challenging to replicate similar designs for different study areas to compare the findings. While sampling designs for an occupancy modelling framework have been investigated theoretically using simulated datasets (Mackenzie and Royle 2005, Bailey et al. 2007, Guillera-Arroita et al. 2010), only a few studies have used empirical field data to explore the precision and accuracy of occupancy estimates (Shannon et al. 2014). The use of field data not only provides an accurate outcome but also provides vital information on species biology as a baseline to be replicated by other field studies.

When species detection probability is imperfect (<1), occupied sites may be classified as unoccupied based on survey data leading to underestimations of occupancy (Guillera-Arroita et al. 2014). To overcome this problem, replicate surveys should be conducted at sampled sites. Replication is commonly achieved by conducting repeated surveys at different points in time (temporal) or by surveying different sectors of each sampled site (spatial). The need for replication creates a trade-off between the number of sites to survey and the number of replicate surveys per site (Bailey et al. 2007). There are still few studies using field datasets that estimate detection probability and occupancy simultaneously to derive the optimal trade-off necessary among a suite of species (Guillera-Arroita et al. 2010). Detection probability was found to be the most significant factor for the estimation of the dynamic occupancy model (McKann, et al. 2013) and critical for estimating optimal survey designs (Guillera-Arroita et al. 2010). However, it was mostly unaddressed or poorly reported in occupancy studies.

We used data of a broad scale camera-trap survey to derive the recommended sampling design to overcome the drawbacks addressed. Here, we implemented landscape-level camera-trap surveys to evaluate how the number of sampling sites (50–400 cameras) in combination with a number of occasions (10–25 survey days) influenced the error associated with estimating occupancy and detection probability. We surveyed a diverse group of terrestrial mammal species varying in size and abundance and included camera-trap locations over the whole study area to make our study independent of habitat-specific factors working at local scales. We also evaluated the relationship between the function of capture frequency (Tobler et al. 2008) and detection probability to determine if the former could be a surrogate for the latter. We used the optimality criterion for both occupancy and detection probability estimates (Guillera-Arroita, et al. 2010) to simulate scenarios and evaluate the estimates for a different combination of days and sites. The terrestrial community of this study-area represents almost the complete body-size spectrum of species that can be photo-captured from Asia as well as other continents. Developing countries with a limited fund for wildlife monitoring and conservation can be benefitted especially from practising outcomes of the study. Using these results, we provide recommendations and general guidelines that can be used by wildlife practitioners to design and implement studies with better allocation of sampling effort.

3.2 Methods:

3.2.1. Study area and design:

This study was conducted in Tadoba-Andhari Tiger Reserve (TATR, 1727 km^2) in Maharashtra, India. The landscape characteristically holds Southern tropical dry-deciduous forests (Champion and Seth 1968), dominated by Bamboo (*Dendrocalamus strictus*) and Teak (*Tectona grandis*) species. Elevation ranges from 212 m to 351 m asl and annual temperature ranges from 3-48ºC. There is a short-wet season (July-September) and a long dry season (October-June); the area gets an annual rainfall of 1175 mm (Khawarey & Karnat, 1997).

We deployed 378 pairs of camera-traps in 1727 sq. km of TATR, dividing the area into 1.42 x 1.42 km (2 sq. km) cells. Individual camera trap sites in adjacent cells were separated by an average of 1 km with some exceptions due to the unavailability of suitable locations and terrain constraints. Within each sampling cell, we maximized detection probability by selecting sites for camera trap deployments where animals were most likely to travel based on topography, vegetation cover and the confluence of roads or animal trails. The placement of camera-traps along roads and animal trails ensures maximum detection of the existing assemblage of the animals specifically the focal group (O'Connell, Nichols and Karanth, 2011). We placed a pair of unbaited, motion-triggered digital camera traps with a white-flash (Cuddeback Blue series C1, Cuddeback Ambush www.cuddeback.com) ~40 cm above ground on the opposite side of roads and trails. Due to logistical constraints (limitation of camera trap units), camera traps were set in four different blocks throughout the study area with an average of 100 camera-trap pairs in each block. The camera trap sampling spanned across the dry season (February to June 2016) to ensure constant occupancy and detection probability. Cameras were programmed to take consecutive images at a 5-second delay while triggered. After placement, cameras were checked once every two weeks for storage memory and battery condition. At any given location in every block, cameras were active for at least 25 days.

3.2.2 Statistical Analysis:

We estimated the detection probability and occupancy of terrestrial mammals that had a minimum of ten detections and defined each day (24-h) as a sampling occasion, and multiple detections within in a day were combined as a single capture. We assumed closure for each sampling block to ensure constant occupancy (no immigration, no emigration) throughout the sampling interval. Species-specific detection histories were generated by pooling presence-absence data across the four blocks. We used detection histories to estimate constant occupancy (ψ) and detection probability (p) with single species–single-season occupancy models (MacKenzie et al. 2002). The single-season occupancy modelling framework is based on a sampling protocol in which 'S' sites are repeatedly surveyed with 'K' replicates to generate species presence/absence matrix for each site and replicate. The model assumes that each site has a probability of being occupied and that the detection process at occupied sites is a series of independent Bernoulli trials. We ran the occupancy models in the software PRESENCE 12.7 (Hines 2006) and the unmarked package (Fiske and Chandler 2011) in the program R 3.4 (R core team 2017). We calculated the average time to first capture and capture frequency, defined as the number of times a species was captured at a particular location, to explore the relationship between capture frequency and detection probability (Tobler et al. 2008). We also explored the relationship between estimated occupancy and species traits (e.g. body size, group size) for all the studied species.

3.2.3 Simulation approach:

The effort of sampling exercised with camera traps can be allocated into number of sites (S) and number of replicates (K). As the number of repeat visits in a sample increases, the precision of the occupancy and detection probability estimates improves. However, when this is performed at the expense of reducing the effort in terms of number of sampling sites and sampling days, it creates a trade-off leading to an optimal number of repeat visits and sampling sites which depends on the characteristics of the species. This also affects the power to detect a difference in occupancy and detection probability. We used the estimated occupancy and detection probability of each species to simulate a S x K matrix and calculate the deviation in the estimates with different scenarios varying the number of camera traps and sampling intervals. For each species, every scenario was simulated 1000 times and the Root-Mean squared error (RMSE) was computed from the estimated occupancy value. We simulated full detection history matrices using a Bernoulli process with probability ψ_i (estimated occupancy) to see whether the site was occupied, and generated another Bernoulli process with probability p_i to model the detection probability. We simulated twenty different scenarios varying the number of occasions (S= 50, 100, 200, 300, 400) and sampling days (K= 10, 15, 20, 25) for each species. We performed simulations using the Unmarked package (Fiske and Chandler 2011) in the program R 3.4 (R core team 2017). RMSE values were grouped into bins of 0.025 for both the occupancy estimate criterion and A-optimality criterion. Given our high survey effort, our sample size was large enough for several asymptotic approximations.

3.2.4 Power analysis:

We used estimated occupancy and detection probability results from our models to evaluate the statistical power of our design (Guillera-Arroita & Lahoz-Monfort 2012). We considered effect size as a function of occupancy to calculate power. Power of a statistical test given by $1 - \beta$ (Type II error) represents the probability of correctly rejecting a false hypothesis and the levels of significance should indicate the relative seriousness of committing Type I and II errors

(Guillera-Arroita & Lahoz-Monfort 2012).Considering our monitoring goal for a large spectrum of species with higher sampling effort, we assumed that making a Type II error (β) would be highly costly and chose 0.8 for β (i.e., not detecting a change in occupancy and detection probability when there is a change) and used a level of 0.05 for α (Type I error). Survey effort using varying number of sites (50-400) and sampling occasions (10-25) was used to investigate the power for individual species. We constructed power curves with estimated occupancy parameters and daily detection probability constant.

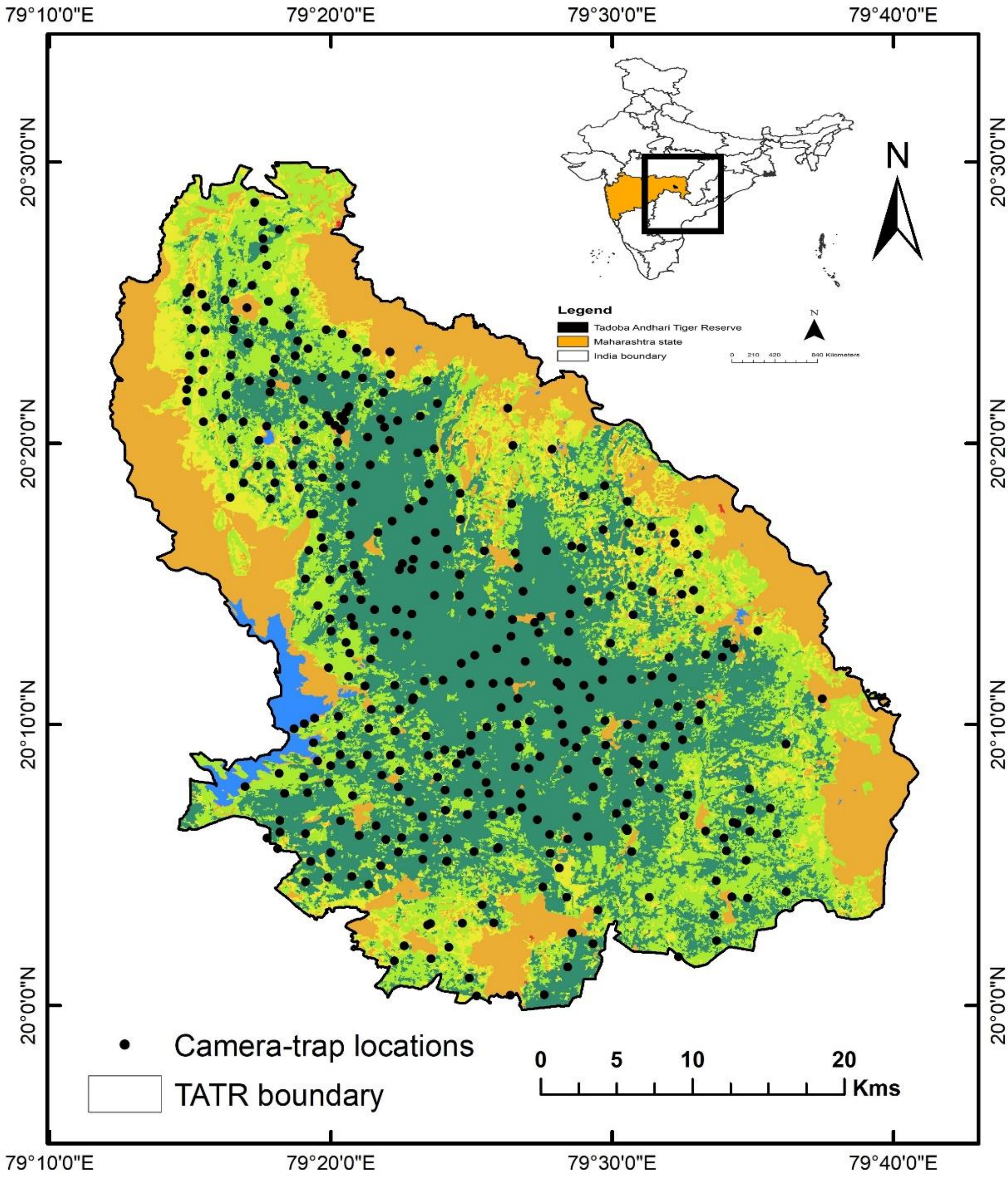

Figure 8: Study area showing camera-trap locations in Tadoba-Andhari Tiger Reserve (TATR). The map shows forested area and villages within the boundary of TATR. Inset: location of study area in India

3.3 Results:

We photographed a total of 22 species over 9,828 trap nights. We did not include the Indian pangolin *(Manis crassicaudata*), Chinkara (*Gazella bennettii*), and Northern palm squirrel (*Funambulus pennantii*) due to a few (<10) number of captures. We analysed camera trap data for 19 resident mammal species totalling 7765 detections (Table 1,2). Sambar was the most frequently captured species (n = 1357), whereas Rusty-spotted cat was the least captured (n = 109). Rusty-spotted cat has the lowest occupancy (ψ = 0.1174) in the study area and wild pig has the highest occupancy estimate (ψ = 1) (Figure 2). Dholes had the lowest daily detection probability (p = 0.036), whereas chital has the highest (p = 0.16) (Figure 2). Estimates of occupancy and detection probability of all the nineteen species are plotted (Figure 2).

Table 1: Overall description of the study species, status in IUCN red-list and number of detctions from motion-triggered camera tap sampling from Tadoba-Andhari Tiger Reserve, India. Species information was compiled from Menon (2015).

Species	**Scientific Name**	**Head to Body Length(cm)**	**Weight (kg)**	**Social status**	**IUCN Red-list Status**	**Number of detections**
Dhole	*Cuon alpinus*	88-135	10-20	group	Endangered	137
Jungle Cat	*Felis chaus*	60-85	2.5-12	solitary	Least Concern	171
Honey Badger	*Mellivora capensis*	60-77	7-13	solitary	Least Concern	206
Mongoose sp.	*Herpestes sp.*	36-45	2-3	solitary	Least Concern	146
Sloth Bear	*Melursus ursinus*	140-190	50-95	solitary	Vulnerable	360

Nilgai	*Boselaphus tragocamelus*	170-210	120-288	group	Least Concern	285
Four-horned antelope	*Tetracerus quadricornis*	90-110	15-25	solitary	Vulnerable	315
Wild pig	*Sus scrofa*	90-200	45-320	group	Least Concern	755
Leopard	*Panther apardus*	180-240	30-77	solitary	Vulnerable	464
Gaur	*Bos gaurus*	250-330	650-1000	group	Vulnerable	415
Muntjac	*Muntiacus muntjak*	90-120	20-28	solitary	Least Concern	143
Rusty-spotted Cat	*Prionailurus rubiginosus*	35-48	1.1-1.6	solitary	Near-Threatened	71
Small-Indian civet	*Viverricula indica*	45-63	2-4	solitary	Least Concern	258
Tiger	*Panthera tigris*	240-310	100-260	solitary	Endangered	695
Grey Langur	*Semnopithecus entellus*	55-75	9-11	group	Least Concern	444
Indian Porcupine	*Hystrix indica*	60-90	11-18	solitary	Least Concern	479
Sambar	*Rusa unicolor*	160-210	130-270	group	Vulnerable	1357
Asian Palm civet	*Paradoxurus hermaphroditus*	42-71	1.5-4.5	solitary	Least Concern	428
Chital	*Axis axis*	140-155	45-85	group	Least Concern	598

They are also classified into groups (low, moderate, high) based on their estimated occupancy and detection probability (Figure 7, Table 2) for estimation of optimal sampling effort. The detection probability estimates showed that a sampling effort of 26 days was large enough to detect nine out of the nineteen species at least once (Figure 8). However, cumulative detection probability (i.e. probability to detect species at least once) converged to 1 if our sampling effort would be for 50 days (Figure 8) except for two of our study species (Dhole and Rusty-spotted cat). Capture probability and detection probability were found to be positively and significantly correlated for the studied species (r = 0.75, p = 0.016).

Table 2: Broad classification of the terrestrial mammals based on occupancy and detection probability calculated from motion-triggered camera trap survey from Tadoba-Andhari Tiger Reserve, India

		Occupancy		
		Low	Mid	High
Detection probability	Low	Dhole -Honey badger-Jungle cat-Mongoose sp. -Rusty-spotted Cat	Sloth bear-Four-horned antelope-Nilgai	
	Mid	Muntjac-Small Indian Civet	Leopard -Gaur	Wild pig
	High	Chital-Palm civet	Langur-Porcupine	Sambar-Tiger

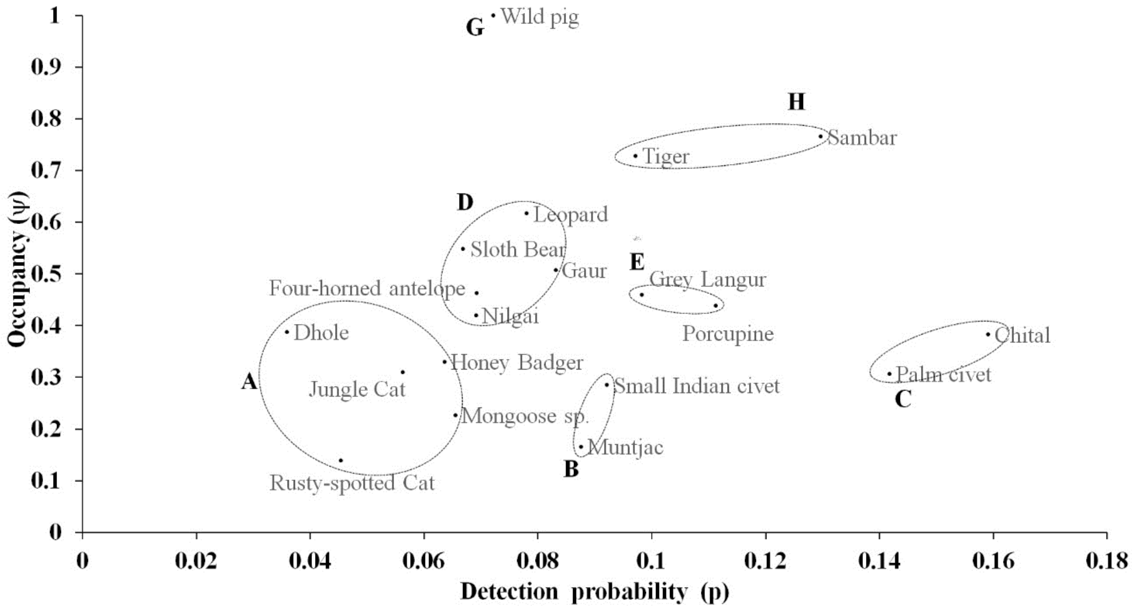

Figure 7: Occupancy estimates and detection probability of nineteen mammals from camera-trapping in Tadoba-Andhari Tiger reserve to explore the sampling design trade-offs for camera-trapping exercise. The species are clustered according to their common characteristics; A) Low occupancy and low detection probability, B) Low occupancy and moderate detection probability, C) Low occupancy and high detection probability, D) Moderate occupancy and low detection probability, E) Moderate occupancy and moderate detection probability, F) Moderate occupancy and high detection probability, G) High occupancy and moderate detection probability, H) High occupancy and high detection probability

The estimated occupancy was positively correlated with the body size ($r = 0.47$, $p = 0.04$) suggesting that large-bodied mammals are captured more frequently at multiple locations than small-bodied mammals. We did not detect a significant relationship between estimated occupancy the group size of the animal, but detection probability increased with group size (chital, gaur, langur, wild-pig etc). While, occupancy was positively correlated with the body size detection probability was significantly correlated neither with body size (r = 0.17, p = 0.49) nor the group size.

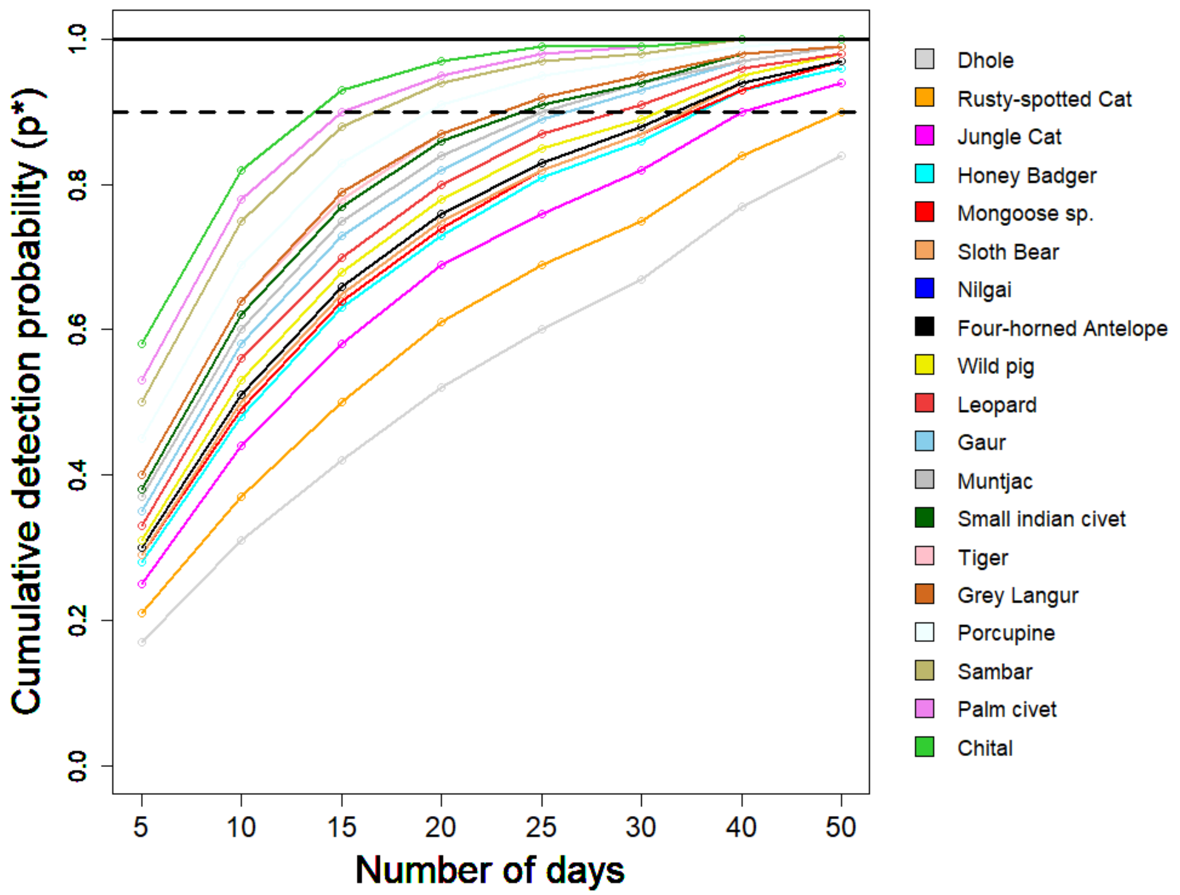

Figure 8: The cumulative detection probability ($p^{*}= 1-(1-p)^{s}$) of capturing an animal at least once over different number of sampling days. As cumulative detection probability converges towards one, chances of detecting species at a site at least once becomes certain. The black solid line denotes cumulative detection probability ($p^{*} =1$) and the dashed black line denotes cumulative detection probability ($p^{*} =0.9$).

With an increase in survey effort, RMSE values decreased for all species, although the optimal number of sites and survey days varied widely across the nineteen species. For rare species with low detection probability and occupancy (dhole, honey badger, rusty-spotted cat), the RMSE values changed significantly (0.21; 100 camera traps x 10 replicates - 0.028; 400 camera traps x 10 replicates) when number of sites decreased. For species with moderate ($0.07 < p < 0.1$) and high detection probabilities ($p > 0.1$) (leopard, chital, sambar, tiger), sampling occasions affected RMSE values more than number of sites (0.117; 100 camera traps x 10 replicates – 0.062; 100 camera traps x 25 replicates). Apart from the rarely detected species (e.g. Dhole, Jungle cat, Honey badger), all the other species show less change in the RMSE values when sampling is done for all the possible sites (Figure 9).

Table 3: Optimal survey design for estimation of occupancy and detection probability of the terrestrial mammals from camera trap survey from Tadoba-Andhari Tiger Reserve, based on three different root mean squared error (RMSE) levels

Species	Occupancy (ψ)	Detection probability (p)	Occupancy criterion (sites x occasions)			A-optimality criterion (sites x occasions)		
			RMSE 0.05	RMSE 0.075	RMSE 0.10	RMSE 0.075	RMSE 0.10	RMSE 0.15
Dhole	0.388	0.04	400x25	300x20	400x15	400x20	300x20	200x20
Rusty-spotted Cat	0.1387	0.048	200x20	200x15	100x15	200x20	200x15	100x10
Jungle Cat	0.31	0.06	200x25	200x20	200x15	200x20	200x15	100x25
Honey Badger	0.33	0.06	200x20	200x15	400x10	300x15	400x10	200x10
Mongoose sp.	0.2268	0.066	200x20	300x15	100x20	300x15	100x20	200x10

Sloth Bear	0.549	0.07	400x20	200x15	300x10	300x15	400x10	200x10
Nilgai	0.42	0.07	200x20	400x10	300x10	300x15	300x10	200x10
Four-horned antelope	0.463	0.07	200x20	200x15	300x10	200x15	300x10	200x10
Wild pig*	1	0.07	200x20	200x15	200x10	200x15	200x10	100x15
Leopard	0.617	0.08	400x20	400x15	300x10	200x20	300x10	100x20
Gaur	0.508	0.08	200x20	300x10	200x10	400x10	300x10	200x10
Muntjac	0.1661	0.09	100x20	200x15	100x15	100x20	200x15	100x15
Small-Indian civet	0.285	0.092	200x15	100x25	100x20	100x25	100x20	100x10
Tiger	0.7285	0.10	200x20	200x15	200x10	200x25	200x10	100x20
Grey Langur	0.46	0.10	200x15	200x10	100x15	300x10	200x10	100x15
Indian Porcupine	0.439	0.11	300x15	100x25	100x15	300x10	100x25	100x15
Sambar	0.766	0.13	200x20	200x15	200x10	200x15	200x10	100x15
Asian Palm civet	0.307	0.142	200x25	100x15	100x10	100x15	100x10	100x10
Chital	0.383	0.16	100x15	100x10	100x10	100x15	100x10	100x10

*naïve occupancy estimate was used for the simulation as the occupancy estimate didn’t converge

Optimal survey design derived with power analysis was in line with the optimum survey effort required for different combinations of the RMSE values for different species (Figure 9, Figure

10). Power increased with the increase in the number of sampling sites and occasions for all the species. However, this change was not significant for the species with higher occupancies (Sambar, Wild pig, Tiger) or higher detection probabilities (Chital, Langur, Porcupine). For species with low detection probabilities (Dhole), we found an 80% chance of detection a 50% change in occupancy, but for species with high detection probabilities (Chital), the same effort can detect a change of 25% (Figure 5) with the effort of 400 cameras with 25 days. With the same effort, it is possible to detect when there is almost fifty percent change in the parameters with a power of eighty percent (Figure 10) but the power decreases sharply with decrease in survey effort decreases for species with the lowest occupancy (Rusty-spotted cat) and lowest detection probability (Dhole). However, species with higher detection probability (chital, palm civet etc.) or higher occupancy estimates (sambar, tiger, wild-pig etc.) show insignificant changes in effect with the changes in sampling effort (Figure 10).

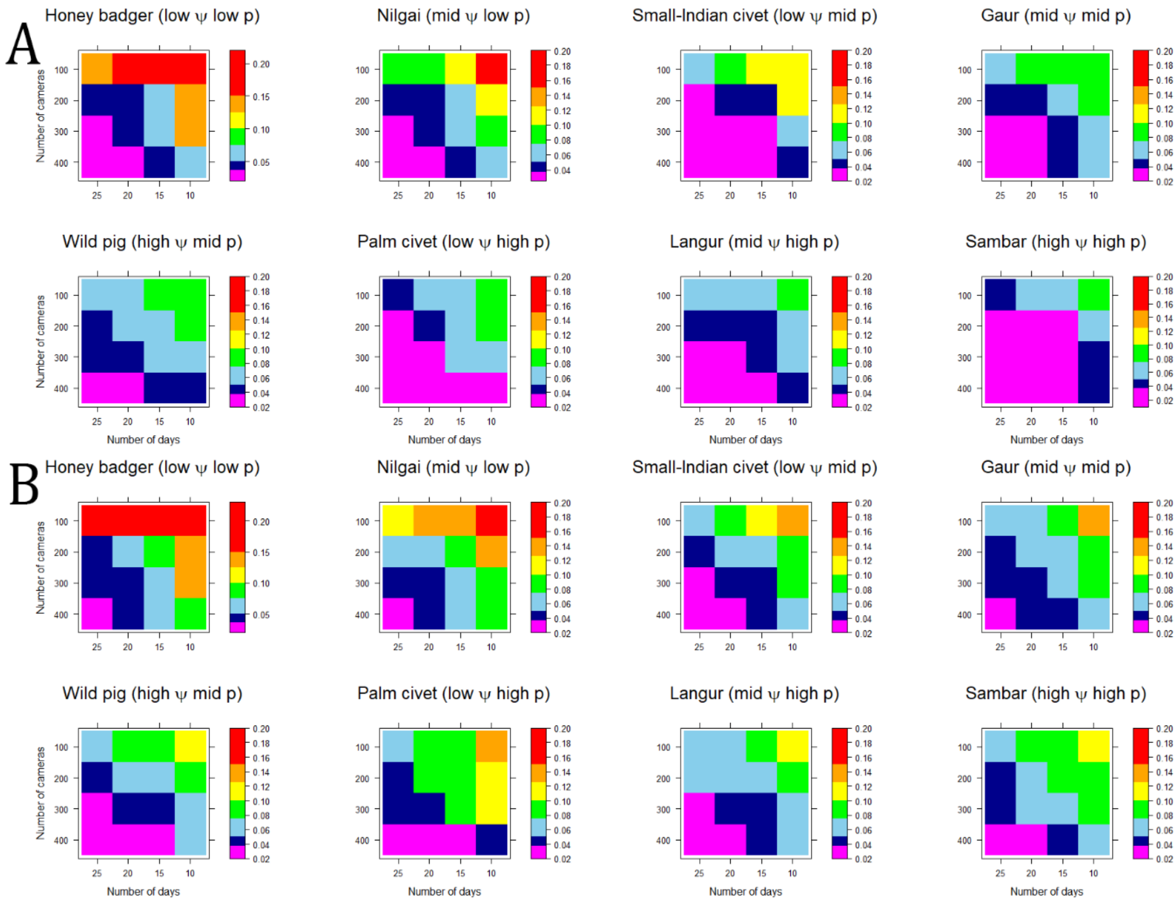

Figure 9: Root-mean squared error (RMSE) errors of (A) simulated occupancy and (B) both occupancy and detection probability (A-criterion Guillera-Arroita, et al. 2010) for different mammals detected. We plotted the errors with at least one species from the eight species classification mentioned in the Table 2. Tile color reflects the RMSE for each combination of of camera traps sites and days.

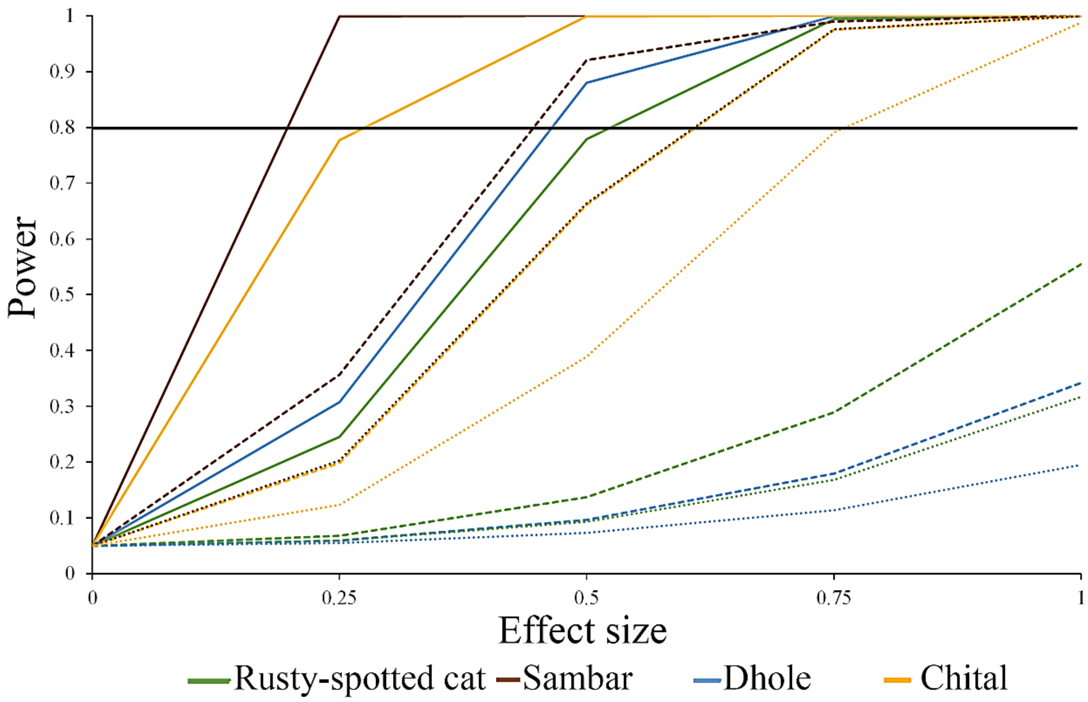

Figure 10: Power curves (α =0.05) as difference in change in occupancy (psi) and detection probability (p) under different sampling design for different species. The Solid line represents S=400, K=25, the dashed line represents S=100, K=10 and the dotted line represents S=50, K=10; where S is the number of sampling sites and K denotes the number of replicates. Black line represents cut-off of 0.8 for power.

3.4 Discussion:

The study examines optimal sampling trade-offs using empirical data on occupancy and detection probability attained from field surveys of a diverse mammalian community in India. We used the detection histories of nineteen mammals representing a broad spectrum of ecological characteristics including varying body sizes, feeding guilds and behavioural aspects. The optimal survey effort for the mammal community encountered in the studies, varied significantly across their body size and ecology of the species. The recommendations presented from this work are intended to provide broad guidelines to managers and researchers for effective design of their study. The findings are based on the largest camera-trapping data set analysed to estimate optimal sampling design for terrestrial mammal community. The resulting design will ensure effective allocation of survey cost that is the most limiting factor of ecological studies in lower-middle income or developing countries.

The trade-off between the number of sampling sites and number of occasions is of fundamental concern for planning and designing a field survey (Mackenzie and Royle 2005, Bailey et al. 2007, Guillera-Arroita, et al. 2010, Shannon et al. 2014). Simulated data has been used to provide theoretical insights for most of the studies except Shannon et al. (2014). Though simulated data can be based for designing studies but field data represents realistic scenarios and provides flexibility with customization of ecological factors (e.g. Body size, group size). Shannon et al. (2014) used only the criteria of occupancy for deriving the sampling trade-offs. The occupancy and detection probability range of the species encountered in this study was ψ = (0.1174-1) and p = (0.036-0.159) was a superset of Shannon et al. (2014) where ψ = (0.245-0.925) and p = (0.023-0.19) as the results in this paper included more terrestrial mammals (19) where Shannon et al. (2014) used data of ten mammals with three virtual species. Moreover, our study used both estimated occupancy and detection probability to develop the design trade-offs to present more robust estimates.

We chose one animal from the eight classifications (Table 2) representing different occupancy and detection probability to estimate the optimal sampling strategy. The mean squared error (MSE) decreased from 0.21 (100 camera traps x 10 sampling days; low ψ low p) to 0.015 (400 camera traps x 25 sampling days; high ψ high p) when only occupancy is used whereas, MSE decreased from 0.228 (100 camera traps x 10 sampling days; low ψ low p) to 0.027 (400 camera traps x 25 sampling days; high ψ high p) when both occupancy and detection probability is used (Figure 4). The result also emphasizes use of detection probability to estimate the optimal sampling that was never executed with empirical data before this study.

Species from highest and lowest extremes of both occupancy and detection probability was used to test the power of our study. Analysis reflected that species from the lowest extremes requires significantly higher sampling effort than the species with high occupancy and/or detection probability (Figure 10). Similar result is also reflected in the optimal survey designs derived using RMSE. We found that species with bigger body size mostly have moderate to high detection probability and thus they require less sampling efforts than the small mammals (Table 3).

The positive relation between body size and occupancy estimate signifies that species with bigger body size have a higher occupancy estimate. This can also be attributed by their larger home-range and higher daily distance movement. We did not find significant relation between group size and occupancy estimate of species. Species like Dhole and Chital are group living but their occupancy estimates were low as compared to other species. The relationship between the function of capture frequency (Tobler et al. 2008) to detection probability was also evaluated to determine if the former could be a surrogate for the latter. Positive significant correlation between these two variables signifies that capture frequency can also be used as an alternative of detection probability. Capture frequency is easier to calculate then detection probability and provide comparable insights with less intensive computations.

Eight of the nineteen mammals encountered during the study are listed in the IUCN red list (www.iucnredlist.org, Table 1) and they are also of higher conservation priority. Though except for the Tiger, the sampling recommendation is not available for most of the species reported in this study (specially the small mammals e.g. Honey badger, Palm civet, Rusty-spotted cat etc.). This study is a first ever attempt to understand significant parameters like detection histories imperative in monitoring rare and elusive species like the Dhole, Rusty-spotted cat and Honey badger that have been hardly studied with such comparative spatial scale.

The outcome of the Mean square values from simulation can be compared with the results of Power analysis to compare the efficacy of our sampling and reliability to detect change in the estimated occupancy and detection probability values. Results from both the analysis were concurring. The optimal survey effort estimated for all the species changed with the different occupancy and detection probability.

3.4.1. Caveats/ Assumptions of the study

The sampling interval for each block of this study was restricted to 25 days to fulfil the assumption of constant occupancy throughout the sampling period (Mackenzie et al 2006). As directed by Long and Zielinski (2008), the probability of detection of a species at least once in the survey duration should be more than 0.80. With the detection probabilities reported in our study, with a 40 day replicate all the species except three (Dhole, Rusty-spotted cat, Jungle cat)

(Figure 8) attained the threshold of the mentioned probability (0.8) whereas our sampling duration of 25 days was very close to the requisite. A study by McKann et al., (2013) addressed a cumulative detection probability (p*) value of 0.9 as a benchmark value beyond which there is no significant change in the estimation bias or the confidence interval. Cumulative detection probability of ten out of the nineteen species was higher than the threshold value (Figure 8) with sampling replicate of 25 days. McKann et al., (2013) have also given the recommendation of requisite of atleast 60 cameras to reduce bias of the occupancy estimate and 120 cameras for further reduction in the interval length. Though the initial occupancy estimate and detection probability for simulation used by McKann et al. (2013), was higher than the estimated from this field study but the design recommendations of both the studies were similar. There are several methods to increase the detectability of species e.g temporal replication of sites, reducing the study-area and/or increasing number of sampling sites, using bait and lures, surveying high animal use areas or combining different sampling methods. We deployed the cameras mostly at animal trails or forest roads to maximise animal captures but did not use any baits or lures. As we had limited number of cameras, we could not extend the sampling to more cells with finer resolution. Also that may violate the assumption of independence of captures if the cameras are placed very close-by.

We have also investigated other assumptions regarding occupancy studies using camera-traps. First, the detections at particular sites are assumed to be independent. Though the assumption is difficult to be followed for the long-ranging species as they are captured at the adjacent locations of their home-range center. We have used detection probability based on their captures in 24-hr frame. The value is assigned as “Presence” or ‘’1’’ even if the animal is captured multiple times in a day in the same camera trap. Also the violations are not found to bias occupancy estimates as the detection probability decreases as they go far from thecenter of their home-range. The camera placement was mostly on roads, trails or animal paths to maximise capture probability of the species. Previous studies (Cusack et al. 2015, Kolowski & Forrester 2017) have shown capture rate significantly varies with camera placement but our primary aim was to increase detection of all the mammal species. Also, the studies (Cusack et al. 2015, Kolowski & Forrester 2017) reported insignificant differences in species richness between trails and random locations as the trap night increases. The sampling in the study was carried out in dry season and thus, we have assumed constant occupancy for the whole sampling period. With this assumption, we can also distinguish the effects from stochastic fluctuation (Field et al. 2005) and small-scale effects. Also pooling data from several camera traps helps us to negate the issues of small-sample size which is prevalent in ecological studies focusing on rare and elusive species (Guillera-Arroita, et al. 2010, McKann et al., 2013).

3.4.2 Global implications

The key objective of the study was to reach the managers and practitioners to guide them properly with realistic scenarios from field data to plan and execute their monitoring work for a diverse range of species rather than the advancement of the analytical framework. Though detection probability is considered as the most significant factor (Mckann et al. 2013) for occupancy modelling and can also play a pivotal role for the recommended survey design (Guillera-Arroita, et al. 2010) but no studies with field data implemented the criteria for sampling design trade-offs. Hence, we have tried to partially fill this gap and included the design criterion with precision of detection probability along with occupancy. Recommended designs (Figure 9) for this broad spectrum of species can be used to guide other camera-traps studies or studies covering large spatial extents focusing on species with comparable occupancy or detection probability.

3.4.3 Future research/Conclusions:

Though occupancy may not be an alternative for abundance estimation but it generates considerable data that can be used for monitoring a range of species in a cost-effective way. Due to the ease of use and potentiality to reflect population status, occupancy is used by the IUCN for 2 of its 5 measures for estimating population threat level. In line with Tempel and Gutiérrez, (2013) and Zielinski and Stauffer, (1996), we have also found occupancy framework suitable for monitoring both territorial & co-occurring species with high precision. Studies focusing on multiple areas covering a larger landscape or data collected over multiple years would be better to evaluate the optimum trade-offs than those derived from studies from a single area and single season.

Our study investigates the sampling design trade-offs for robust estimation of occupancy and detection probability with different level of errors for a range of mammalian species using camera-traps. In addition to practical lessons of this study, our data showed the importance of including detection probability to estimate the optimal sampling trade-off. Our findings clearly show that increasing survey effort is not the most efficient strategy for all the species. We recommend future works to include detection probability with spatial and temporal replicates to estimate optimal sampling design. Broad range of nineteen terrestrial mammal species used in this study emphasize use of camera trapping surveys as a potentially powerful tool for monitoring over large spatial areas. Our approach to analysing camera trapping surveys with empirical dataset could be extended for other terrestrial or aquatic ecosystems for monitoring species of conservation concern.

Chapter 4

Population Estimation of unidentifiable Felidae and Mustelidae species

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4.1 Introduction:

Carnivores naturally occur at low densities owing to their apex position in the food web. Concurrently they continue to face rapid population decline caused by contracting range sizes and fragmentation of existing habitat (Ripple et al. 2014). Asia holds more than 60% of the global diversity of cats (Macdonald et al. 2010), harbouring 21 out of 36 species. India, a mega-biodiverse country, is home to 15 among them (Nowell & Jackson 1996). The geographical distribution range of most of these cats lies within protected areas with an average size of less than 400 km^2, which contributes to only five percent (http://wiienvis.nic.in/Database/Protected_Area_854.aspx) of the total landmass of the country. Furthermore, these protected areas are located within high densities of human populations dependent on local resources and surrounded by land which is undergoing an upsurge in anthropogenic developmental activities. Given these escalating pressures on felid species in Asia (Macdonald & Loveridge 2010, Dickman et al. 2015, D'Cruze & Macdonald 2015), an in-depth understanding of their population status and habitat use would be fundamental for designing effective conservation and management policies. Additionally, as a number of the species do not have unique pelage patterns, capture-recapture techniques (Efford 2004) cannot be applied for population estimation and owing to their elusive nature, direct encounters are also rare. We addressed these issues using the spatial presence-absence model (Ramsey et al. 2015) based on field-based sampling using automated camera-traps.

Among the small cats native to India, the jungle cat (*Felis chaus*) and rusty-spotted cat (*Prionailurus rubiginosus*) are the two, most widespread species. The former belongs to the house cat lineage, whereas the latter to the leopard cat lineage (Johnson et al. 2006). Rusty-spotted cat, the smallest cat in the world (average body weight 1.6 kg), is also reported to use the arboreal habitat alongside the terrestrial domain (Nowell & Jackson 1996). However, no such adaptation has been reported for the jungle cat (average body weight of 5 kg). Both species are known to be nocturnal and elusive (Nowell & Jackson 1996, Majumdar et al. 2011). The jungle cat is categorized as “Least Concern” in IUCN red list (Gray et al. 2016) due to its large distribution range from south-eastern Asia to middle east and eastern Europe, while the rusty-spotted cat was recently downgraded to “Near Threatened” from “Vulnerable”, owing to new records from previously unknown locations (Mukherjee et al. 2016). Honey badgerMellivora capensis is one of the largest (6–14 kg) mustelids and is distributed over Africa, Arabian Peninsula, West Asia, and the Indian subcontinent (Do Linh San et al., 2016). Owing to the wide distribution range, the species has been categorized as Least Concern in the International Union for Conservation of Nature red list of Threatened species (Do Linh San et al., 2016). However, despite its widespread distribution range, limited knowledge exists about its ecology except in southern Africa (Begg, 2001, Begg et al., 2003, Begg et al., 2016, Ramesh et al., 2017, Kheswa et al., 2018). In India, the species is relatively rare and is categorized as Scheduled-I in the Wildlife (Protection) Act, 1972 providing it with the highest level of protection. The species is known as a solitary forager and primarily prefers a carnivorous diet (Begg, 2001). Their fossorial behavior and nocturnal activity pattern (Gubbi et al., 2014),make them highly elusive in nature and difficult to encounter for a population estimation study.

Although taxonomy and phylogeography of these small cats have been studied (Mukherjee et al. 2010, Kitchener et al. 2017), fundamental ecological information on parameters like demography, habitat use, and activity pattern is majorly lacking. Previous studies have not attempted to estimate the population of any of these species, nevertheless, the population trend of both the species is presumed to be decreasing (Gray et al. 2016, Mukherjee et al. 2016). Most studies on the rusty-spotted cat are based on opportunistic sightings (Davate et al. 2015, Mali & Srinivasulu 2015). A single study discussed the habitat use, seasonal abundance (Kalle et al. 2014), and distribution pattern (Kalle et al. 2013) of small carnivores from one protected area in the Western Ghats. The study (Kalle et al. 2014) had limited inference owing to a small sample size (n=11) but indicated a positive relationship of the abundance of the rusty-spotted cat with deciduous forest and that of jungle cat with dry thorn forest. there is only one study estimating population density of Honey Badger in India (Gupta et al., 2012). The population estimation would fill the existing knowledge gap of these species using camera-trap captures as our study is the first attempt to estimate the population density of these individually unidentifiable small carnivores.

4.2 Materials and Methods:

4.2.1 Study sites:

We conducted the study in Tadoba-Andhari Tiger Reserve (TATR) (20°04´-28°025´N, 79°13´-79°33´E) in the state of Maharashtra in Central India. The reserve spreads across an area of 1700 km^2 in the Deccan plateau. The terrain of TATR is mostly undulating and hilly in the north and flat in the southern part (Paliwal & Mathur 2014). The climate is characterized by a hot and long summer and a short and mild winter (Paliwal & Mathur 2014). Annual average precipitation is around 1,200 mm, received mainly from south-western monsoons between June and September (Khawarey & Karnat 1997). The vegetation of the reserve has been classified as Southern Tropical Dry Deciduous forest (Champion & Seth 1968) dominated by bamboo

(*Dendrocalamus strictus*) and teak (*Tectona grandis*). The habitat is majorly homogenous comprising of dense forest cover in 68%, open forest in 10% and human habitation in 21% of the total area of the reserve.

More than 20 mammal species have been recorded from the reserve through camera-trapping studies (Habib et al. 2015). These include four species of felids (tiger, leopard, jungle cat and rusty-spotted cat), an ursid (sloth bear), two species of canids (dhole, jackal) and one species of mustelid (honey badger). Wild pig and chital are the major prey species followed by sambar, nilgai and gaur.

4.2.2 Field methods:

We conducted camera-trap surveys in the dry season from February to June 2016. A pair of automated motion-triggered digital camera-traps (Cuddeback C1 or Cuddeback Ambush www.cuddeback.com) was deployed at 397 locations without using lure or bait (Fig 1). Due to the limited availability of camera-traps, sampling in the reserve was carried out in the tiger reserve dividing the whole area into four different blocks with an average of 100 stations per block. Cameras were shifted to consecutive blocks after sampling was done in one block. The cameras were deployed dividing the area following a grid size of 2 km^2, equivalent to the home-range size (2-5 km^2) of another small cat, the leopard cat which is widespread across the country (Rajaratnam et al. 2007). Camera traps deployment was aimed for proportional representation of different habitat types (except human habitation) across the reserve. The average distance between two adjacent camera traps was 1.03 km, ensuring no large gaps in camera placement for the detection of individual small cats and to avoid pseudo-replication. Cameras were placed on both sides of roads, animal trails and fire-lines facing each other, placed around 30-40 cm above the ground. Camera-trap placement at trails optimizes the capture of large as well as small carnivores (Chen et al. 2009, Johnson et al. 2009). Also, the placement of two camera-traps at every site increased the detectability of these small felids (Evans et al. 2019). Cameras were programmed to take three photographs per trigger with an interval of 5 sec. Photographs taken within 30 min from the first trigger were not used for analysis to maintain the independence of captures. All the camera-traps were active for 24 hours continuously for 26-30 days and checked once in 15 days. Sampling interval was restricted to 26-30 days to ensure demographic closure (Kendall 1999).

4.2.3 Density estimates:

In this study individuals of neither species are uniquely identifiable from photographs. Therefore, we used spatial presence-absence (SPA) models (Ramsey et al. 2015), an extension of the spatial count model of Chandler & Royle (2013). Spatial count models the latent encounters of spatially referenced individuals with sampling devices using data augmentation and Markov chain Monte Carlo (MCMC) sampling in a Bayesian framework (Ramsey et al. 2015). SPA models are structurally similar to spatial capture-recapture (SCR) models (Efford 2004). We assumed a half-normal detection function to model the probability of detection. Similar to SCR models, SPA models estimate g_0 (baseline encounter rate), σ (scale/movement parameter related to home-range of the species) and N (population size) (Ramsey et al. 2015).

For each camera site, the detection or non-detection of these cats were recorded on each 24h sampling interval. The state-space (S) was comprised of the sampled area and a surrounding buffer area that is large enough to include all individuals potentially exposed to sampling. We estimated σ from the body-size and daily-movement distance equation (Garland 1983). We employed multiple buffer (σ, 2σ and 5σ) values around the state spaces to test the effect of buffer size on the density estimates of the SPA model. Following the equation of (Garland 1983), the estimates of the home-range size of these cats were calculated as 0.8 -1.2 km^2 and 2-5 km^2 for rusty-spotted cat and jungle cat respectively. A vague uniform prior, U (-10,10), was placed on the logit of g_0, whereas an informative prior was used for the home-range-scale parameter σ. To incorporate this, we used an informative prior of gamma (40,35) for jungle cat, an informative prior of gamma (45,40) for honey badger, and gamma (50,60) for rusty-spotted cat respectively. We also compared the density estimates using the informative priors with estimates of uninformative priors (e.g. U (0,10) prior for sigma) to understand the role of priors. We used 50,000 MCMC iterations (with the initial burning of 5,000) and the thinning rate of the chains was fixed as 1. As we estimated the parameters following iterations in the Bayesian framework, it was necessary to check the convergence of chains. Geweke diagnostic scores (Geweke 1992) were used to test the convergence of the MCMC chains in the "coda" package (Plummer et al. 2006) in R 3.4 (R Development Core Team 2017). Geweke score of less than 1.6 indicated convergence of the estimated parameters in the chain.

4.3 Results

The total survey effort comprised of 10332 trap nights from 397 camera-traps. We photographed 23 mammals during the camera-trap survey including 171 photo-captures of jungle cat and 66 photo-captures of rusty-spotted cat. Of the 397 camera-trap locations, jungle cat was detected at 91 locations and rusty-spotted cat was detected at 38 locations respectively. Both the species were detected together at 9 locations. We obtained 206 captures of honey badgers in 102 camera traps. Out of the 206 captures, 22 captures had 2 individuals in 1 photograph and 1 instance had 3 individuals.

The model estimated densities of 4.01 (95% CI 2.65- 6.12) individuals/100 km^2 for jungle cat 14.09 ± 3.15 individuals/100 sq. km for honey badgers and 6.67 (95% CI 4.07-10.74) individuals/100 km^2 for rusty-spotted cat (Table 4). Extrapolating estimated density for the survey area, we estimated 72 (95% CI 48-111) jungle cats, 233 (95% CI 166-368) honey badgers and 100 (95% CI 61-161) rusty-spotted cats in the tiger reserve. The baseline encounter rate (g_0) and home-range scale parameter were greater for jungle cat than rusty-spotted cat (Table 4, Figure 10-11). There was no significant difference in density estimates with increase in buffer sizes (σ, 2σ and 5σ) for both the species (t(rusty)=25.03, $p<0.001$ and t(jungle) = 7.84, $p<0.001$). Population estimates using uninformative priors overlapped with the informative priors for both the species but the coefficient of variation (CV) was much smaller with informative prior in case of Jungle cat. Informative priors had a CV of 22.4 % whereas uninformative priors had a CV of 70.5% and for rusty-spotted cat CV was 25.8% for informative prior and 25.3% for uninformative prior. The density estimate for rusty-spotted cat was higher with the uninformative prior while the density estimate of jungle cat was similar.

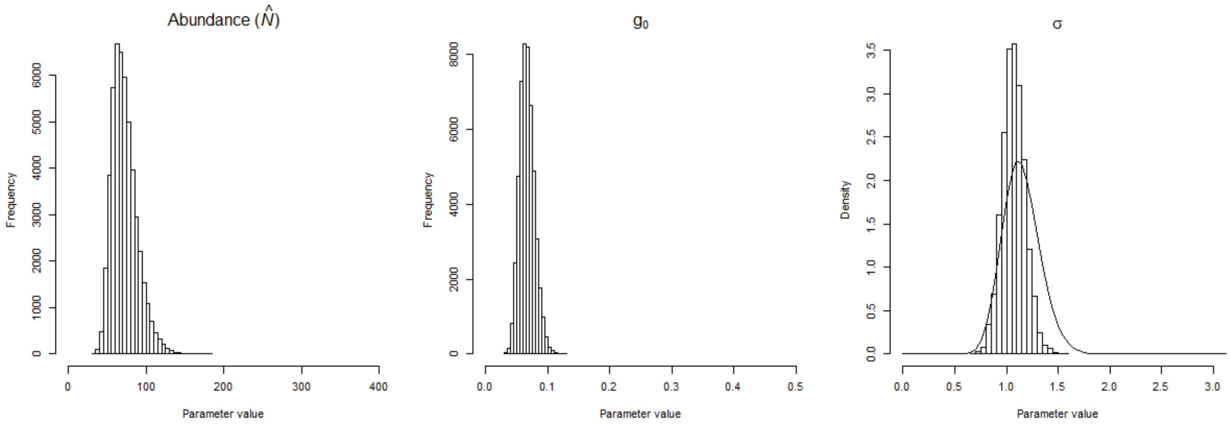


Figure 10: Estimated abundance (N), baseline encounter rate (g0) and movement parameter (σ) of jungle cat using Gamma (40,35) prior. The black curve indicates the prior distribution of sigma. The solid line overlaid on the posterior distribution of σ is the prior gamma distribution used for the species.

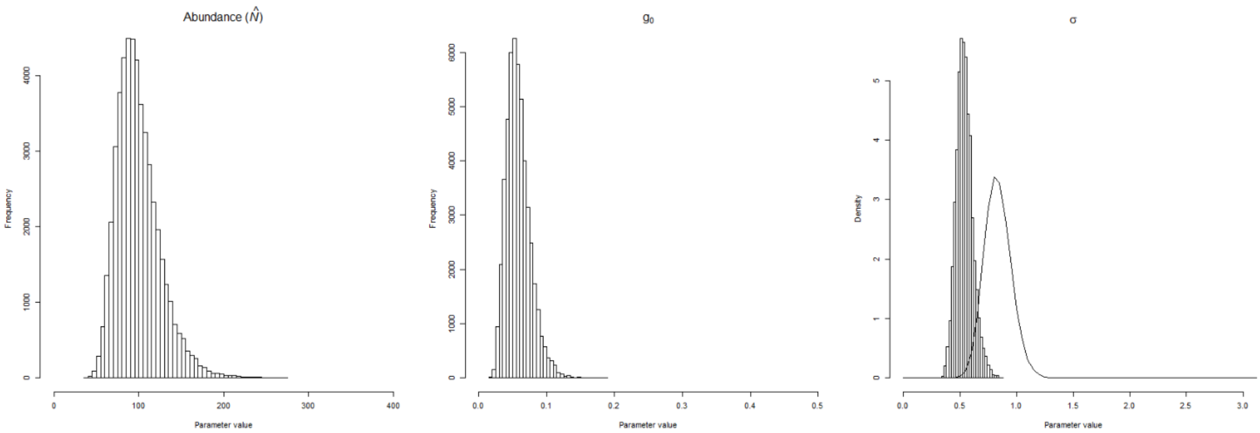


Figure 11: Estimated abundance (N), baseline encounter rate (g0) and movement parameter (σ) of rusty-spotted cat using Gamma (50,60) prior. The black curve indicates the prior distribution of sigma. The solid line overlaid on the posterior distribution of σ is the prior gamma distribution used for the species.

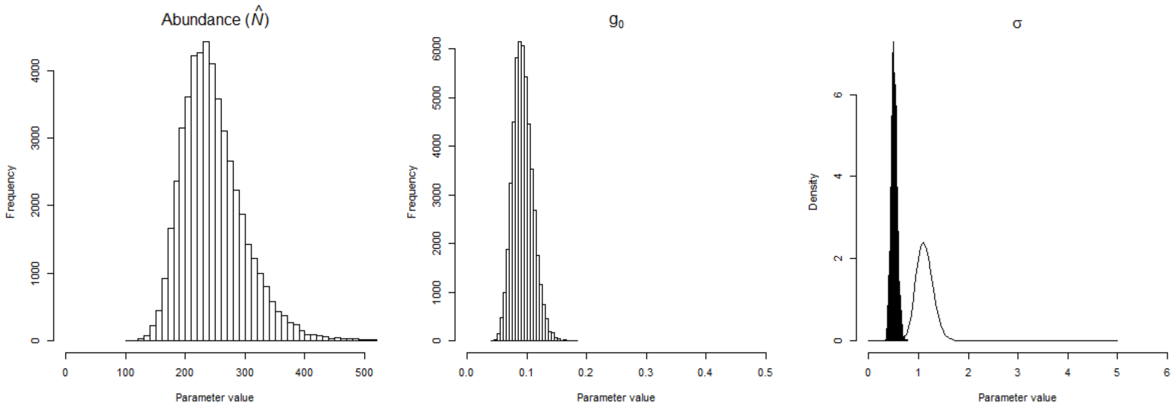


Figure 12: Estimated abundance (N), baseline encounter rate (g0) and movement parameter (σ) of honey-badger using Gamma (45,40) prior. The black curve indicates the prior distribution of sigma. The solid line overlaid on the posterior distribution of σ is the prior gamma distribution used for the species.

Table 4: Parameter estimates of population size N, density and parameters of detection function (detection probability g_0, spatial-scale parameter σ) from the spatial presence/absence model for Jungle cat, rusty-spotted cat and honey badger are given in the table.

	No. of independent captures	Density per 100 sq.km (95% CI)	Posterior N (95% CI)	Sigma estimate (95% CI)	g_0 estimate (95% CI)
Jungle cat	171	4.01 (2.65- 6.12)	72 (48-111)	1.069 (0.858-1.294)	0.067 (0.046-0.092)
Rusty-spotted cat	66	6.67 (4.07-10.74)	100 (61-161)	0.539 (0.412-0.703)	0.058 (0.030-0.099)
Honey badger	206	14.09 (10.94-18.24)	233 (166-368)	0.509 (0.401-0.631)	0.092 (0.063-0.127)

The Geweke diagnostic scores reflected convergence of all parameters of SPA models for both the species as the z statistic values was <1.6. Also, we tested the geweke scores of each parameter against $z=1.6$ and reported the p-value, which was found to be significantly different for all the parameters. The geweke scores with the p values in the parenthesis of the jungle cat SPA models are given by, sigma =1.17 (0.86), g_0 = -0.94 (0.824), psi = -1.198 (0.09), N = -1.26 (0.073) while the geweke scores of the rusty-spotted cat SPA models are given by, sigma = -1.02 (0.16), g_0 = 1.55 (0.94), psi= -0.77 (0.22), N= -0.72 (0.24). The z statistic values for SPA model of honey-badger are given by, sigma = 0.047(0.519), g0 = 0.741(0.771), psi = 0.577(0.718), N = 0.528(0.701).

4.4 Discussion

This study attempted to estimate the population of two sympatric and individually unidentifiable small cat species and understand their habitat preference. We report the first ever population density estimates of jungle cat and rusty-spotted cat that ranges from 3-7 individuals per 100 km^2. The estimates, based on the largest camera trapping dataset available for these small cat species, are comparable to density estimates of other small cats (Mohamed et al. 2013, Srivatsa et al. 2015, Hearn et al. 2016). The estimated densities of these elusive cats can significantly contribute to conservation strategies. We also observed fine-scale spatial segregation supporting our hypothesis, facilitating co-occurrence between these small cat species.

4.4.1 Population density estimates:

There are no previous records of population density estimates for both of the studied species. But estimates of this study are comparable to population density of other individually identifiable small cats of comparable body sizes, the leopard cat (*Prionailurus bengalnensis*) (Mohamed et al. 2013, Srivatsa et al. 2015) and the marbled cat (*Pardofelis marmorata*) (Hearn et al. 2016, Singh & Macdonald 2017). Contrary to the non-spatial models, spatial models provide site-specific detection probability and a scale of animal space use (sigma). Estimates of the movement parameter (sigma) of this study are comparable with that of leopard cat (Srivatsa et al. 2015) and marbled cat (Hearn et al. 2016) but smaller than the sigma estimates of leopard cat (Mohamed et al. 2013) or marbled cat (Singh & Macdonald 2017). Difference in the analytical procedure (spatial presence-absence vs spatial capture-recapture) prevented direct comparison of the parameter estimates. In our study, the number of captures of jungle cat was greater but their density estimate was lower than that of rusty-spotted cat. This was attributed to the assumption of a larger home-range of jungle cat compared to rusty-spotted cat.

Earlier studies found the density of small cats reflected top-down competition from other large predators present as has been evidenced in a study on leopard cats from the Western Ghats in India (Srivatsa et al. 2015). Moreover, when the carnivore community remained similar, species density was found to be associated with other biotic factors. Studies on neotropical small cats (ocelot) revealed dependence on primary productivity (Di Bitetti et al. 2008), density estimates ranging from 2.3 per 100 km^2 (Chiquibul, Belize) to 94.7 per 100 km^2 (Peruvian Amazon) (Dillon & Kelly 2007, Kolowski & Alonso 2010). Future studies should consider these factors along with the presence of other carnivores as covariates to model density of these small cat species.

The only density estimate of this species from the Indian subcontinent was available from Sariska Tiger Reserve (Gupta et al., 2012) based on repeated presence-absence model (Royle and Nichols, 2003). The study estimated summer and winter densities as 5.48 ± 4.33 individuals per 100 km2 and 6.43 ± 2.79 individuals per 100 km2, respectively (Gupta et al., 2012). Another study on small nocturnal carnivores from Serengeti National Park (Waser, 1980) estimated the density of honey badger around <10 individual per 100 km^2 from transect counts. Our density estimates of 14.1 ± 3.15 individuals per 100 km^2 was the highest among these studies. This could be attributed to the area devoid of any anthropogenic disturbance, higher productivity of the area compared with the other study areas and also temporal segregation of honey badger from the activity period of other large carnivores. Moreover, the study site is a tiger reserve and has less human presence which may lead to lower disease prevalence ensuring higher survival probability. The sigma parameter from the SPA was estimated as 0.509m (95% CI 0.401–0.631m) which was much lower from the daily movement parameter estimated from Africa (Begg et al., 2016). The difference in analytical procedures (spatial presence-absence vs. radio-telemetry), however, hindered direct comparison of the parameter estimates. Still, our study used a robust methodology with a recently developed framework incorporating spatial information to estimate the population.

As honey badgers are not individually identifiable and are of small size, it is challenging to use their sex or age class unambiguously as a covariate in the capture-recapture model. Moreover, the extended period of the dependence of cubs on mothers (Begg, 2001) made group identification more challenging from photo captures. Also, a precise estimate of the home-range of the species is required as a prior for the movement parameter in the SPA model (Ramsey et al., 2015). Parameters derived from further studies on movement pattern and home-range of the species may aid in more precision in the estimated parameters.

4.4.2 Caveats and Limitations:

Although the population estimation and habitat use pattern in our study where based on a robust analytical framework, there are certain inevitable limitations similar to other field studies. We could not employ a finer grid size for camera-trap sampling due to logistical constraints. Prior distributions for the spatial count model were selected based on the data available for leopard cat (Rajaratnam et al. 2007) and allometric equations of daily-movement, home-range and body mass. Radio-telemetry studies can aid in providing refined estimates for the prior distributions and robust estimates using spatial capture-recapture (Efford et al. 2004) or spatial mark-resight (McClintok et al. 2009) framework. Further studies can evaluate the efficacy of the spatial presence-absence model by comparing estimates from other frameworks. Alongside remotely sensed environmental variables, micro-habitat variables collected from sampling sites can be collated to understand multi-scale habitat preferences. The presence of other species as a predictor variable can also reveal the effect of species interaction in shaping habitat use patterns. The study was restricted to a tiger reserve whereas both the study species are also known to occur outside protected areas. It would be useful for future studies to look at density estimates across various gradients of natural and anthropogenic disturbances and varied mammal community as well.

4.4.3 Conclusions:

Lack of proper baseline data and ordinated conservation policies have led to local extinction of species from varied habitats globally (Weber & Rabinowitz 1996, Lotze & Worm 2009). Reliable estimates of species abundance and knowledge of their habitat preference are of fundamental importance as they facilitate management goals and policy decisions for successful conservation of species. The understanding of the unique ecological role of small carnivores (Roemer et al. 2009) can be adequately supplemented by baseline data as provided by our study. In addition to providing the estimates of the population density of two sympatric small cats that cannot be individually identified, our study demonstrates the utility of spatial count models for the population estimation of unidentifiable species. The study highlights the importance of different habitat types explaining fine-scale habitat segregation between co-occurring species. With carefully designed field surveys and maintaining proper caution in the generalisation of results, our model may be extended and applied to other species which lack individually identifiable morphological features like pelage patterns (such as civets, bears, and foxes) and are cryptic and elusive besides being of high conservation priority. Trends of population estimates and habitat use from this study can contribute to the assessment of conservation status and devising mitigation principles. Long term studies assessing other life-history parameters of small cats are imperative in our understanding of their ecological role in carnivore communities thriving across varied landscapes.

Chapter 5

Population Estimation of unidentifiable Canidae species

5.1 Introduction

Reliable population estimate is one of the key interests of wildlife ecology and biodiversity conservation studies. The continuous decline in the population of large carnivores and range contraction (Ripple et al. 2014, Wearn & Glover-Kapfer 2019) has made it necessary to estimate such demographic parameters with high precision. Motion triggered cameras have been widely used (Burton et al. 2015) for robust population estimation of elusive and cryptic animals over other field sampling methods. These population estimation studies primarily used capture-recapture sampling and were focused on uniquely identifiable animals (e.g. tiger Panthera tigris Karanth 1995, jaguar Panthera onca Silver et al. 2004, ocelot Felis pardalis Maffei et al. 2004). The conventional capture-recapture studies (Karanth & Nichols 1998) and the advanced spatial capture-recapture (SCR) (Borchers & Efford 2008) robustly estimated the density of uniquely identifiable species. For the unidentifiable species various approaches (e.g. N-mixture models, Royle 2004; Random Encounter Model (Rowcliffe et al. 2008); Spatial Count Model (Chandler & Royle 2013); Camera-trap Distance Sampling (Howe et al. 2017) have been developed. All these approaches have their typical advantages and disadvantages (Gilbert et al. 2020). Moreover, field applications and validations are limited to a handful of studies (Rovero & Marshall 2009, Gilbert et al. 2020) as the model assumptions are difficult to meet in field conditions.

The challenges of density estimation of uniquely identifiable species get exacerbated for group-living species lacking such unique marks. For social group-living species, there are two different detection probabilities (group detection probability and individual detection probability) associated with the population estimation. These are fundamental parameters which can bias the abundance and detection probability. A recent study by Bischof et al. (2020) showed high aggregation and cohesion among individuals in a group resulted in positive bias and overdispersion in the population density and scale parameter estimate. A limited number of studies on population estimation of social species used a gamut of methods (genetic SCR Lopez-bao et al. 2018; Camera-trap SCR Mattioli et al. 2018, Integrated population models Ngoprasert et al. 2019, Mark-resight models Gabriele-Rivet et al. 2020) but a thorough evaluation is not available. A recent study from Thailand (Ngoprasert et al. 2019) which used Integrated Population models (IPM) assimilated counts and presence-absence data to estimate the dhole population. They also used extensive simulation to test their models against different group size and the correlation between group members. Although the model took into account the heterogeneity in terms of spatial covariate but could not estimate the density surface using the framework. A genetic SCR study (Lopez-bao et al. 2018) did not account for the groups but a camera-trap SCR study (Mattioli et al. 2018) estimated both group and population density of wolves. Spatial count model (Chandler & Royle 2013) was applied for a few species for population estimation (Red fox Ramsey et al. 2015; American Black bear Evans & Rittenhouse 2018; Small cats Chatterjee et al. 2020) but application on group-living species is limited. Density estimates using the Random Encounter Model (Rowcliffe et al. 2008) also require an unbiased estimate of group-size that would be challenging to obtain for elusive and rare animals.

To overcome the existing challenges and drawbacks for population estimation of unidentifiable group-living species, we developed a model utilizing a hierarchical clustering approach in this study. We used the maximum number of individuals from a photo-capture sequence as weightage with capture locations in the clustering model. Using simulation, we evaluated our model efficacy and bias with the change in the number of photographs and distance between the centers of the pack-operating area. We also demonstrated the use of this model for camera-trap photo-captures of Dhole (Cuon alpinus), an endangered social canid from south-east Asia. We validated our findings from telemetry and genetic studies from the same study site. Finally, we compared the precision of our estimate with the existing methods (e.g. Spatial count model (Chandler & Royle 2013), Integrated population model (Ngoprasert et al. 2019)) for population estimation of unidentifiable species. Our approach aims to use fewer numbers of assumptions to postulate a generic method applicable to population estimation of group-living species without individual identifications.

5.2 Materials and Methods:

5.2.1 Field methods:

We conducted camera-trap surveys in the dry season from February 2014 to June 2018. A pair of automated motion triggered camera-traps were deployed at 240, 397 and 328 locations respectively for year 2014,2016,2018 (Figure 6, Figure 8) across the core and buffer area of the tiger reserve following a 2 sq. km grid. Each location had 2 camera-traps placed on either side of roads, animal trails, fire-lines facing each other, placed around 30-40 cm above the ground. Camera-trap placement at the trails optimises capture of large as well as small carnivores (Chen et al. 2009, Johnson et al. 2009). Also, two camera-traps increased detectability of these small carnivores. Higher number of camera sites in the reserve area ensured coverage of the complete forested habitat. Each station consisted of a pair of Cuddeback C1 or ambush (www.cuddeback.com) digital camera-trap placed at a location to maximise capture probabilities. At each site, both camera-traps was active for 24 hours for 26-30 days. We assumed sampling interval of 26-30 days would be enough to ensure demographic closure (Kendall 1999). Camera-trap sampling was carried out throughout the tiger reserve in four different blocks.

5.2.2 Density estimates for Dhole:

The Dhole is a pack living, terrestrial member of the canidae family. They usually live in packs of 5-10 individuals, but there is also reporting of larger packs (Johnsingh 1982). They share their home-range with other sympatric carnivores like-tiger, leopard but two different packs have very little overlap in their home-range (Venkataraman 1995). Though they have a range from Tibet to Thailand, Habitat fragmentation and hunting has limited the distribution of the species to a little fraction of the historical range and classified the species as ‘endangered’ in the IUCN Red list (Kamler et al. 2015). Peninsular India is now one of the very good strongholds for the species.

5.2.2.1 Identification of number of packs:

As the number of packs is not known, we used hierarchical clustering algorithm on the capture location of dhole to investigate the spatial correlation structure. We used one hour as the independent time between two capture sequences and merged all captures happened between 10 minutes to obtain the number of members in a pack. The maximum number of individuals captured in a photograph is used as weights in the clustering method. We used Euclidean distance between spatial point coordinates for clustering. We used several criteria like (Hubert’s C, Hubert’s Gamma (Hubert and Arabie 1985); pairwise biserial correlation, Average silhouette width and Pseudo R^2 (Kaufman and Rousseeuw 1990); Studer et al. 2011) to estimate an optimal number of clusters in the hierarchical approach. We also validated the number of clusters using radio-telemetry of individuals of a pack for the year 2018. We radio-collared three individuals of three different packs and used these radio-collared as known individuals to compare with the estimated clusters. We used the consensus of these methods to estimate optimal cluster number. Analysis was carried out in the package 'WeightedCluster' (Studer M & Studer MM 2014) in R 3.6 (R core development team 2019).

From the available methods of clustering, we have chosen 'ward-linkage' as it minimizes the sum of square criterion that we are taking as our distance measure whereas 'single linkage' calculates the distance between nearest two points of the clusters and 'complete linkage' calculates the distance between farthest two points of the clusters. The similarity measure for expressing the distance between cluster k and cluster i+j by merging cluster i and cluster j is given by,

$d(i+j, k) = a_i d(i, k) + a_j d(j, k) + b d(i, j) + c\,|d(i, k) - d(j, k)|$ (Lance-Williams formula)

5.2.2.2 Number of individuals in each pack:

The packs being separated out; we can calculate the probability of miss in captures of the pack. If a pack is captured t times and the number of individual captured is n_i i=1,2,…t.

$$\text{Let, } n = \max_{1 \le i \le t} n_i$$

So the number of missed individual is $(n - n_i)$ i=1,2,…t

The probability of missing an individual is,

$$p = \frac{\sum_{i=1}^{t} (n - n_i)}{t} \qquad \text{Eqn 1}$$

Hence the probability of capturing an individual is, 1-p

So, the estimate of the pack size would be,

$$\widehat{n} = \frac{n}{1-p} \qquad \text{Eqn 2}$$

From the missed history we can get a missing probability for the pack. It takes 5-15 second for the camera to take photos in consecutive image mode so the assumption of missing individuals of a pack is justified. For the estimate of the pack size we divide the maximum number of individuals captured in a trap with the probability of capturing an individual.

5.2.3 Simulation

5.2.3.1. Simulation to study effect of varying photograph:

To illustrate the effect of number of photographs affecting the proportion of detection and estimation of pack size, we carried out a simulation study in which we generated data for number of photographs and different pack size. We ran the simulation study for 1000 replicates. We assumed the number of individuals captured in photos follow poisson distribution and simulated for two different scenarios when the pack-size was small (4-5) and pack-size was large (8-10). For each of the two pack-sizes mentioned above, we simulated data where the number of photographs of a pack is 10,25,50.

We also compared the population estimate of our model with a population estimation method given by Ngoprasert et al. (2019). They used number of individual captures in a photograph at various sampling locations and modelled the population following a beta-binomial distribution in an Integrated population model (Ngoprasert et al. 2019) framework.

Simulation to study the efficiency of our method:

The efficacy of the clustering method is majorly regulated by how efficiently it can formulate different clusters from different packs. We performed a simulation study to evaluate the efficacy of the method. Considering the radius of a home range of two Dhole pack is r1 and r2 kilometre and the distance between the centers of two pack-operating areas d kilometre. We evaluated the efficacy of the clustering with the ratio of the radius of the pack-operating area and the distance between the centers. The clustering algorithm was assumed to be inefficient as the ratio (r1 + r2/d) value approaches or crosses one. We estimated the average radius of the area used by a dhole pack from the different clusters we obtained from the camera-trap capture.

We used average dhole home-range radius from radio-collared individuals as initial values for the simulation. We simulated different cases starting from when the ratio is 0.5 to, 0.7, 0.8, 0.90, 0.95, 1, 1.2 and calculated the classification probability of the clustering algorithm. We simulated 10000 cases of each scenario and reported the classification probability.

5.2.4 Other Population estimation methods:

We compared population estimates of the clustering methods with other methods like Integrated population models (Ngoprasert et al. 2019) and Spatial count Models (Chandler and Royle 2013). The Integrated population model used number of individual captures (count and presence-absence) in a photograph at various sampling locations and modelled the population following a beta-binomial distribution in an Integrated framework. We used 30 sites for count data in 2014 and 50 sites for count data in 2016 and 2018. As a prior distribution of movement parameter (σ) in the Spatial count model, we used an informative gamma prior with parameter (20,5) and an uninformative uniform prior for baseline encounter rate (g0). We ran 55000 iterations and discarded the first 5000 iterations as burn-in. We also compared the movement parameter estimate of spatial count model with the average radii of the polygons obtained from the clustering algorithm.

5.3 Result:

Among the 240 camera traps installed in 2014, we got Dhole captures in 55 of them. From the 207 photographs of the wild dog available for our study, most of them are of a single individual (n=97). The highest number of individual captures in a single photograph is 5. In 2016, we got dhole captures in 70 camera traps among the 397 camera traps. In 2018, we photographed dhole at 149 cameras out of the 328 camera-trap stations.

We estimated 7 packs operating in the surveyed area in 2014 and 9 different packs operating in the surveyed area in 2016 and 2018 (Figure 17, Figure 20). The radius of the pack operating area was calculated as 3-3.5 km for all the three years which was comparable with the earlier home-range estimates of dhole as ~50-80 sq. km (Bhaskar acharya 2005, Venkataraman et al. 1995).

We calculated number of individuals in a pack using eqn. 2 and the estimated the total population and population density. The density was calculated as varying from 8.25 (95% CI 5.03-30.48) to 4.7 individuals per 100 sq km (95% CI 2.97-10.19) from year 2014 to 2018 (Figure 16). The population density using IPM varied from 18.86-31.73 individuals per 100 sq. km (Figure 16) and spatial count model estimates varied from 9.18-27.41 individuals per 100 sq.km (Figure 16). The population abundance estimate for the study area was estimates as 82 (95% CI 51-218) in 2014 and 97 (95% CI 43-147) in 2016 and 2018. The movement parameter of spatial count (CV 7%-58%) model was highly variable compared to the movement parameter of the clustering (CV 16%-25%).

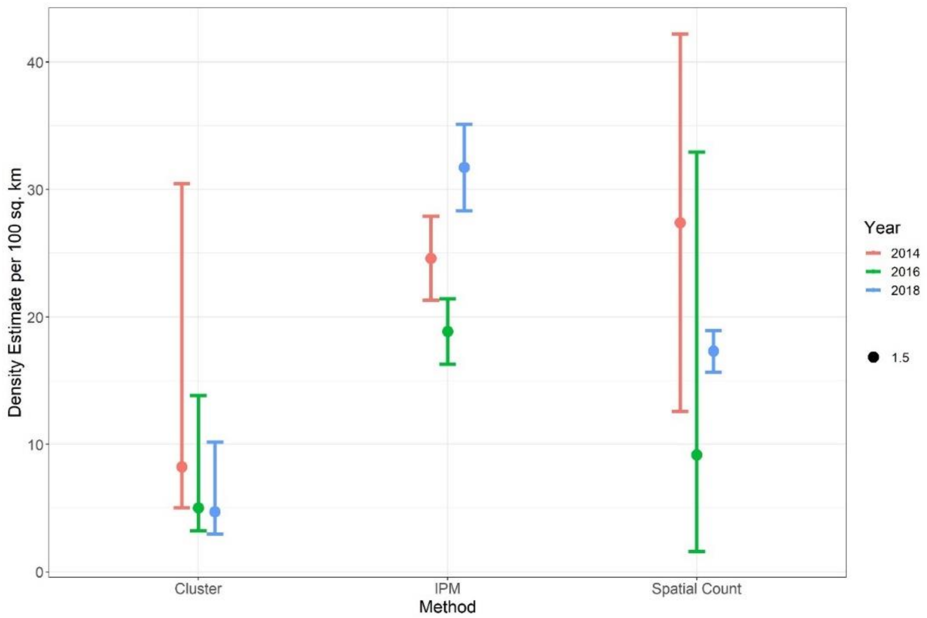


Figure 16: Comparison of population density estimates of dhole using three different methods (clustering, Integrated population model and Spatial count) for three years (2014, 2015, 2016). The dot represents mean population estimate and the bars represent 95% confidence interval.

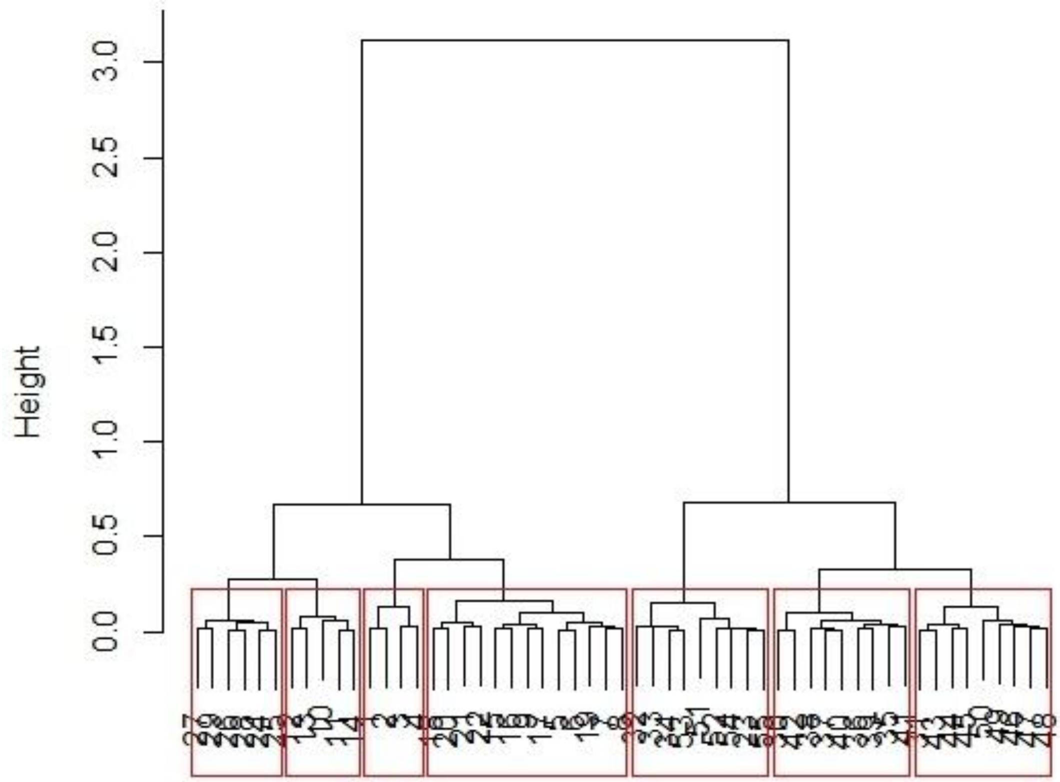
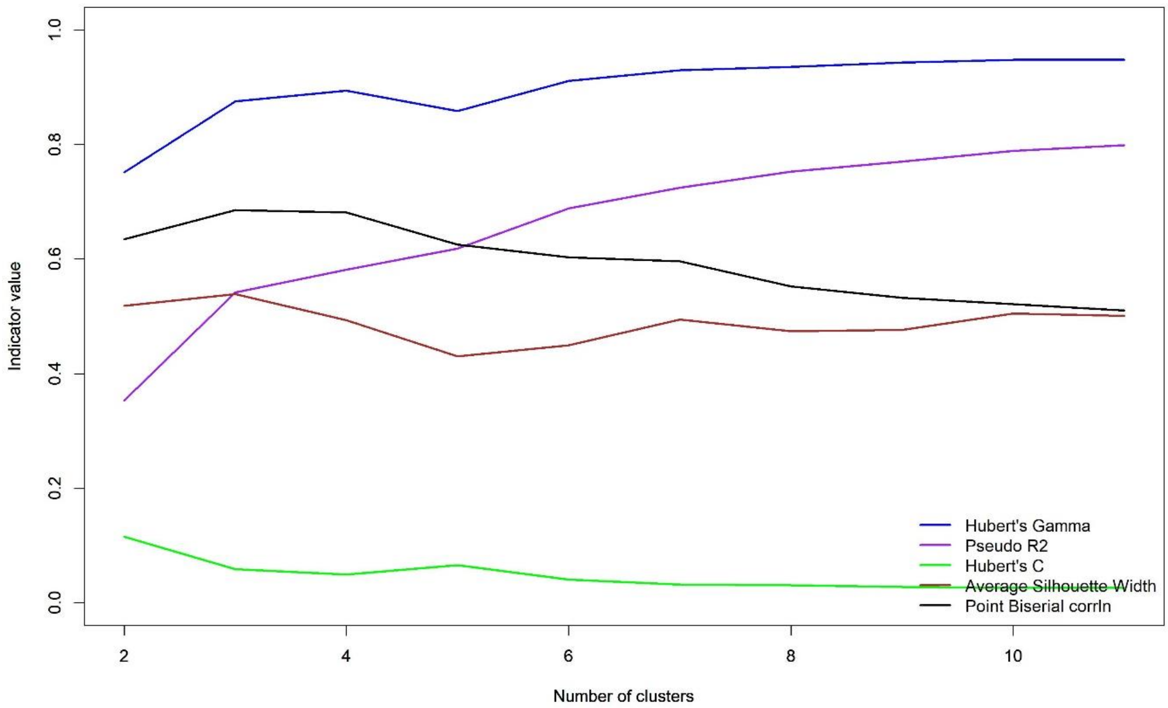


Figure 17: Dendrogram of the weighted clusters from the captures of wild dog in Tadoba-andhari Tiger reserve. These red rectangles depict the different packs present in the study area in the year 2014.



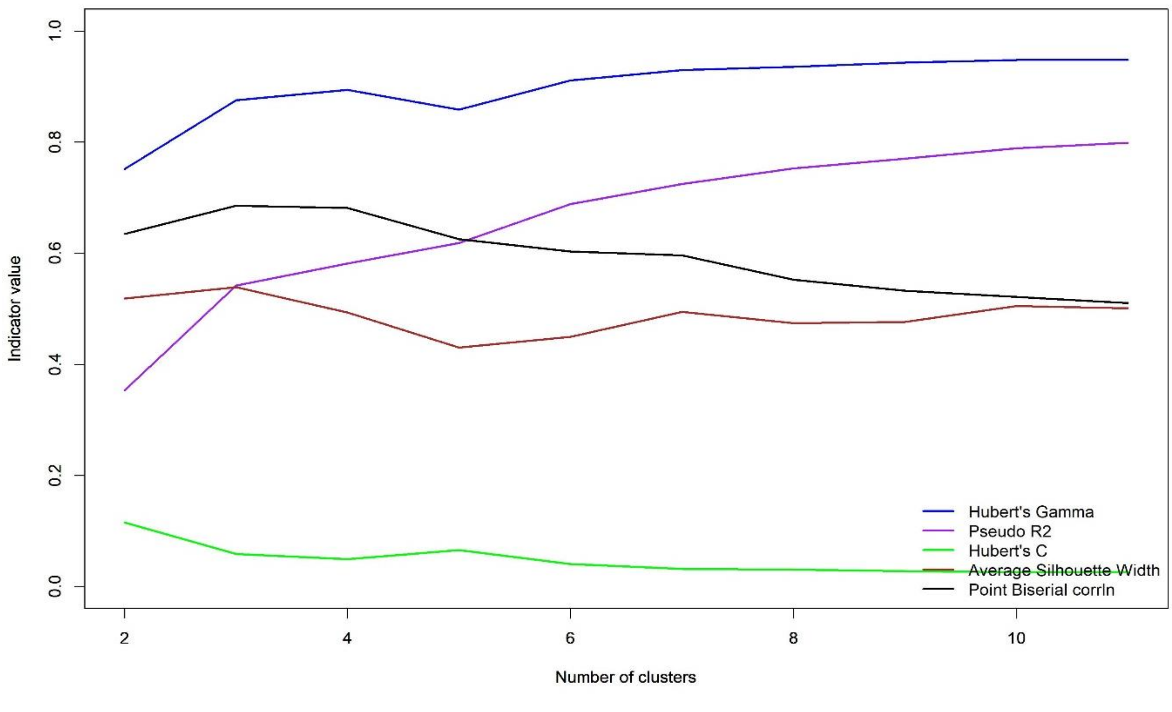
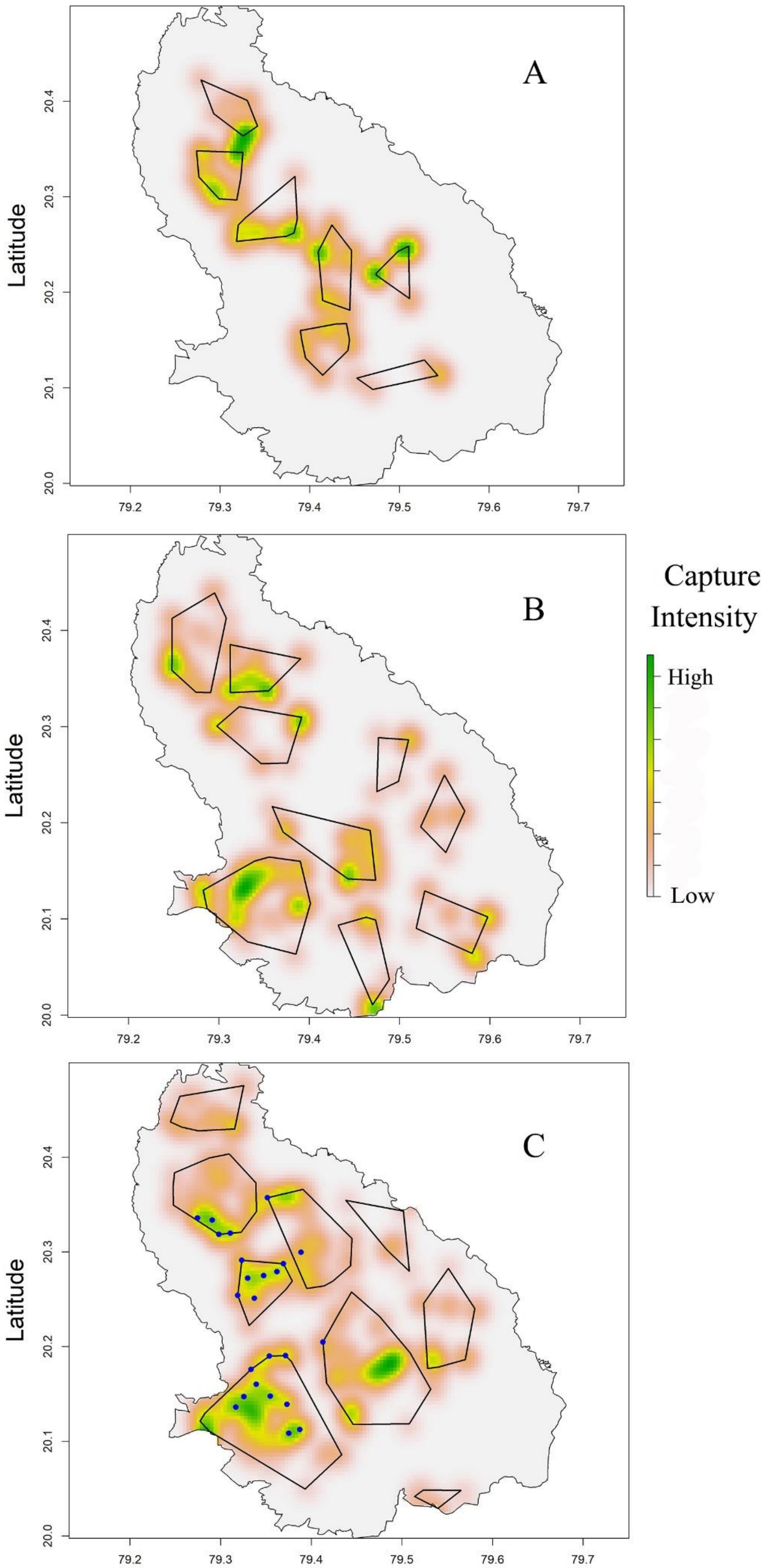


Figure 18: Comparison of different methods to estimate the optimal number of clusters of the hierarchical clustering of dhole locations of (A)2014 and (B)2016 using the “weighted clustering” approach


A
B
C
Capture
Intensity
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20.0
20.1
20.2
20.3
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79.3
79.4
79.5
79.6
79.7

Figure 19: Convex polygons of estimated dhole pack clusters for the year (A) 2014, (B) 2016 and (C) 2018 in Tadoba-Andhari Tiger reserve. The blue dots represent capture of radio-collared individuals. The maps were plotted on a surface generated using intensity of the number of captures.

5.3.2 Simulation Study:

5.3.2.1 Effect of varying photograph:

We did not detect any significant change in the estimation of pack-members with change in number of photographs. For both the three scenarios the error range was almost same for the different number of photographs (Figure 20). Although there was a difference in estimation of pack-members across different size of group. For smaller groups, the number of individuals were overestimated while for larger group the number of individuals were unbiased.

As smaller groups are more tightly knit than the larger groups, most of the times all the members of the larger groups were not photographed together. This led to the bias in the estimation of number of individual. This also supports the requirement of deploying camera-traps for shorter interval as it can ensure the assumption of population closure and can also be used unbiased for estimation of number of individuals of a pack.

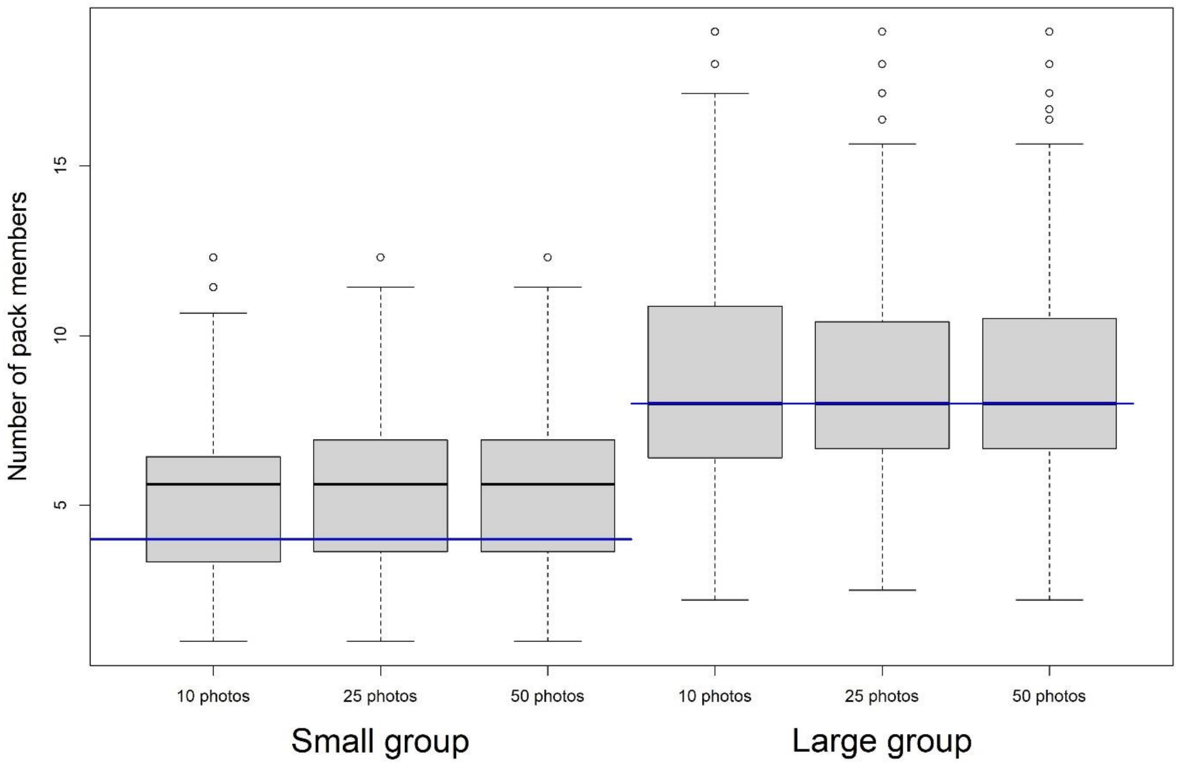

Figure 20: Bias in estimation of number of individuals from photographs using simulation methods for two different group-sizes (Small with 4 individuals and large with 8 individuals).

5.3.3 Efficiency of the clustering algorithm:

Simulation study also showed a similar trend as the real data. Our method is performing very well when the ratio of the distances is less than 0.75. After that the misclassification error increases and around 0.95 the method is unable to form separate cluster of two packs as their core area lies adjacent to each other. In reality this is justified as the core area of two packs lies apart and overlap between core activity areas is very rare as we have used sampling interval to be very small (Venkataraman 1995).

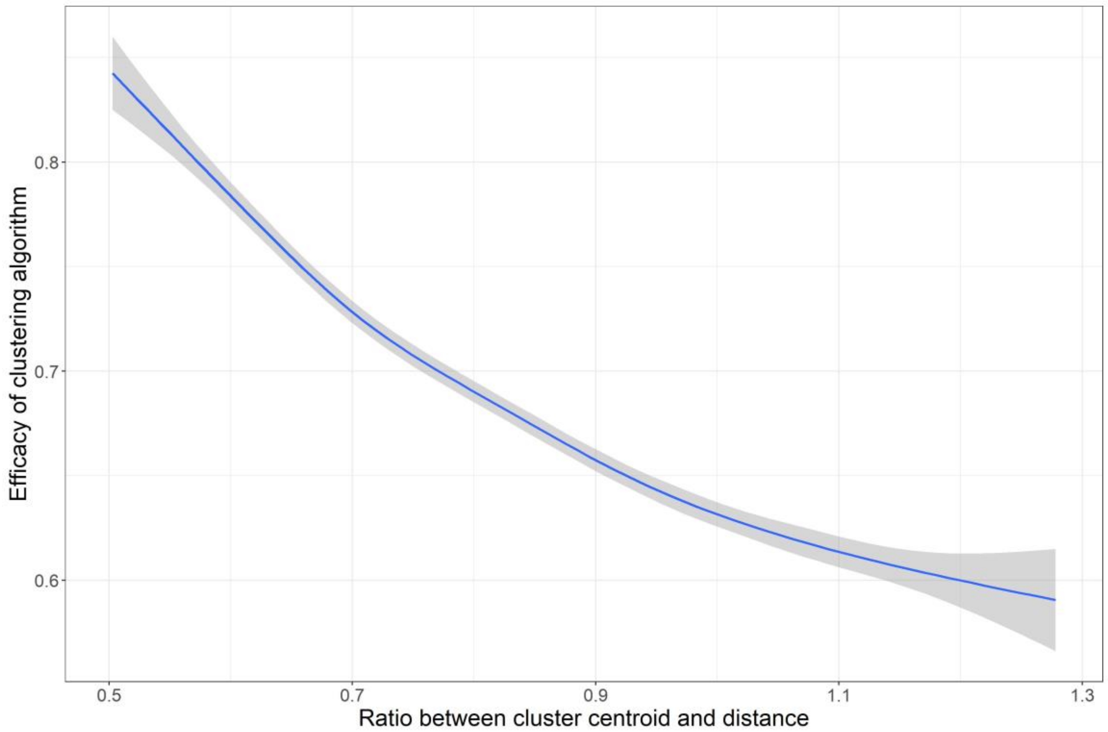

Figure 21: Efficiency of the weighted hierarchical clustering method with the ratio of distance from the pack operating radius and distance between two pack centroids. As the ratio approaches 1 the efficiency of the method decreases.

5.4 Discussion:

Capture-recapture studies are now a very popular method to get the estimates of density when the species is uniquely identifiable. The standard method of conventional capture-recapture studies (Karanth & Nicholas 1998) estimated the density of uniquely identifiable species. For the unidentifiable animal, the density estimates lack robustness and applicability to be implemented in field studies. Recent advances in the topic tried to use a combination of spatially capture-recapture (Borchers and Efford 2008) and N-mixture models. From the capture-recapture models, the activity centers and movement parameters are modeled and the N-mixture models deal with the issue of uniquely identifying an individual (Chandler and Royle 2013).

In this study, we tried to develop a method to estimate the density and abundance of a social and territorial species from spatial capture-recapture data from camera trap. Camera traps are now used as an extension in the design as the organization of individuals in space can also be known from the spatial data of captures. The information can be used to increase precision in estimates (Gopalaswamy et al. 2012) by multiple sampling methods. We applied the model by estimating the number of packs active in the study area and to estimate the number of individuals in a pack, developed a probability function based on the proportion of the individuals captured. Dholes are territorial canids and they defend their territory by scent-marking. The assumption of no overlap in the core activity area was followed from their territorial behavior observed in the studies (Venkataraman 1995, Johnsingh 1982). Also, the sampling interval of camera trapping was kept as less as possible to ensure the assumption population closure and non-overlap of core activity areas.

5.4.1 Comparison with other methods:

Our results showed the clusters formed from the clustering algorithm using the number of individuals captured as weights, could be used as a robust approach to estimate number of packs and population. There has been only a single study (Ngoprasert et al. 2019) to estimate the number of dholes. Also, they are difficult to observe in the wild as they are elusive, rare and often dominated by other large predators (Tiger, Leopard) present in the current range. The population estimation of our study demonstrated the population estimates using Integrated Population model (IPM) of Ngoprasert et al. (2019) overestimated in our case. Although their confidence interval was substantially smaller than the population estimates of the clustering approach but the model estimates was almost twice than estimates from our approach (Figure 16). Similarly, for spatial count model (Chandler and Royle 2013), the population estimates were not quite precise (Figure 16) compared to the Integrated population model. The integrated population model used both count data and presence-absence data and the increase in naïve occupancy in 2018 could have led to significant increase in population estimate of IPM. Even though the estimates were highly varying among each other, all the estimates have overlapping confidence interval (Figure 16). Earlier application of spatial capture-recapture for group-living species reported an underestimation from previous studies (Lopez-bao et al. 2018) but we did not find any such effect in the spatial count estimates.

The density estimates of dhole from this study area was comparable with the previous published estimates from Thailand (Ngoprasert et al. 2019). Population density from the previous studies were estimated as 2.2 and 3.0 individuals per 100 sq. km where the estimate from this study was estimated as 4.7-8.25 individuals per 100 sq. km. This is the first density estimates from central Indian landscape which is a stronghold of the remaining dhole population. With proper caution this method can also be extended to genetic sampling and compared with spatial capture-recapture estimates to test the efficacy of the model. Density estimates are available for only a few group-living carnivores that are not individually identifiable (wolf Lopez-bao et al. 2018, Mattioli et al. 2018; Dhole Ngoprasert et al. 2019;). Lack of individual identification and rarity are the major reason for the shortcomings. Unlike wolf, dhole have lost most of their distribution range and is categorized as "Endangered" according to IUCN red list (Kamler et al. 2015). Moreover, interference competition from other large carnivores overlapping with their distribution have also led to decline in their population (Bhandari et al. 2020).

With the help of the simulation studies, we tried to assess the efficacy of this clustering method and the effect of the number of photographs to estimate the dhole pack size. The simulation results for the number of photographs show a similar trend as our results of the camera trap.

There is very little change in the probability function with the change in the number of photographs. In the second simulation the new method performs well when there is no overlap in the core area but as the distance between the centroid decrease i.e. the ratio of the radius of the core home-range radius and distance between the centroids increase, there is a problem with the formation of the cluster. As the ratio tends to one the method face issue to separate the different classes and often merge them to form one single cluster. To ensure no overlap in the core area sampling period should be kept for less number of days and that will validate the closure of the population also.

One major limitation of the study is that, we assumed the pack-size variation between different groups would be reflected in the photo-captures of the groups. For very small groups or single individuals it would be almost impossible to take into account the variation. This may lead to clumping of multiple groups as a single group. Further information from other sources like radio-telemetry, genetic sampling would be effective in these situations.

Camera trap has been adopted widely for surveying different wildlife species. This is an attempt to estimate the density and population estimate of the social and territorial animal using a novel clustering method following a non-invasive sampling technique (camera trap photographs). With proper caution, the model can also be extended to other social species using different sampling frameworks like camera-traps, genetic sampling etc.

Chapter 6

Comparison of density estimates between different sampling techniques

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6.1 Introduction:

Robust population density estimates are fundamental for effective conservation and management of wild species, but such evaluation is challenging when the study species is elusive, rare and difficult to detect. Density estimation of species with unique stripes (Tiger Karanth & Nichols 1998) or spots are comparatively easier to implement as they can be enumerated in capture-recapture framework, whereas species lacking such marks are difficult to be identified with higher precision. There has been a lot of analytical developments (e.g. Random Encounter model (Rowcliffe et al. 2008), Spatial Count model (Chandler & Royle 2013) and Camera-trap Distance sampling (Howe et al. 2017) for such unmarked species but these studies has not been evaluated rigorously in field-studies. A thorough evaluation of the underlying assumptions of these models is yet to be done with varying ecological parameters.

Camera traps are one of the new tools to monitor wildlife species non-invasively (Burton et al. 2015). Dataset generated using camera-trap sampling can be treated in different framework to study different objectives like species occupancy, activity-pattern, interaction with other species and density of uniquely identifiable species (Burton et al. 2015). The assumptions of population estimation models of uniquely unidentifiable species are difficult to meet in field-studies. N-mixture model (Royle 2004) assumes the same individual is not encountered in multiple sites. The Random Encounter Model developed by Rowcliffe et al. (2008) to estimate species absolute density modelling detections as particles of the gas model. Although there are quite some applications of the model (Balestrieri et al. 2016, Caravaggi et al. 2016, Sanchez et al. 2017), there are very few robust evaluations of the model effectiveness. Moreover, the model assumes animal movement independent of each other which are difficult to hold in empirical data. Recently developed Spatial Count model (Chandler and Royle 2013) models the spatial correlation in the proximate site and estimate the population based on the movement/home-range information of the species. There are few applications of the model but majorly on solitary species (American Black Bear Evans & Rittenhouse 2018, Small cats Chatterjee, Nigam & Habib 2020). Camera-trap distance sampling (CTDS) (Howe et al. 2017) was the most recent development for unmarked population estimation where camera-traps were formulated as point transects following distance sampling approach (Buckland et al. 2001). The method was applied for chimpanzees (Cappelle et al. 2019) and terrestrial mammal community (Bessone et al. 2020).

We expanded the camera-trapping approach further for species lacking uniquely identifiable marks following camera-trap based distance sampling approach (Howe et al. 2017). We used one group-living and one solitary species to understand the effect of snapshot timings and dial-activity pattern of these species. Also, we compared the bias and precision of camera-trap distance sampling and line-transect sampling techniques. As CTDS framework is based on the availability of animal for detection at such predetermined snapshot intervals, delineating their effect would be fundamental for robust estimation of species population density. The outcomes of this study can inform future survey designs with a trade-off between cost and effort. Moreover, this snapshot timing and activity pattern can be applied effectively for population estimation of other elusive species lacking robust population density estimates.

6.2 Materials and Methods:

6.2.1 Study area:

The study was carried out in Tadoba-Andhari Tiger Reserve distributed over an area of 1700 sq. km. The reserve consists of Tadoba National park and Andhari Wildlife Sanctuary. The landscape consists of southern tropical dry deciduous forests (Champion and Seth 1968), dominated by bamboo (*Dendrocalamus strictus*) and teak (*Tectona grandis*). Elevation ranges from 212 m to 351 m asl and annual temperatures range from 3-48ºC. There is a short, wet season (July-September) and a long, dry season (October-June) with an annual rainfall of 1175 mm (Khawarey & Karnat 1997).

6.2.2 Camera-trapping:

We deployed 378 pairs of camera traps throughout the extent of TATR (1727 km^2), dividing the area into 1.42 x 1.42 km (2 sq. km) cells (Figure 22A). Individual camera trap sites in adjacent cells were separated by an average of 1.032 km with some exceptions (n=68) due to the unavailability of suitable locations and terrain constraints. Camera trap sampling with this design was carried out especially focusing on large predators like Tiger (*Panthera tigris*), Leopard (*Panthera pardus*). Within each sampling cell, we maximized detection probability by deploying cameras along roads and animal trails as these are most preferred for animal movement (O'Connell et al. 2010). We placed a pair of unbaited, motion-triggered digital camera traps with a white-flash (Cuddeback Blue series C1, Cuddeback Ambush, www.cuddeback.com) 30-40 cm above the ground on opposite sides of roads and trails, approximately 5-6 m apart. Camera traps were set in four different blocks throughout the study area with an average of 200 camera-trap units (100 sites) in each block. Camera trap sampling spanned across the dry season (February to June 2016) to avoid seasonal variation in animal detection probability and movement. Cameras were programmed to take consecutive images (n=3) at a 5-second delay when triggered and were checked once every two weeks, with each deployment lasting at least 25 days (range 25-32 days).

6.2.3 Camera-trap distance sampling:

We calculated radial distance from the camera sensor for two herbivore species (one group living spotted deer *Axis axis*, one solitary species Indian Muntjac *Muntiacus muntjac*). We used the framework given by Howe et al. (2017) and used the camera-traps as point transects. We calculated trap-wise effort using different snapshot timings ranging from 5-s (minimum time between two shutters) to 30 min. Distance sampling analysis was carried out in "Distance" software ver 7.3.

We calculated the species-specific availability and corrected for that available times using the formula given by Cappelle et al. (2019). Activity analysis was carried out in "activity" package in R 4.0.2 (R Core team 2020).

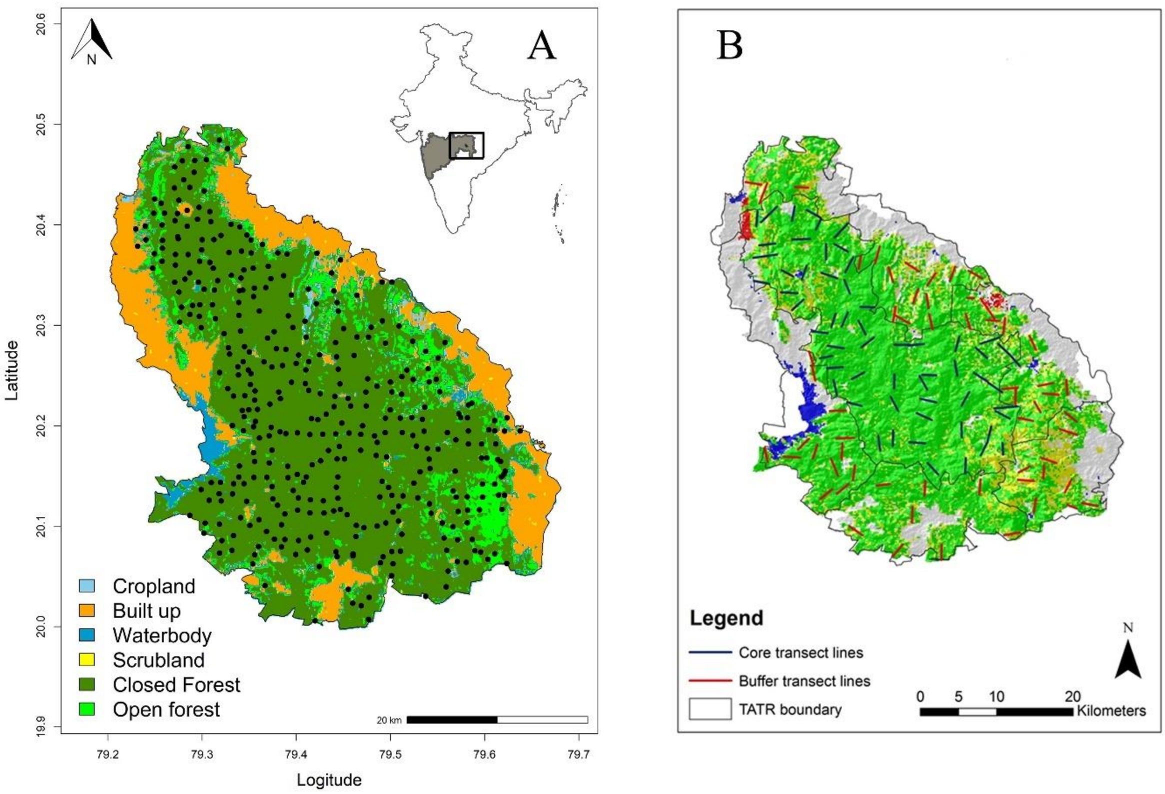


Figure 22: Study-area showing locations of camera-trap (A) and line-transects (B) in Tadoba-Andhari Tiger Reserve (TATR). Inset: location of study-area in India.

6.2.4 Line-transect:

A total of 95 transects of 2 km distributed all over the tiger reserve (Figure 22B) were walked 7 times to estimate prey species density. Transects were walked in March to record the prey species. In each transect, whenever herbivore species were encountered group-size, GPS location, distance from the observer and angular bearing of the animal were recorded. We used half-normal and hazard rate detection function with 'cosine', and 'simple polynomial' adjustment terms to model the species detection. We selected the best model of detection functions using Akaike Information Criterion values. Analysis of the data was carried out in "Distance" software ver 7.3.

6.3 Results:

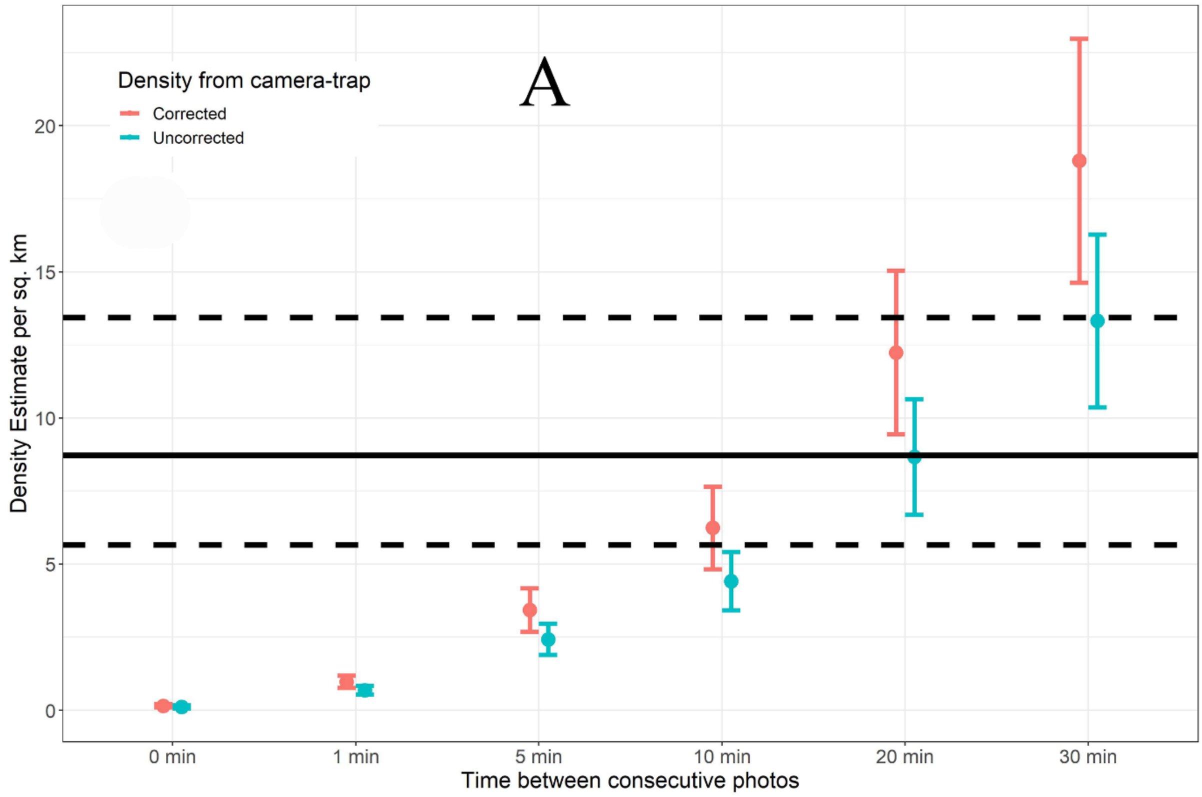
We accumulated a total of 306 detection of chital and 217 detections of Indian muntjac in camera traps using an effort of 10322 camera-days. A total of 812 observations of ten different prey species were recorded in line-transects. Chital was recorded 129 times and Indian muntjac was recorded 65 times in transect sampling.

The density estimation using line-transect distance sampling was estimated as 8.48 (95% CI 5.31-13.54) and 1.16 (95% CI 0.7-1.91) individuals per sq. km for spotted deer and Indian muntjac respectively (Table 1). Average group size estimate for spotted deer and Indian muntjac was 7.68 (95% CI 5.95-9.91) and 1.1 (95% CI 1.01-1.21) respectively.

In CTDS, the density of both the species was increasing as we increased the snapshot interval. The density was comparable with the line-transect density when the snapshot interval was chosen as 20 minutes (Figure 23A). The density of Chital was estimated as 8.67 (95% CI 6.69-10.65) with 20-minute snapshot interval and density of Indian Muntjac was estimated as 1.16 (95% 0.62-2.18) (Figure 23B). For camera-trap distance sampling hazard rate model with a simple polynomial, adjustment term was the best performing model for detection probability modelling of spotted deer and Indian Muntjac (Figure 24) based on AIC values.

Table 5: Species density, number of observations and effective strip width of line-transect distance sampling for both the species are given in the table

Species	Number of records	Density (95% CI)	CV	Effective Strip width (95% CI)
Chital	129	8.48 (5.31-13.54)	24.01	42.96 (34.3-53.7)
Indian Muntjac	65	1.16 (0.7-1.91)	25.37	23.26 (17.1-31.6)



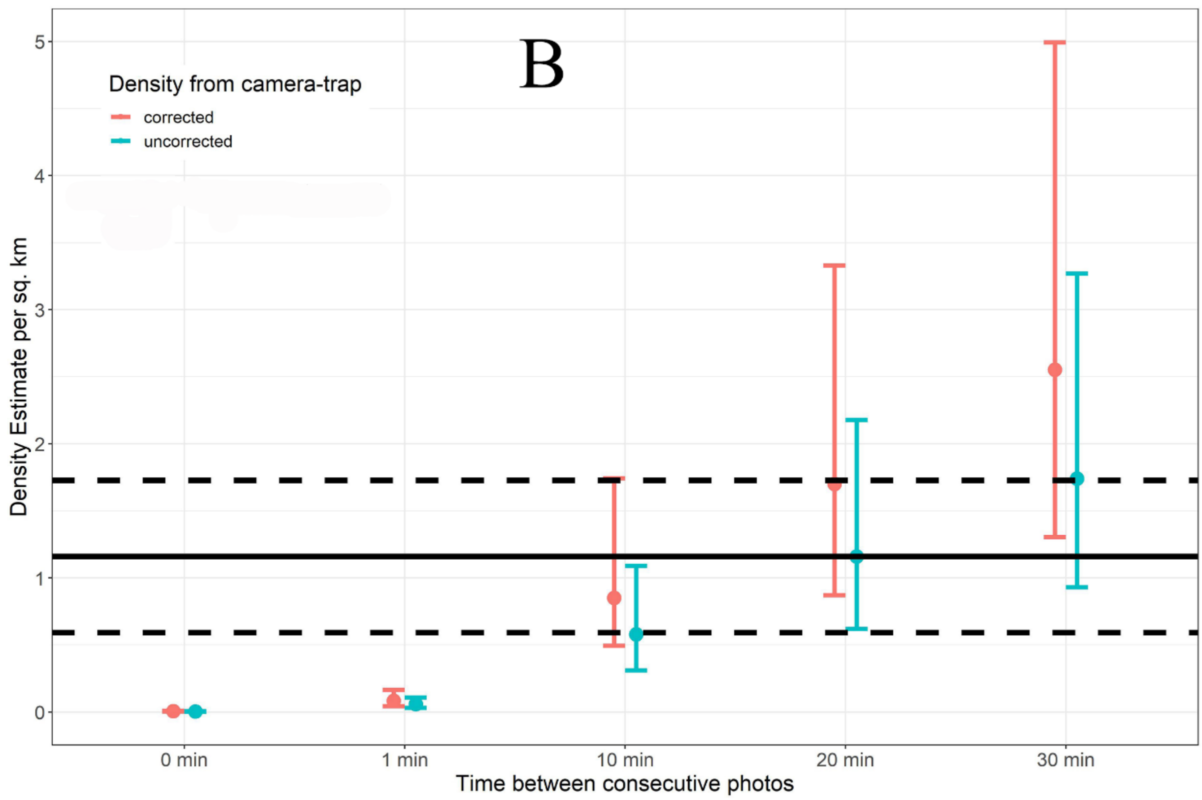


Figure 23: Comparison of density estimates of two herbivores (A) Spotted deer *Axis axis* and (B) Indian Muntjac *Muntiacus muntjac* with different snapshot times (0 min-30 min). The black

horizontal line with the dashed line represents the line-transect density estimates and 95% confidence intervals.

Activity plot of both the ungulate species showed a lower activity around midday (Figure 25). The dip in the activity was much pronounced in Indian muntjac compared to chital. This low activity is also used to compute the availability factor for detection. We used 15 hour activity time for Indian Muntjac and 17 hour activity time for spotted deer. Incorporating the activity time in the CTDS estimates, we found an increase of 46-60% for Indian Muntjac and 24-40% increase in density estimates of spotted deer.

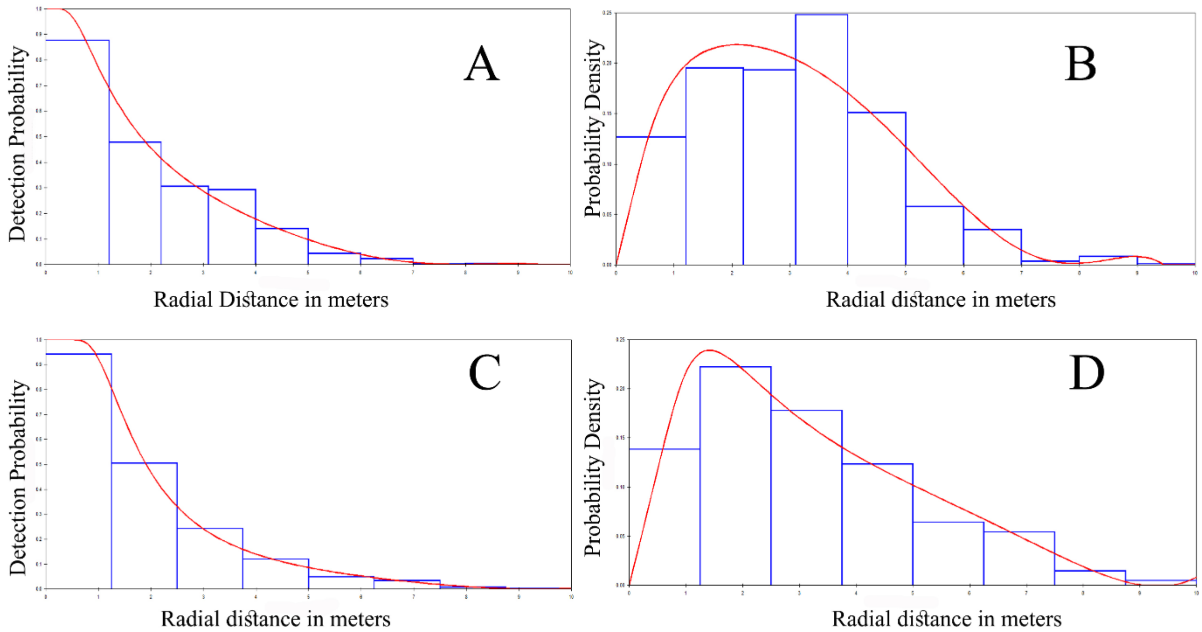


Figure 24: Detection probability as a function of distance (A, C) and probability density functions of observed distances (B, D) and from hazard-rate detection models fitted to data from Spotted deer (A, B) and Indian Muntjac (C, D) collected from camera-trap photo-captures.

6.4 Discussion:

We estimated population density of two ungulate species from line-transect distance sampling and camera-trap distance sampling (CTDS). We compared the estimates from both the sampling framework with different snapshot timings for CTDS. Our analysis revealed a snapshot timing of 20 minutes was effective for comparison of density estimates from these two sampling methods. This is the first study where density estimates of camera-trap sampling were compared with other methods to evaluate the effects of snapshot timings.

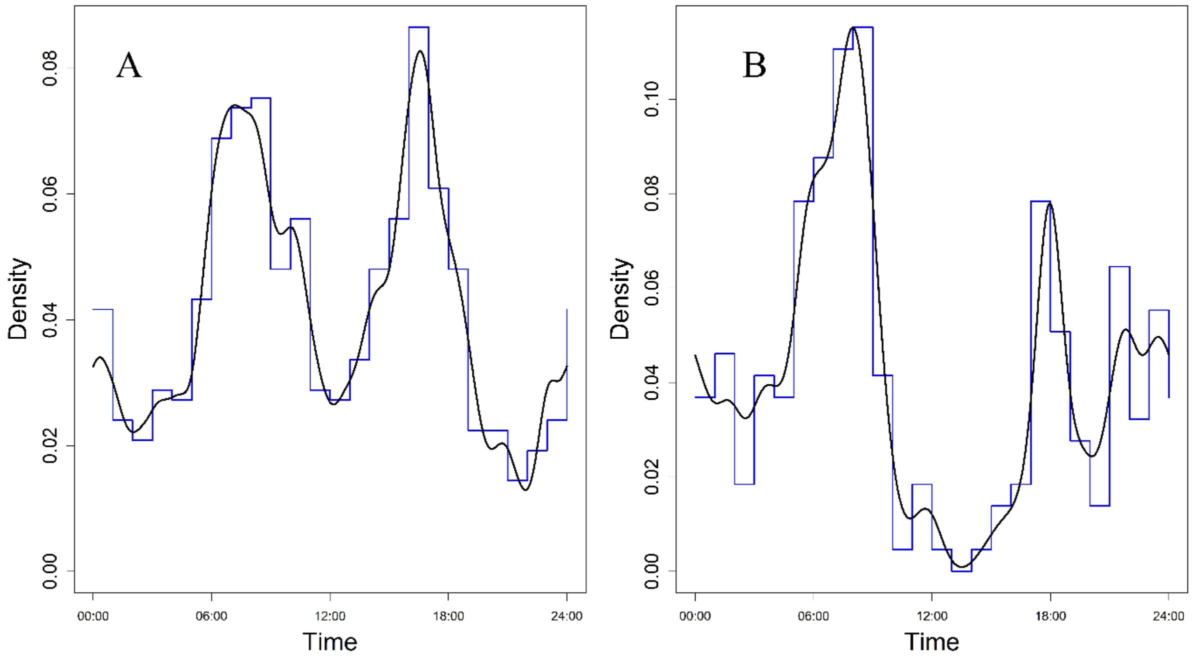


Figure 25: Radial activity pattern of (A) Chital and (B) Indian muntjac. The blue line represents the number of captures per hour and the black line is fitted on the histogram. There is a drop in the activity around midday for Indian Muntjac but chital was active throughout the day.

Earlier application of camera-trap distance sampling compared the density estimates with Spatial Capture-Recapture (SCR) (Cappelle et al. 2019) and REM (Bessone et al. 2020). These studies found no significant differences between the density estimates of different sampling approaches. Cappelle et al. (2019) also compared the cost-effectiveness and processing time of these methods. CTDS and SCR required similar efforts in the field but CTDS required more time for processing the data for analysis. Also, CTDS estimate was less precise compared to density estimates of SCR but more precise compared to Line-transect distance sampling. We also found similar results in our comparison of line-transect and CTDS estimates. While evaluating the effect of activity timing on density, we found an increase in density estimate when we included only the photo-captures from the peak activity period of the species. Previous studies of Howe et al. (2017) also reported a similar pattern when they compared the density estimates between daytime and peak activity hours of the species. The change is majorly attributed to the decrease in sampling effort. Also, the snapshot interval for camera-trap distance sampling can be visualized as an independent point count to evaluate population density. While comparing the density for increasing snapshot interval we reported an increasing trend in the population density. This increase was contributed majorly by two factors, site-wise sampling effort and the number of photo-captures. As we increased sampling interval, site-wise sampling effort decreased led to a smaller number of point counts. We had to drop photo-captures while using the different snapshot timings but that can ensure the independence between two photo-captures. Surprisingly, both group-living and solitary species exhibited similar snapshot timings. Although, line transect density estimates are known to be underestimation for forest-dwelling herbivores (Jathanna, Karanth & Johnsingh 2003), here we found the ideal snapshot timing from CTDS for unbiased density estimation.

One major limitation of this camera-trap approach was deploying the cameras at habitat features preferred by animals (e.g. animal trails, roads). Placing the cameras at random locations at directed by Howe et al. (2017) may alter the findings compared to the preferential placement. This bias arising from non-random placement of cameras was also reported similarly for population estimation of lions (Cusack et al. 2015) and Lynx (Garrote et al. 2019) while using Random encounter model (Rowcliffe et al. 2008). Although the studies (Cusack et al. 2015, Garrote et al. 2019) reported overestimation from non-random camera placement, we found underestimation of density for non-random camera placement. This study also explored the scope of using camera-trap distance sampling for such deployment of cameras. In this study, we followed the recommendation provided by Howe et al. (2017) using a large sample of distance observations to increase the precision of estimated density using CTDS. We improved precision of density estimates with an increase in higher snapshot intervals and also recommended using higher sampling effort for robust population density for future studies employing CTDS.

The recently proposed CTDS method has huge potential for population estimation of unmarked animals as compared to other methods (Spatial Count model Chandler & Royle 2013; Mark-resight model Rich et al. 2014) it has a huge advantage to be a less computationally intensive and easier approach. It can harness the power of open-source software “Distance” (Thomas et al. 2010) and can be extended for robust population estimation of multispecies simultaneously (Bessone et al. 2020). As the approach does not require other ecological information like animal speed and movement parameter, this method can be effectively applied to a broad range of species.

Chapter 7

Conclusion and Synthesis

The thesis explored optimal sampling design using camera-traps and estimated population density of several uniquely unidentifiable carnivore species. Also, the work compared between different sampling methodologies and commented on the accuracy and cost-effectiveness. The study was majorly based on camera-trap sampling as it is one of the most promising sampling techniques to explore terrestrial mammal community (Burton et al. 2015).

We explored the current status of research in the literature review, estimated the optimal sampling strategy in the first technical chapter, estimated population density and investigated whether they are the most cost-effective and accurate sampling methodology or not.

7.1 Significant Outcomes

The literature review of the thesis in chapter 1 found that camera-trap studies are majorly distributed in countries developed countries with higher Gross Domestic Product (GDP) and higher proportion of English speakers. Species richness of mammal orders like carnivora and certiodactyla is not a major driver of camera trap studies especially in the speciose tropical areas.

In Chapter 3 we estimated optimal sampling design for species with different body-size species over a range of occupancy and daily detection probability. We found that increasing sampling effort is not the best strategy and it depends on species ecology and body-size.

Chapter 4 and Chapter 5 described population density of different carnivore species. We estimated the population density of Dhole, Jungle cat, Honey-badger and Rusty-spotted cat. We compared the effectiveness of informative priors in estimating the population density of these small carnivores and evaluated how closely simulation matches with the estimated population density.

In chapter 6, we compared density estimated between different sampling methods and evaluated which is the most cost-effective, labour intensive and precise estimator to estimate different state variables (density, occupancy).

7.2 Recommendations

The major recommendations from the study are given below for management and conservation implementations.

1. Species specific camera trap should be deployed. Although there has been a rise in multi-species occupancy studies, the assumptions are difficult to follow when movement of the species are significantly different from other.

2. For common species, around 100 camera traps for two weeks can give robust estimate but for rare and elusive species (ψ <0.25), camera must be placed at least for more than three weeks.

3. Small carnivores have very specific habitat requirements and unlike large carnivores their strong affinities toward the specific habitat can act as an adverse effect for their survival. There is a pertinent requirement for population estimate of such species that cannot be identified individually based on their pelage patterns. Occupancy of such species can serve as an indicator for large scale monitoring but reserve specific population estimates are also necessary to gather insights of their ecology.

7.3 Challenges and Limitations

This study was carried out in one protected area in central Indian landscape. The terrestrial mammal community would be different in other landscapes where landscape specific factors would be acting in multiple scales. We deployed the camera traps at animal trails and roads to maximise animal captures. Random deployment of the cameras would be nessacery for the data to be analysed in Random encounter Model (Rowcliffe et al. 2008) framework. Also, recent studies (Rich et al. 2019) exploring the hybrid deployment of cameras to maximise species specific captures and comparison of multiple sampling methods (Bessone et al. 2020) to evaluate species density is required to comment about various sampling protocols. We could not evaluate such protocols for a number of species and was restricted with the carnivore community for such analysis.

Moreover, this work was limited to one session of camera trapping exercise. Multi-year analysis of same dataset with the same protocol can help us accumulating more in-depth understanding of the ecology of these small carnivores.

7.4 Future Work

The optimal survey design was based on one protected area and terrestrial mammal community of the area. Although we have generalised the findings of the optimal design part to be applicable for other areas and ecosystems, careful application of this model to other ecosystems can illustrate further the shortcomings of this model and guide future development. Park managers, practitioners can certainly take advantage of this work and employ it for their particular area.

We have explored all the methods available to estimate population density of the uniquely unidentifiable species. We have also commented about the particular advantages and shortcomings of the unmarked spatial capture-recapture (Spatial count/ Spatial presence-absence) for a range of carnivore species. We evaluated the limitations of trap-spacing mentioned in the earlier works and remarked how that could be overcome for the model to be applied for more species. We calculated home-range of the species from body-size allometric equations. Future works can incorporate radio-telemetry studies for calculation of home-range to be used as informative prior in the model. Also, the radio-collared species can be used as marked individual and the data can be used in the Spatial partial-identity model (Augustine et al. 2019) framework. This can improve the robustness of the estimate as shown in earlier simulations (Chandler and Royle 2013). The dhole model needs to be validated on other identifiable group living animals and this we can evaluate the efficacy of such approach.

Also, multi-session data collected using similar protocol can help us in understanding the population trend of these small carnivores. That would be much more robust than the density estimated from a single session data. Future studies keeping in mind these recommendations can improve density estimate as well as can advance our perception about the little known elusive small carnivores.

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Papers and presentations

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RESEARCH ARTICLE

Population density and habitat use of two sympatric small cats in a central Indian reserve

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Abstract

Despite appreciable advances in carnivore ecology, studies on small cats remain limited with carnivore research in India being skewed towards large cats. Small cats are more specialized than their larger cousins in terms of resource selection. Studies on small cat population and habitat preference are critical to evaluate their status to ensure better management and conservation. We estimated abundance of two widespread small cats, the jungle cat, and the rusty-spotted cat, and investigated their habitat associations based on camera trap captures from a central Indian tiger reserve. We predicted fine-scale habitat segregation between these sympatric species as a driver of coexistence. We used an extension of the spatial count model in a Bayesian framework approach to estimate the population density of jungle cat and rusty-spotted cat and used generalized linear models to explore their habitat associations. Densities of rusty-spotted cat and jungle cat were estimated as 6.67 (95% CI 4.07–10.74) and 4.01 (95% CI 2.65–6.12) individuals/100 km^2 respectively. Forest cover and evapotranspiration were positively associated with rusty-spotted cat occurrence whereas both factors had a significant negative relation with jungle cat occurrence. The results directed habitat segregation between these small cats with affinities of rusty-spotted cat and jungle cat towards well-forested and open scrubland areas respectively. Our estimates highlight the widespread applicability of this model for density estimation of species with no individual identification. Moreover, the study outcomes can aid in targeted management decisions and serve as the baseline for species conservation as these models allow robust population estimation of elusive species along with predicting their habitat preferences.

Introduction

Carnivores naturally occur at low densities owing to their apex position in the food web. Concurrently they continue to face rapid population decline caused by contracting range sizes and fragmentation of existing habitat [1]. Asia holds more than 60% of the global diversity of cats [2], harbouring 21 out of 36 species. India, a mega-biodiverse country, is home to 15 among them [3]. The geographical distribution range of most of these cats lies within protected areas with an average size of less than 400 km^2, which contributes to only five percent (http://wiienvis.nic.in/Database/Protected_Area_854.aspx) of the total landmass of the country. Furthermore, these protected areas are located within high densities of human populations dependent on local resources and surrounded by land which is undergoing an upsurge in anthropogenic developmental activities. Given these escalating pressures on felid species in Asia [4–6], an in-depth understanding of their population status and habitat use would be fundamental for designing effective conservation and management policies. Additionally, as a number of the species do not have unique pelage patterns, capture-recapture techniques [7] cannot be applied for population estimation and owing to their elusive nature, direct encounters are also rare. We addressed these issues using the spatial presence-absence model [8] based on field-based sampling using automated camera-traps.

Among the small cats native to India, the jungle cat (*Felis chaus*) and rusty-spotted cat (*Prionailurus rubiginosus*) are the two, most widespread species. The former belongs to the house cat lineage, whereas the latter to the leopard cat lineage [9]. Rusty-spotted cat, the smallest cat in the world (average body weight 1.6 kg), is also reported to use the arboreal habitat alongside the terrestrial domain [3]. However, no such adaptation has been reported for the jungle cat (average body weight of 5 kg). Both species are known to be nocturnal and elusive [3, 10]. The jungle cat is categorized as "Least Concern" in IUCN red list [11] due to its large distribution range from south-eastern Asia to middle east and eastern Europe, while the rusty-spotted cat was recently downgraded to "Near Threatened" from "Vulnerable", owing to new records from previously unknown locations [12].

Although taxonomy and phylogeography of these small cats have been studied [13, 14], fundamental ecological information on parameters like demography, habitat use, and activity pattern is majorly lacking. Previous studies have not attempted to estimate the population of any of these species, nevertheless, the population trend of both the species is presumed to be decreasing [11,12]. Most studies on the rusty-spotted cat are based on opportunistic sightings [15, 16]. A single study discussed the habitat use, seasonal abundance [17], and distribution pattern [18] of small carnivores from one protected area in the Western Ghats. The study [17] had limited inference owing to a small sample size (n = 11) but indicated a positive relationship of the abundance of the rusty-spotted cat with deciduous forest and that of jungle cat with dry thorn forest.

In this context, as both species have overlapping distribution ranges, we aimed at predicting fine-scale segregation in a habitat that enables the coexistence of these sympatric small cats. We hypothesized that habitat segregation at a fine-scale between these two species as a major driver for the cooccurrence. Also, the population estimation would fill the existing knowledge gap of these species using camera-trap captures as our study is the first attempt to estimate the population density of these individually unidentifiable small cats.

Materials and methods

Study sites

We conducted the study in Tadoba-Andhari Tiger Reserve (TATR) (20˚04´-28˚025´N, 79˚13´-79˚33´E) in the state of Maharashtra in Central India. The reserve spreads across an area of 1700 km^2 in the Deccan plateau. The terrain of TATR is mostly undulating and hilly in the north and flat in the southern part [19]. The climate is characterized by a hot and long summer and a short and mild winter [19]. Annual average precipitation is around 1,200 mm, received mainly from south-western monsoons between June and September [20]. The vegetation of the reserve has been classified as Southern Tropical Dry Deciduous forest [21] dominated by bamboo (*Dendrocalamus strictus*) and teak (*Tectona grandis*). The habitat is majorly homogenous comprising of dense forest cover in 68%, open forest in 10% and human habitation in 21% of the total area of the reserve.

More than 20 mammal species have been recorded from the reserve through camera-trapping studies [22]. These include four species of felids (tiger, leopard, jungle cat and rusty-spotted cat), an ursid (sloth bear), two species of canids (dhole, jackal) and one species of mustelid (honey badger). Wild pig and chital are the major prey species followed by sambar, nilgai and gaur.

Field methods

We conducted camera-trap surveys in the dry season from February to June 2016. A pair of automated motion-triggered digital camera-traps (Cuddeback C1 or Cuddeback Ambush www.cuddeback.com) was deployed at 397 locations without using lure or bait (Fig 1). Due to the limited availability of camera-traps, sampling in the reserve was carried out in the tiger reserve dividing the whole area into four different blocks with an average of 100 stations per block. Cameras were shifted to consecutive blocks after sampling was done in one block. The cameras were deployed dividing the area following a grid size of 2 km^2, equivalent to the home-range size (2–5 km^2) of another small cat, the leopard cat which is widespread across the country [23]. Camera traps deployment was aimed for proportional representation of different habitat types (except human habitation) across the reserve. The average distance between two adjacent camera traps was 1.03 km, ensuring no large gaps in camera placement for the detection of individual small cats and to avoid pseudo-replication. Cameras were placed on both sides of roads, animal trails and fire-lines facing each other, placed around 30–40 cm above the ground. Camera-trap placement at trails optimizes the capture of large as well as small carnivores [24, 25]. Also, the placement of two camera-traps at every site increased the detectability of these small felids [26]. Cameras were programmed to take three photographs per trigger with an interval of 5 sec. Photographs taken within 30 min from the first trigger were not used for analysis to maintain the independence of captures. All the camera-traps were active for 24 hours continuously for 26–30 days and checked once in 15 days. Sampling interval was restricted to 26–30 days to ensure demographic closure [27].

Density estimates

In this study individuals of neither species are uniquely identifiable from photographs. Therefore, we used spatial presence-absence (SPA) models [8], an extension of the spatial count model of [28]. Spatial count models the latent encounters of spatially referenced individuals with sampling devices using data augmentation and Markov chain Monte Carlo (MCMC) sampling in a Bayesian framework [8]. SPA models are structurally similar to spatial capture-recapture (SCR) models [7]. We assumed a half-normal detection function to model the probability of detection. Similar to SCR models, SPA models estimate g_0 (baseline encounter rate), σ (scale/movement parameter related to home-range of the species) and N (population size) [8].

For each camera site, the detection or non-detection of these cats were recorded on each 24h sampling interval. The state-space (S) was comprised of the sampled area and a surrounding buffer area that is large enough to include all individuals potentially exposed to sampling. We estimated σ from the body-size and daily-movement distance equation [29]. We employed multiple buffer (σ, 2σ and 5σ) values around the state spaces to test the effect of buffer size on the density estimates of the SPA model. Following the equation of [29], the estimates of the home-range size of these cats were calculated as 0.8–1.2 km^2 and 2–5 km^2 for rusty-spotted cat and jungle cat respectively. A vague uniform prior, U (-10,10), was placed on the logit of g_0,

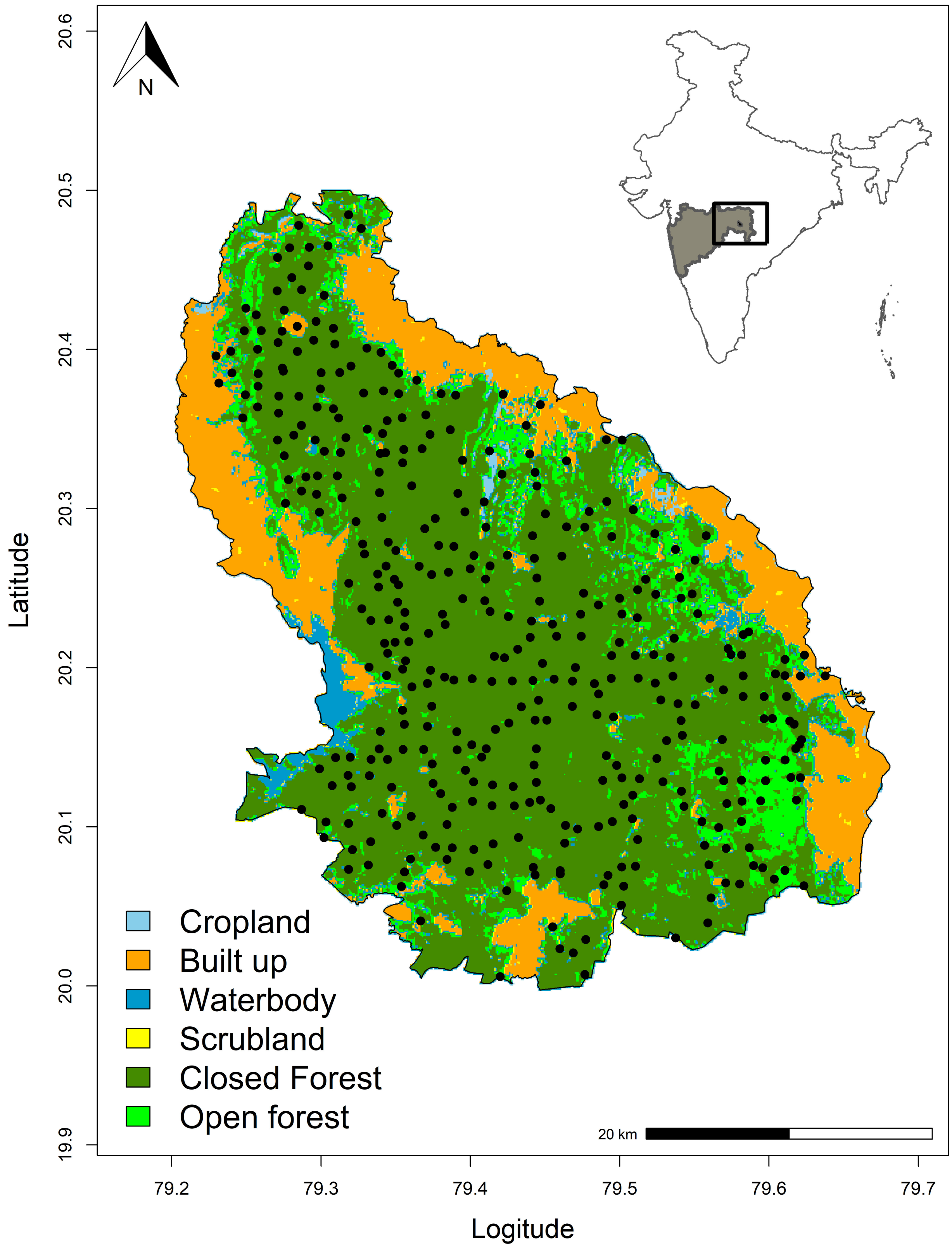
20.6
20.5
20.4
20.3
20.2
20.1
20.0
19.9
Latitude
N
Cropland
Built up
Waterbody
Scrubland
Closed Forest
Open forest
20 km
79.2
79.3
79.4
79.5
79.6
79.7
Logitude

Fig 1. Study area showing camera trap locations in Tadoba-Andhari Tiger Reserve (TATR). Inset: Location of the study area in India. The map shows closed forest areas (in dark green), open forest (in light green), scrublands (in yellow), waterbodies (in blue) and human habitation (in orange) within the boundary of Tadoba-Andhari Tiger Reserve. Land-use data were obtained from Copernicus Global Land Service (https://land.copernicus.eu/) under CC 4.0 License.

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whereas an informative prior was used for the home-range-scale parameter σ. To incorporate this, we used an informative prior of gamma (40,35) for jungle cat and gamma (50,60) for rusty-spotted cat respectively. We also compared the density estimates using the informative priors with estimates of uninformative priors (e.g. U (0,50) prior for sigma) to understand the role of priors. We used 50,000 MCMC iterations (with the initial burning of 5,000) and the thinning rate of the chains was fixed as 1. As we estimated the parameters following iterations in the Bayesian framework, it was necessary to check the convergence of chains. Geweke diagnostic scores [30] were used to test the convergence of the MCMC chains in the "coda" package [31] in R 3.4 [32]. Geweke score of less than 1.6 indicated convergence of the estimated parameters in the chain.

Habitat use

We investigated the habitat associations of the small cats using generalized linear models (GLM). We enumerated total counts at each site considering a 24-hour sampling interval as one sampling occasion and used this as a response variable. Data were pooled from all the four blocks for the analysis. Values of remotely sensed habitat variables; land use/landcover, evapotranspiration, forest-cover, elevation, normalised difference vegetation index (NDVI), distance from village, distance from waterbody were extracted from camera-trap locations with a 100-meter buffer and used as covariates for modelling the species count across sites. We restricted the buffer to 100 meters as we were interested in understanding the habitat preferences of species at a fine scale. Land use/landcover and forest cover were categorical variables while the remaining covariates were continuous variables (S1 Table). Forest cover was classified into very dense (cover >70%), moderately dense (cover 40–70%), open forest (cover 10–40%), scrub (cover <10%) and non-forest (www.fsi.nic.in). Similarly, land use/landcover was classified as human-habitation, agriculture, open forest, deciduous forest and waterbody (bhuvan.nrsc.gov.in). The main purpose of using these habitat variables was to model the species occurrence with habitat heterogeneity. Moreover, these variables were found to be effective predictors of small carnivore distribution from previous studies in India [18]. Evapotranspiration was used as a surrogate for aridity while forest cover and NDVI represented the canopy and vegetation cover of the habitat. Distance from village was used as a surrogate for human use.

We standardized all covariates using z-transformation and tested them for correlation. Significantly correlated variables ($|r| < 0.4$) were dropped for further analysis. Generalized linear models were fitted with a "poisson" link function and model fitting was carried out in R 3.4 [32]. The best-fit model was chosen based on the difference between AIC of two models, ($\Delta AIC > 2$). We used model averaging for predictor variable coefficient estimate when multiple models were satisfying the ΔAIC criterion. Model averaging was carried out in "MuMIn" package in R 3.4 [32].

Results

The total survey effort comprised of 10332 trap nights from 397 camera-traps. We photographed 23 mammals during the camera-trap survey including 171 photo-captures of jungle cat and 66 photo-captures of rusty-spotted cat. Of the 397 camera-trap locations, jungle cat

Table 1. Parameter estimates of population size N, density and parameters of detection function (detection probability g_0, spatial-scale parameter σ) from the spatial presence/absence model are given in the table.

	No. of independent captures	Density per 100 sq.km (95% CI)	Posterior N (95% CI)	Sigma estimate (95% CI)	g_0 estimate (95% CI)
Jungle cat	171	4.01 (2.65–6.12)	72 (48–111)	1.069(0.858–1.294)	0.067 (0.046–0.092)
Rusty-spotted cat	66	6.67 (4.07–10.74)	100 (61–161)	0.539(0.412–0.703)	0.058 (0.030–0.099)

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was detected at 91 locations and rusty-spotted cat was detected at 38 locations respectively. Both the species were detected together at 9 locations.

The model estimated densities of 4.01 (95% CI 2.65–6.12) individuals/100 km^2 for jungle cat and 6.67 (95% CI 4.07–10.74) individuals/100 km^2 for rusty-spotted cat (Table 1). Extrapolating estimated density for the survey area, we estimated 72 (95% CI 48–111) jungle cat and 100 (95% CI 61–161) rusty-spotted cats in the tiger reserve. The baseline encounter rate (g_0) and home-range scale parameter were greater for jungle cat than rusty-spotted cat (Table 1, Fig 2). There was no significant difference in density estimates with increase in buffer sizes (σ,

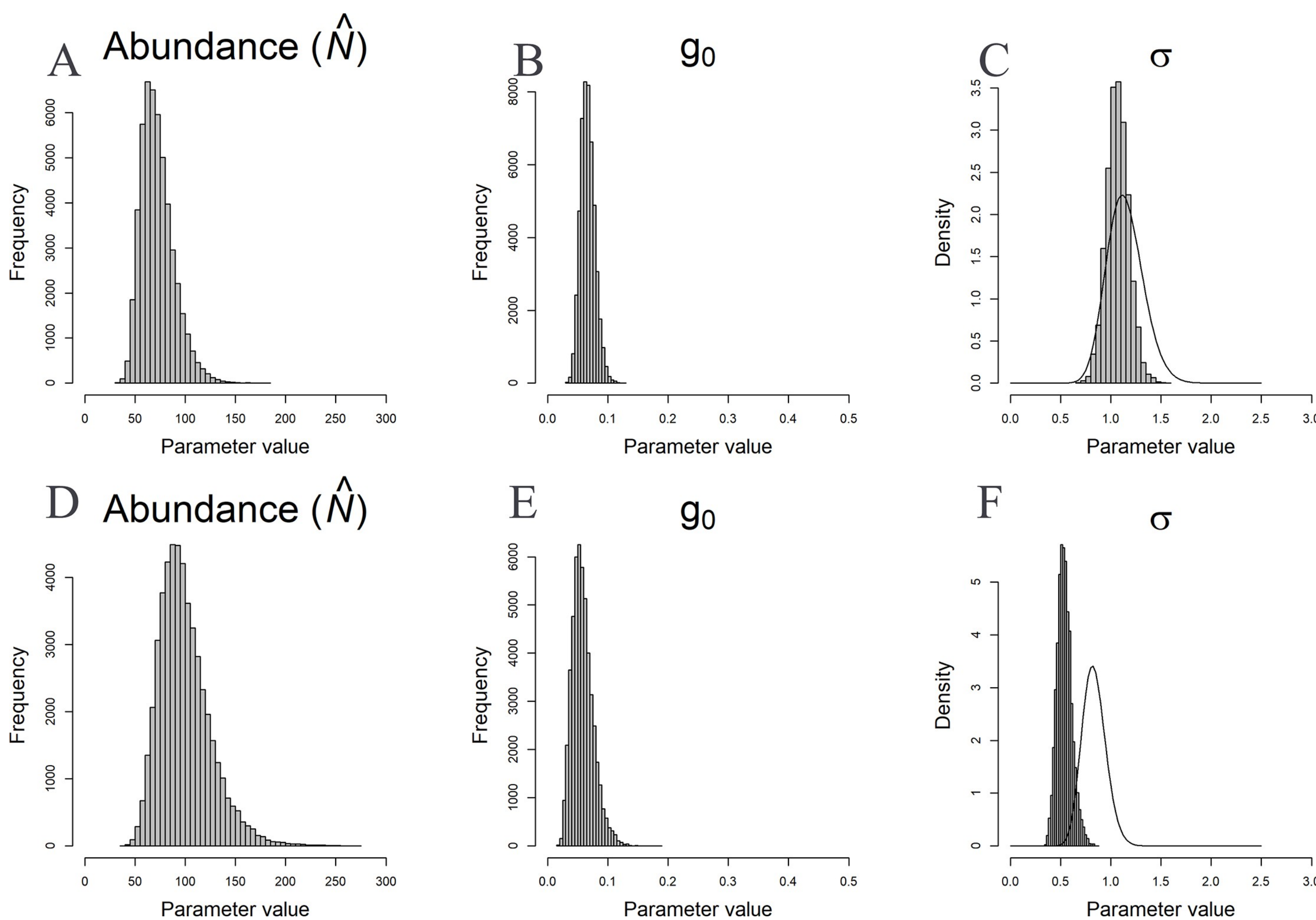

Fig 2. Posterior distributions of Jungle cat abundance (A) and Rusty-spotted cat abundance (D) ($N^{\wedge}$), and parameters of detection function (detection probability g_0 (B & E), spatial-scale parameter σ (C & F)) using the spatial presence-absence model applied to jungle cat and rusty-spotted cat detections in camera traps from the Tadoba-Andhari Tiger Reserve. The solid line overlaid on the posterior distribution of σ is the prior gamma distribution used for the species. These estimates were derived following a Gamma (50,60) and (40,35) prior on σ for Rusty-spotted cat and Jungle cat respectively and uniform (-10,10) prior on g_0.

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2σ and 5σ) for both the species (t(rusty) = 25.03, $p<0.001$ and t(jungle) = 7.84, $p<0.001$). Population estimates using uninformative priors overlapped with the informative priors for both the species but the coefficient of variation (CV) was much smaller with informative prior in case of Jungle cat. Informative priors had a CV of 22.4% whereas uninformative priors had a CV of 70.5% and for rusty-spotted cat CV was 25.8% for informative prior and 25.3% for uninformative prior. The density estimate for rusty-spotted cat was higher with the uninformative prior while the density estimate of jungle cat was similar.

The Geweke diagnostic scores reflected convergence of all parameters of SPA models for both the species as the z statistic values was <1.6. Also, we tested the geweke scores of each parameter against z = 1.6 and reported the p-value, which was found to be significantly different for all the parameters. The geweke scores with the p values in the parenthesis of the jungle cat SPA models are given by, sigma = 1.17 (0.86), g_0 = -0.94 (0.824), psi = -1.198 (0.09), N = -1.26 (0.073) while the geweke scores of the rusty-spotted cat SPA models are given by, sigma = -1.02 (0.16), g_0 = 1.55 (0.94), psi = -0.77 (0.22), N = -0.72 (0.24).

Habitat use patterns using the generalized linear modelling reflected differential habitat use by both species. Coefficients of the predictor variables were generated using model-averaged equations satisfying the criteria ΔAIC <2. The occurrence of rusty-spotted cat was best predicted by forest cover (0.72 ± (SE) 0.24), evapotranspiration (0.71 ± (SE) 0.18) and distance from water (-0.53 ± (SE) 0.16) (Table 2, Table 3, Fig 3). Jungle cat occurrence was associated with NDVI (2.33 ± (SE) 1.12), evapotranspiration (-0.47 ± (SE) 0.09) and distance to water (0.27 ± (SE) 0.09) (Table 2, Table 4, Fig 4). The coefficient of the significant variables reflected the varied habitat preference for the species. Jungle cat preferred xeric habitats with negative association with forest cover while rusty-spotted cat was positively associated with dense forest cover and more humid areas.

Discussion

This study attempted to estimate the population of two sympatric and individually unidentifiable small cat species and understand their habitat preference. We report the first ever population density estimates of jungle cat and rusty-spotted cat that ranges from 3–7 individuals per 100 km^2. The estimates, based on the largest camera trapping dataset available for these small cat species, are comparable to density estimates of other small cats [33–36]. The estimated

Table 2. GLM coefficient with associated standard error values (in parenthesis) depicting habitat associations of the jungle cat and rusty-spotted cat. The coefficients and the associated standard errors were derived by averaging suitable models satisfying the ΔAIC <2 criteria.

Model covariate	Jungle cat	Rusty-spotted cat
Forest cover	-0.13 (0.067) $^{+}$	0.73 (0.24) **
Normalised difference vegetation index	2.34 (1.12) *	2.17 (1.80)
Evapotranspiration	-0.47 (0.09) ***	0.71 (0.18) ***
Distance from water	-0.27 (0.09) **	-0.53 (0.16) **
Landuse/ landcover	0.002 (0.034)	0.13 (0.09)
Distance from villages	-0.002 (0.047)	0.03 (0.13)
Elevation	0.06 (0.07)	-0.23 (0.22)

(Significance codes

*** < 0.001

** < 0.01

* < 0.05

$^{+}$ < 0.1)

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Table 3. Result of generalized linear models used to evaluate the habitat use patterns of rusty-potted cat based on remotely sensed habitat covariates around camera trap locations. elev- elevation; aet- actual evapotranspiration; lulc—Landuse/landcover, fcm- forest cover; ndvi–Normalised Difference Vegetation Index; waterdist- distance from water; villdist–distance from villages.

Covariates	Degrees of freedom	AICc	ΔAIC	weight
fcm+lulc+ndvi+aet+waterdist	6	395.34	0.00	0.25
fcm+lulc+elev+aet+waterdist	6	395.63	0.29	0.22
fcm+lulc+ndvi+elev+aet+waterdist	7	396.21	0.87	0.16
fcm+ndvi+elev+aet+waterdist	6	396.57	1.23	0.14
fcm+lulc+villdist+aet+waterdist	6	396.68	1.34	0.13
fcm+lulc+ndvi+villdist+aet+waterdist	7	397.57	2.03	0.09

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densities of these elusive cats can significantly contribute to conservation strategies. We also observed fine-scale spatial segregation supporting our hypothesis, facilitating co-occurrence between these small cat species.

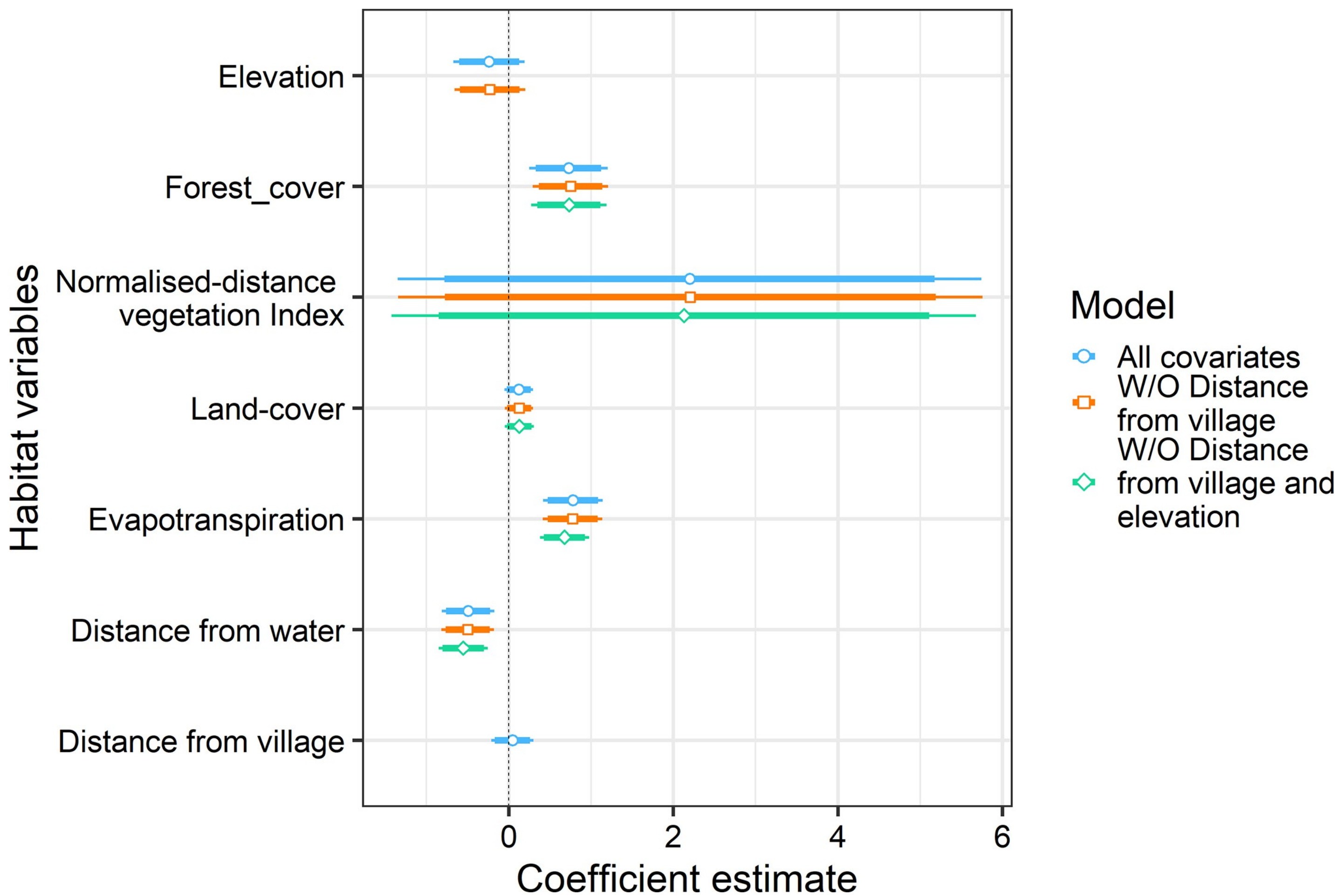

Fig 3. Scaled coefficients with standard deviation of habitat covariates from generalized linear model estimates for rusty-spotted cat. Broad horizontal lines depict the 95% confidence interval of each variable, while the narrow lines represent 90% confidence interval. Non-significant habitat variables, dropped from subsequent equations are represented by absence of the coefficient and standard deviation line.

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Table 4. Result of generalized linear models used to evaluate the habitat use pattern of jungle cat based on remotely sensed habitat covariates around camera trap locations. elev- elevation; aet- actual evapotranspiration; lulc-Landuse/landcover, fcm- forest cover; ndvi–Normalised Difference Vegetation Index; waterdist- distance from water; villdist–distance from villages.

Covariates	Degrees of freedom	AICc	ΔAIC	weight
fcm+elev+ndvi+aet+waterdist	6	395.34	0.00	0.38
fcm+villdist+ndvi+aet+waterdist	6	395.63	1.51	0.18
fcm+lulc+ndvi+aet+waterdist	6	396.21	1.55	0.17
fcm+lulc+ndvi+elev+aet+waterdist	7	396.57	2.04	0.14
fcm+villdist+ndvi+elev+aet+waterdist	7	396.68	2.06	0.13

https://doi.org/10.1371/journal.pone.0233569.t004

Population density estimates

There are no previous records of population density estimates for both of the studied species. But estimates of this study are comparable to population density of other individually identifiable small cats of comparable body sizes, the leopard cat (*Prionailurus bengalnensis*) [33, 34] and the marbled cat (*Pardofelis marmorata*) [35,36]. Contrary to the non-spatial models, spatial models provide site-specific detection probability and a scale of animal space use (sigma).

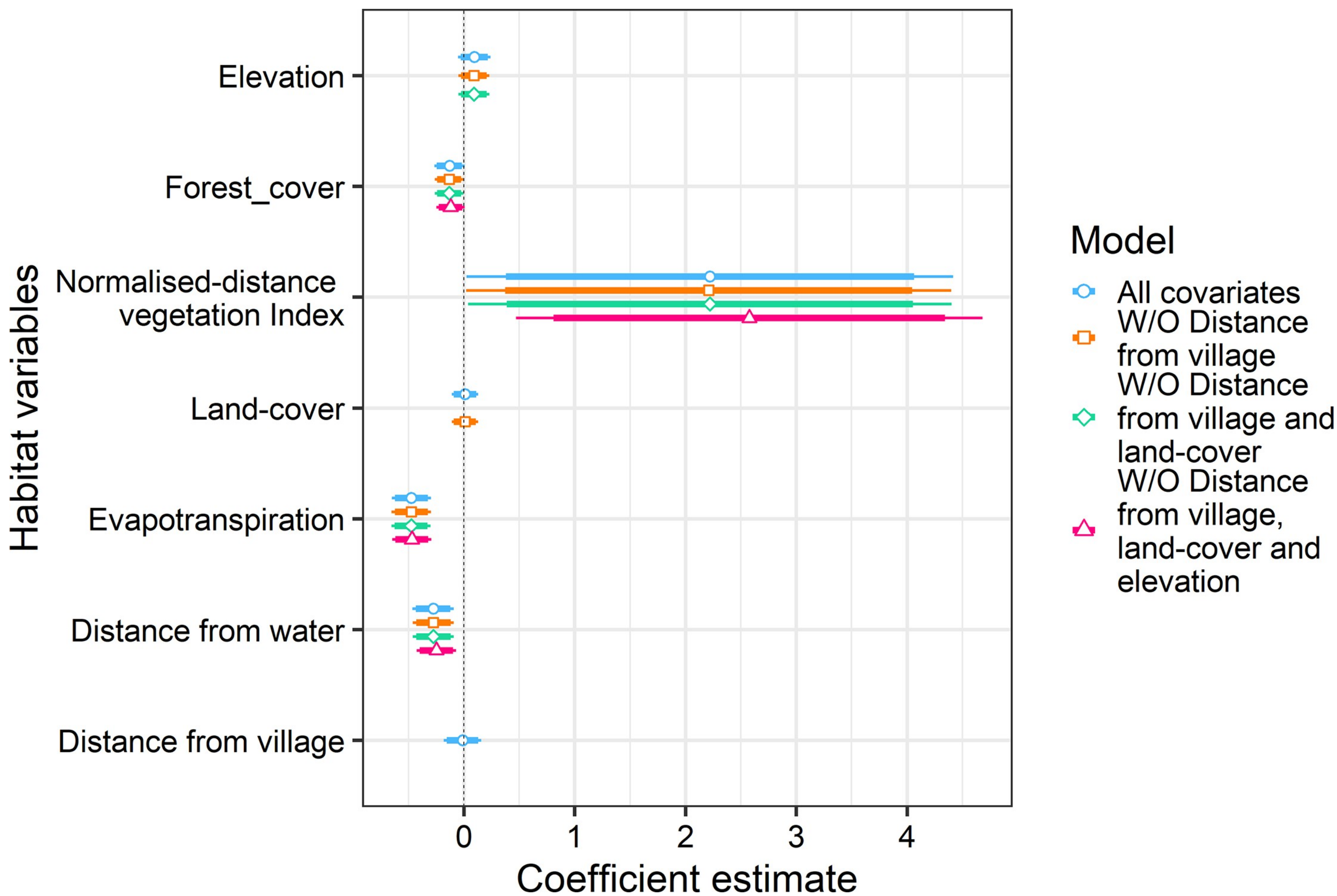

Fig 4. Scaled coefficients with standard deviation of habitat covariates from generalized linear model estimates for jungle cat. Broad horizontal lines depict 95% confidence intervals of each variable, while the narrow lines represent 90%. Non-significant habitat variables, dropped from subsequent equations are represented by the absence of the coefficient and standard deviation line.

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Estimates of the movement parameter (sigma) of this study are comparable with that of leopard cat [34] and marbled cat [35] but smaller than the sigma estimates of leopard cat [33] or marbled cat [36]. Difference in the analytical procedure (spatial presence-absence vs spatial capture-recapture) prevented direct comparison of the parameter estimates. In our study, the number of captures of jungle cat was greater but their density estimate was lower than that of rusty-spotted cat. This was attributed to the assumption of a larger home-range of jungle cat compared to rusty-spotted cat. Earlier studies found the density of small cats reflected top-down competition from other large predators present as has been evidenced in a study on leopard cats from the Western Ghats in India [34]. Moreover, when the carnivore community remained similar, species density was found to be associated with other biotic factors. Studies on neotropical small cats (ocelot) revealed dependence on primary productivity [37], density estimates ranging from 2.3 per 100 km^2 (Chiquibul, Belize) to 94.7 per 100 km^2 (Peruvian Amazon) [38, 39]. Future studies should consider these factors along with the presence of other carnivores as covariates to model density of these small cat species.

Habitat use patterns

We found evidence supporting our hypothesis that there exists fine-scale habitat segregation between the two sympatric cat species. Although the species have a majorly overlapping distribution range in the Indian subcontinent, at a fine-scale of camera trap sampling sites they hardly cooccur. The factors that significantly affected rusty-spotted cat occurrence were those associated with dense forest while jungle cat occurrence was associated with open forests and scrublands. Our results reported a similar pattern as reported by Kalle et al. [18] from the Western Ghats where the presence of jungle cat and rusty-spotted cat was positively related to open forest and deciduous forest respectively. The affinity of rusty-spotted cat for deciduous forest supports the semi-arboreal adaptation of this species [18] which likely facilitates avoiding competition with other carnivores within similar habitats. Similar studies on sympatric meso-predators from other landscapes [40] found negligible spatial avoidance between species but adaptations of segregation in their activity patterns. The fine-scale segregation in habitat niches might have aided in the evolution of sympatry between these species with overlapping distribution ranges.

Caveats and limitations

Although the population estimation and habitat use pattern in our study where based on a robust analytical framework, there are certain inevitable limitations similar to other field studies. We could not employ a finer grid size for camera-trap sampling due to logistical constraints. Prior distributions for the spatial count model were selected based on the data available for leopard cat [23] and allometric equations of daily-movement, home-range and body mass. Radio-telemetry studies can aid in providing refined estimates for the prior distributions and robust estimates using spatial capture-recapture [7] or spatial mark-resight [41] framework. Further studies can evaluate the efficacy of the spatial presence-absence model by comparing estimates from other frameworks. Alongside remotely sensed environmental variables, micro-habitat variables collected from sampling sites can be collated to understand multi-scale habitat preferences. The presence of other species as a predictor variable can also reveal the effect of species interaction in shaping habitat use patterns. The study was restricted to a tiger reserve whereas both the study species are also known to occur outside protected areas. It would be useful for future studies to look at density estimates across various gradients of natural and anthropogenic disturbances and varied mammal community as well.

Conclusions

Lack of proper baseline data and ordinated conservation policies have led to local extinction of species from varied habitats globally [42, 43]. Reliable estimates of species abundance and knowledge of their habitat preference are of fundamental importance as they facilitate management goals and policy decisions for successful conservation of species. The understanding of the unique ecological role of small carnivores [44] can be adequately supplemented by baseline data as provided by our study. In addition to providing the estimates of the population density of two sympatric small cats that cannot be individually identified, our study demonstrates the utility of spatial count models for the population estimation of unidentifiable species. The study highlights the importance of different habitat types explaining fine-scale habitat segregation between co-occurring species. With carefully designed field surveys and maintaining proper caution in the generalisation of results, our model may be extended and applied to other species which lack individually identifiable morphological features like pelage patterns (such as civets, bears, and foxes) and are cryptic and elusive besides being of high conservation priority. Trends of population estimates and habitat use from this study can contribute to the assessment of conservation status and devising mitigation principles. Long term studies assessing other life-history parameters of small cats are imperative in our understanding of their ecological role in carnivore communities thriving across varied landscapes.

Supporting information

S1 Table. Details of the remotely sensed variables used as covariate in the occupancy framework to evaluate the habitat use of small cats in Tadoba-Andhari Tiger Reserve.
(DOCX)

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Population Estimate, Habitat-Use and Activity Patterns of the Honey Badger in a Dry-Deciduous Forest of Central India

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Studies on carnivores are skewed toward larger species in India, limiting ecological information of the smaller ones. Basic ecological understanding like population density, distribution, habitat-use patterns of small carnivores is lacking. This inadequate knowledge has led to disagreement between conservation approaches in different landscapes. Honey badgers (*Mellivora capensis)* are cryptic carnivores distributed across large areas of Africa and Asia; however, fundamental ecological knowledge is scarce. The species is thought to exist at low population densities throughout its range. We used a large camera trap dataset from a tiger reserve in Maharashtra State, India to understand the population density, habitat preference, and diel activity pattern of the species. We applied an extension of the spatial count model for the estimation of population. Habitat preference analyses were carried out using generalized linear models and activity patterns were analyzed using kernel-density functions. The population density was estimated as 14.09 (95% CI 10–22.25) individuals per 100 km^2. Habitat use revealed a positive association with forest cover and negative association with elevation. This may expose the species to other large carnivores in the habitat but honey badger activity pattern peaked at midnight retaining minimum temporal overlap with other large carnivores (e.g., tiger *Panthera tigris*, leopard *Panthera pardus*, and dhole *Cuon alpinus*) and moderate overlap with small carnivores (e.g., jungle cat *Felis chaus*, rusty-spotted cat *Prionailurus rubiginosus*). These behaviors, in turn, may facilitate the coexistence of species at such high density even with high carnivore density. We hope the findings of this study will fill the existing knowledge gap of this species and aid in guiding the conservation of the species in other landscapes and reserves.

Keywords: camera-trapping, competitive exclusion, dial activity pattern, *Melivora capensis*, small carnivores, spatial capture-recapture models, Tadoba-Andhari Tiger Reserve

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INTRODUCTION

Mammalian carnivores are one of the most threatened among all biodiversity, experienced a major population decline and suffered the greatest contraction of their range (Ripple et al., 2014; Di Minin et al., 2016). Moreover, their low density, slow population growth rate, large area requirement has made them susceptible to habitat loss and fragmentation (Cardillo et al., 2004). Small carnivores though outnumber their larger cousins, studies on them are scarce and limited to few families. Out of 150 odd small carnivores, most of the populations (39%) are decreasing or unknown (37%) (http://www.iucn-scsg.org/). They are also known to occur across different habitat types-like forest, savanna, grassland, or human-modified landscapes and in different carnivore communities. As conservation efforts are mostly focused on charismatic large carnivores, it may be detrimental to meso or small carnivores. Hence, understanding species interaction and habitat preference is fundamental to direct conservation efforts to such small carnivores.

Honey badger *Mellivora capensis* is one of the largest (6–14 kg) mustelids and is distributed over Africa, Arabian Peninsula, West Asia, and the Indian subcontinent (Do Linh San et al., 2016). Owing to the wide distribution range, the species has been categorized as Least Concern in the International Union for Conservation of Nature red list of Threatened species (Do Linh San et al., 2016). However, despite its widespread distribution range, limited knowledge exists about its ecology except in southern Africa (Begg, 2001, Begg et al., 2003, Begg et al., 2016, Ramesh et al., 2017, Kheswa et al., 2018). In India, the species is relatively rare and is categorized as Scheduled-I in the Wildlife (Protection) Act, 1972 providing it with the highest level of protection. The species is known as a solitary forager and primarily prefers a carnivorous diet (Begg, 2001). Their fossorial behavior and nocturnal activity pattern (Gubbi et al., 2014), make them highly elusive in nature and difficult to encounter for a population estimation study. Owing to these limitations, so far there is only one study estimating population density in India (Gupta et al., 2012). In the Indian subcontinent, the species has been reported from diverse habitats like scrub and dry deciduous forest (Gubbi et al., 2014), and dry grassland (Mathur et al., 2011) and it shares its range with other carnivores of different body sizes and ecology (Do Linh San et al., 2016; Ramesh et al., 2017). However, niche segregation and interspecies' interactions are poorly understood. Radio-telemetry studies from Africa found strong resource-driven seasonal shifts in its activity pattern from diurnal to nocturnal (Begg et al., 2016). Similar ecological understanding is majorly lacking for populations from this sub-continent. Hence, there is a need for in-depth ecological insights from the species.

Reliable population estimates are an indispensable tool for species conservation and management policies (Williams et al., 2002). The focal species of this study, the honey badger, has no unique pattern, hence individual identification is not feasible. This poses a major challenge for robust population estimation of this species. Additionally, the species, being a carnivore, is at the top of the food pyramid and exists naturally at low densities. Hence, to overcome the challenges of low encounter and unidentifiability, we conducted our sampling with the help of camera traps. Camera traps have been demonstrated as one of the most efficient and non-invasive tools which are currently being used globally to document and study elusive wildlife species (Burton et al., 2015).

We used large scale camera trap data to understand population density, habitat use, and daily activity patterns of honey badger from Tadoba-Andheri Tiger Reserve in central India to develop a better understanding of its ecology. We analyzed habitat use pattern using generalized linear models. Along with that, we used a recently developed method, spatial presence-absence (SPA) approach (Ramsey et al., 2015) to estimate the population of this species. The method (Ramsey et al., 2015) have been reported to be effective for population estimation of individually unidentifiable species with higher accuracy (Chatterjee et al., 2020). We also investigated activity patterns of the honey badger and estimated temporal overlaps with other sympatric carnivores. As the species is known to occur in different habitats with varied activity pattern (Do Linh San et al., 2016), it is difficult to hypothesize about the habitat preference and temporal activity of the species. However, we expected the species to avoid competition (Schuette et al., 2013) with other large carnivores (e.g., tiger, *Panthera tigris*, leopard *Panthera pardus*, and dhole *Cuon alpinus*) by exhibiting minimal spatial and temporal overlap. Informed by this study, we aimed to generate critical information on the species ecology and fill the existing knowledge gap. We believe this information can assist in characterizing management policies and identify challenges for conservation of honey badger in the Indian subcontinent and be useful in understanding the occurrence pattern throughout the distribution range of the species.

MATERIALS AND METHODS

Study Area

We conducted the study in Tadoba-Andhari Tiger Reserve (20°04′−28°025′N, 79°13′−79°33′E) located in Maharashtra State in Central India. The reserve, a part of the Deccan plateau is mostly undulating and hilly in the north and almost plain in the southern part (Paliwal and Mathur, 2014). The reserve spreads across an area of 1,700 km^2. The climate is characterized by a hot and prolonged summer while winter is short and mild (Paliwal and Mathur, 2014). Annual average precipitation is 1,200 mm, received mainly from southwestern monsoons between June and September (Khawarey and Karnat, 1997).

The vegetation of the reserve has been classified as Southern Tropical Dry deciduous forest (Champion and Seth, 1968) dominated by bamboo (*Dendrocalamus strictus*) and teak (*Tectona grandis*). Camera-trapping exercises revealed the presence of more than 20 mammal species from the reserve (Habib et al., 2015). This includes four species of felids, tiger *Panthera tigris*, leopard *Panthera pardus*, jungle cat *Felis chaus*, rusty-spotted cat *Prionailurus rubiginosus*, one species of ursids, sloth bear *Melursus ursinus,* and two species of canids (dhole *Cuon alpinus*, jackal *Canis aureus*), one species of Mustelidae, the honey badger *Mellivora capensis*.

Field Methods

We conducted camera-trap surveys in the dry season from February 2016 and June 2016 to control the seasonal variability. We divided the whole study area into 2 km^2 grids and deployed a pair of automated motion-triggered digital camera-traps at 397 locations across the core and buffer area of the tiger reserve (**Figure 1**). Sampling was carried out in the reserve in four different blocks with an average of 100 locations per block. Camera-traps were placed on both side of roads,

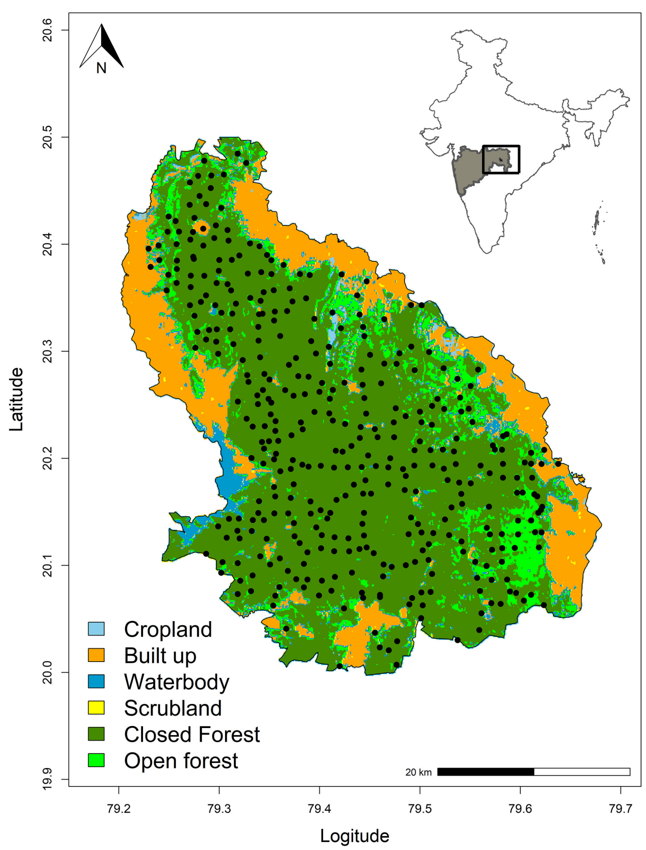

FIGURE 1 | Study area showing camera trap locations in Tadoba-Andhari Tiger Reserve (TATR). Inset: Location of the study area in India. The map shows forested areas (in dark green) and villages (in yellow) within the boundary of TATR. Forest cover used in the map was obtained from Forest Survey of India (www.fsi.nic.in).

animal trails, fire-lines facing each other, placed around 30–40 cm above the ground. Camera-trap placement at the trails optimizes capture of large as well as small carnivores (Chen et al., 2009, Johnson et al., 2009). Each station consisted of a pair of Cuddeback C1 or Cuddeback ambush (www.cuddeback.com) digital camera-trap placed facing each other at every location to maximize capture probabilities of small carnivores. Camera trap stations were active for 26–30 days to ensure close population structure (Kendall, 1999). Camera trap stations were checked once in every 15 days. As the research work was carried out with non-invasive methods, no approval from animal care and handling was not required. Fieldwork was carried out under the permit number D-22(8)/WL/Research/CT-722/ (12-13)/2934/2013 issued by the principal chief conservator of forests (Wildlife) office of Maharashtra State, India.

Density Estimates

Individual honey badgers are not identifiable from camera-trap photographs and marking individuals was not feasible given the low detectability and elusive nature of the species. To overcome these shortcomings, we used SPA (Ramsey et al., 2015), an extension of the spatial count model of Chandler and Royle (2013). Spatial count models the latent encounters of spatially referenced individuals with sampling devices using data augmentation and the Markov Chain Monte Carlo (MCMC) sampling in a Bayesian framework (Ramsey et al., 2015). Thus, it models the range of individuals with respect to capture locations and estimate population using that prior information of home-range. SPA models are structurally similar to spatial capture-recapture (SCR) models (Efford, 2004). Similar to SCR models, SPA models estimate N (population size) along with g_0 (baseline encounter rate), and σ (scale/movement parameter related to home-range of the species). We assumed a half-normal detection function to model the probability of detection.

For each camera site, the detection or non-detection of the species was recorded for each 24 h sampling interval. The state-space (S) comprised of the sampled area and a buffer area surrounding that, large enough to include all individuals potentially exposed to sampling. To generate a buffer area in the state spaces in the SPA model, we estimated σ from a body-size and daily-movement distance equation (Garland, 1983). A vague uniform prior, U (−10,10), was placed on the logit of g_0, whereas an informative prior was used for the home-range-scale parameter σ. The estimates of the home-range size of the species were estimated as 1–10 km^2. To incorporate this, we used the equation given in Royle et al. (2011) and selected an informative prior of gamma (20,15) for sigma. We used 50,000 MCMC iterations (with the initial burning of 5,000) and the thinning rate of the chains was fixed as 1. Geweke diagnostic scores (Geweke, 1992) were used to test the convergence of the MCMC chains in the "coda" package (Plummer et al., 2006) in R 3.4 (R Development Core Team, 2017).

Habitat Use

We used generalized linear models with the Poisson link function to model honey badger habitat use with different environmental covariates and capture numbers of other carnivores at every camera trap site. We calculated total independent captures at every sampling site considering the 24-h sampling interval as one sampling occasion. We extracted values at each camera-trap sampling site from remotely sensed raster datasets using a buffer size of 50 m. Among the habitat covariates, land use/land cover and forest cover were categorical variables while the remaining covariates were continuous variables (**Supplementary Table 1**). Forest cover was classified into the following categories; very dense (cover >70%), moderately dense (cover 40–70%), open forest (cover 10–40%), scrub (cover <10%), and non-forest (www.fsi.nic.in). Similarly, land use/land cover was classified into built-up, agriculture, open forest, deciduous forest, and waterbody categories. These natural and anthropogenic covariates were incorporated to predict the species occurrence. Forest cover, NDVI provided the heterogeneity in vegetation and canopy while actual evapotranspiration was a surrogate for aridity and land-use-landcover was used to understand the heterogeneity in different habitats. Earlier studies of honey badger diet (Begg et al., 2016) from Kalahari found that the majority of the species diet consists of small mammals and

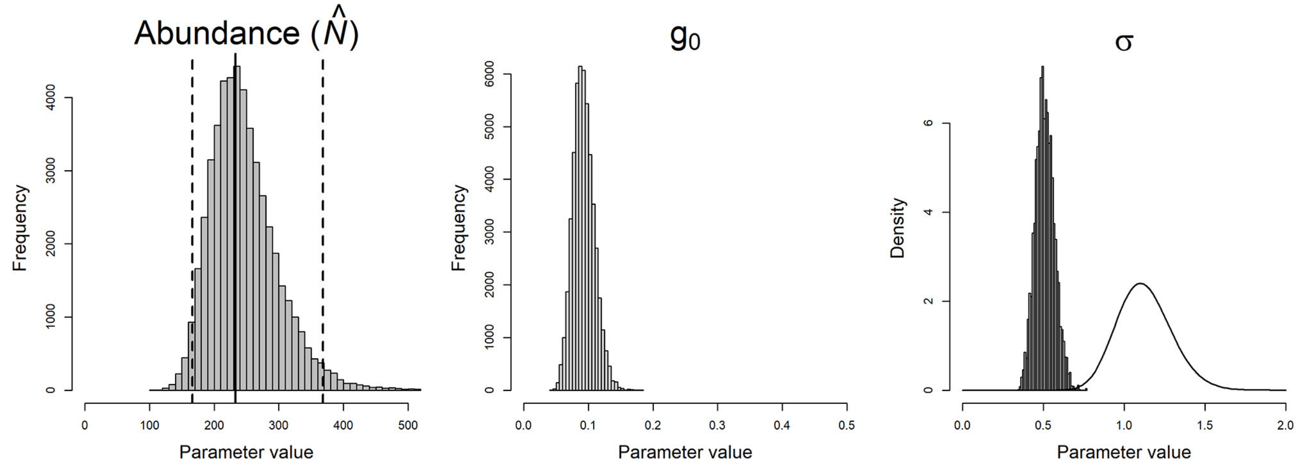

FIGURE 2 | Posterior distributions of Honey badger abundance ($\hat{N}$), and the parameters of the half-normal detection function (detection probability g_0, spatial-scale parameter σ) using the spatial presence-absence model applied to honey badger detections in cameras in the Tadoba-Andhari Tiger Reserve in central India, 2016. The solid line overlaid on the posterior distribution of σ is the prior gamma distribution (45,40) used for the species.

reptiles (<100 g). Although we did not particularly survey for those species, we believe heterogeneous habitat with good forest cover will harbor a higher density of prey species. We transformed all covariates using z-transformation. All the analyses were carried out in R 3.6 (R Core Team, 2017). We used AIC (ΔAIC >2) criterion to choose the best-fit model and applied model averaging in case multiple models were satisfying the AIC criterion. Model averaging was carried out in "MuMIn" package (Barton and Barton, 2015) in R.

Daily Activity Pattern

We used non-parametric kernel-density functions (Ridout and Linkie, 2009) to determine daily activity periods of honey badgers and other sympatric carnivores from the camera-trap photo-captures. Independent capture events were used to calculate the density function. We considered two capture events independent if the time between consecutive photographs of one species from the same camera traps had a time interval of 30 min (O'Brien et al., 2003). We used the "overlap" package (Meredith and Ridout, 2014) in R 3.4 (R Development Core Team, 2017) to understand the temporal activity overlap of a honey badger with other sympatric carnivores. This method generates a coefficient of overlap between 0 and 1, indicating the complete temporal separation between two species at 0 and complete overlap at 1 (Ridout and Linkie, 2009). We considered $\Delta > 0.8$ to be strong overlap and $0.5 < \Delta < 0.8$ as moderate overlap (Lynam et al., 2013). We used the Δ_4 estimator (Dhat4) for sample sizes >75 and the Δ_1 estimator (Dhat1) for smaller sample sizes, <less than 50, following the recommendations provided by Meredith and Ridout (2014). We calculated 10,000 bootstraps for each species analyzed and generated 95% confidence intervals (CIs) for temporal overlap estimates following the recommendations given by Meredith and Ridout (2014).

RESULTS

Total survey effort comprised of 9,828 trap nights from 397 camera-trap sites. We photographed 23 mammal species (**Supplementary Table 2**) during the camera-trap survey and obtained 206 captures of honey badgers in 102 camera traps. Out of the 206 captures, 22 captures had 2 individuals in 1 photograph and 1 instance had 3 individuals.

Density Estimates

We obtained density estimates of 14.1 (95% CI 10–22.25) individuals per 100 km^2 using the SPA model. The baseline encounter rate (g_{-0}) and home-range scale parameter (σ) was estimated to be 0.093 (95% CI 0.063–0.127) and 0.509 m (95% CI 0.401–0.631), respectively. Extrapolating the density estimates for the surveyed area, the population was estimated as 233 (95% CI 166–368) individuals (**Figure 2**).

The Geweke diagnostic scores indicated convergence of all parameters of SPA models for honey badger as the z statistic values was <1.6. The z statistic values for SPA model of honey badger are given by, sigma = 0.047(0.519), g0 = 0.741(0.771), psi = 0.577(0.718), N = 0.528(0.701) (**Supplementary Figure 3**).

Habitat Use

We found forest cover (coefficient 0.28 ± 0.091, p = 0.002) and NDVI (coefficient 3.14 ± 0.96, p = 0.001) to be the most significant factor explaining honey badger habitat use (**Tables 1**, **2**). Elevation was also related negatively and was a significant variable explaining habitat use (coefficient −0.19 ± 0.08, p = 0.02). Distance from water and distance from villages did not have a substantial effect on the habitat use of the species (**Table 2**, **Figure 3**). These associations of the species with these variables reflect affinity of the species toward dense forest areas of lower elevation.

We did not find any significant negative interaction based on the capture number of honey badger and other large and small carnivores (**Supplementary Figures 4–6**).

Diel Activity Patterns and Activity Overlap

We calculated temporal activity patterns and activity overlaps (**Figure 4**) for four species of felids (tiger, leopard, jungle cat, and rusty-spotted cat) ($n = 1696$), one canid (dhole) ($n = 70$), and one Mustelidae (honey badger) ($n = 206$). All the carnivores except dhole displayed very low activity between (0600 and 1,800 h) (**Figure 4**). Honey badgers showed an activity peak around midnight with <10% of the photographs between 0600 and 1,800 h. Honey badgers showed their highest daily activity overlap with other small carnivores, the jungle cat 0.75 (95% CI 0.67–0.83) and the rusty-spotted cat 0.73 (95% CI 0.61–0.85) (**Figure 4**). The lowest activity overlap of the honey badger was with dhole (0.35, 95% CI 0.26–0.45) as dholes exhibited a relatively diurnal activity peak. Tiger and leopard showed a bimodal activity pattern with two activity peaks around dawn (0500–0700 h) and dusk (1,700–2,000 h). However, the tiger showed a drop in the activity period between (0000–0030 h) but in the case of leopards, the period was less prominent. Except for honey badger, the other two small carnivores also engaged in this decline in activity period between (2,300–0300 h) (**Figure 4**). The results showed that honey badger minimizes encounters with other large carnivores temporally. This supported our hypothesis of niche segregation of honey badger with other large carnivores.

TABLE 1 | Result of generalized linear models used to evaluate the habitat use pattern of honey badger based on remotely sensed habitat covariates extracted around camera trap sites.

Covariates	Degrees of Freedom	AICc	ΔAIC	Weightage of model
fcm+lulc+ndvi+elev	5	884.52	0	0.43
fcm+lulc+ndvi+elev+waterdist	6	885.63	1.11	0.25
fcm+lulc+ndvi+elev+aet	6	886.43	1.91	0.17
fcm+lulc+ndvi+elev+villdist	6	886.58	2.06	0.15

elev, elevation; aet, actual evapotranspiration; lulc, Landuse/landcover; fcm, forest cover; ndvi, normalized difference vegetation Index; waterdist, distance from water; villdist, distance from villages.

TABLE 2 | GLM coefficient with associated standard error values and *p*-values depicting habitat associations of honey badger with different environmental covariates.

Habitat covariate	Coefficient	SD (coefficient)	*p*-Value
Intercept	−2.48	0.698	<0.001
Forest cover	0.28	0.09	0.002
Normalized difference vegetation index	3.14	0.96	0.001
Land-use/land cover	−0.10	0.04	0.016
Elevation	−0.19	0.083	0.02
Distance from villages	0.002	0.075	0.97
Evapotranspiration	0.033	0.085	0.69
Distance from waterbody	−0.08	0.082	0.33

The coefficients and the associated standard errors were derived by averaging of suitable models satisfying the ΔAIC <2 criteria.

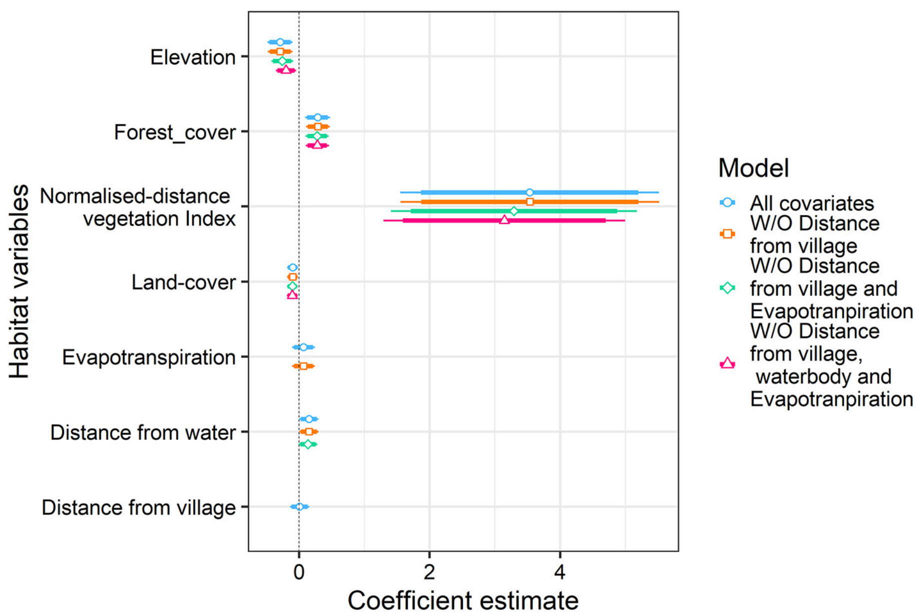

FIGURE 3 | Scaled estimates of environmental covariates used in glm model to evaluate habitat-use are given for honey badger. Broad lines depict the 95% confidence interval of each habitat covariate, while the narrow lines represent 90% confidence interval.

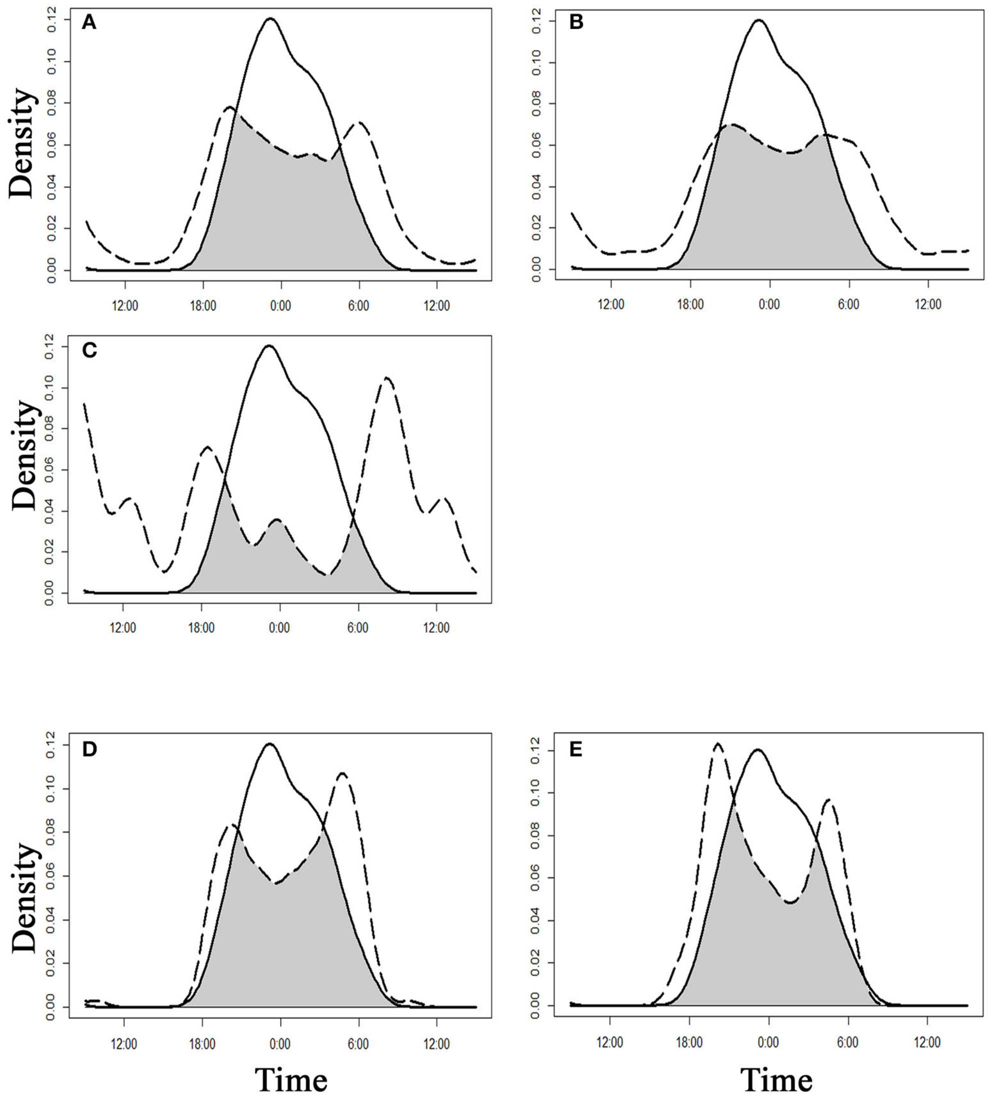

FIGURE 4 | Overlap of activity patterns between sympatric carnivores in Tadoba-Andhari Tiger Reserve (TATR), central India, calculated using a kernel-density function. The activity overlap between paired predators is depicted in gray. The solid line represents the activity pattern of honey badger and the dotted line represents the activity of other carnivores. **(A)** tiger and honey badger, **(B)** leopard and honey badger, **(C)** dhole and honey badger, **(D)** jungle cat and honey badger, **(E)** rusty-spotted cat and honey badger.

DISCUSSION

Our study provides the first density estimates of honey badger from the central Indian landscape. Habitat preference pattern of the species revealed an association with the forested landscape and lower elevation. Honey badger activity pattern showed maximum activity at midnight avoiding other large predators. Combination of all these behavioral traits may have resulted in a high density of honey badger from this protected area.

Density Estimates

The only density estimate of this species from the Indian subcontinent was available from Sariska Tiger Reserve (Gupta et al., 2012) based on repeated presence-absence model (Royle and Nichols, 2003). The study estimated summer and winter densities as 5.48 ± 4.33 individuals per 100 km^2 and 6.43 ± 2.79 individuals per 100 km^2, respectively (Gupta et al., 2012). Another study on small nocturnal carnivores from Serengeti National Park (Waser, 1980) estimated the density of honey badger around <10 individual per 100 km^2 from transect counts. Our density estimates of 14.1 ± 3.15 individuals per 100 km^2 was the highest among these studies. This could be attributed to the area devoid of any anthropogenic disturbance, higher productivity of the area compared with the other study areas and also temporal segregation of honey badger from the activity period of other large carnivores. Moreover, the study site is a tiger reserve and has less human presence which may lead to lower disease prevalence ensuring higher survival probability.

The sigma parameter from the SPA was estimated as 0.509 m (95% CI 0.401–0.631 m) which was much lower from the daily movement parameter estimated from Africa (Begg et al., 2016). The difference in analytical procedures (spatial presence-absence vs. radio-telemetry), however, hindered direct comparison of the parameter estimates. Still, our study used a robust methodology with a recently developed framework incorporating spatial information to estimate the population.

As honey badgers are not individually identifiable and are of small size, it is challenging to use their sex or age-class unambiguously as a covariate in the capture-recapture model. Moreover, the extended period of the dependence of cubs on mothers (Begg, 2001) made group identification more challenging from photo captures. Also, a precise estimate of the home-range of the species is required as a prior for the movement parameter in the SPA model (Ramsey et al., 2015). Parameters derived from further studies on movement pattern and home-range of the species may aid in more precision in the estimated parameters.

Habitat Use

In our study, we found that habitat use of honey badger was affected by the heterogeneity in vegetation structure. Also, the species preferred lower elevation indicating usage of the valley floors rather than cliffs and plateau-tops. This probably reflects the burrowing habit (Begg et al., 2003) of the species as lowland plain areas would be more suitable for burrows. Habitat use studies from Africa (Kheswa et al., 2018) found the distance from vegetation and dominance of plantation trees as the most significant indicator for the species occupancy. The current study also indicated the positive relationship between forest cover and species capture but the distance to water was not found to be significant in this study. This can be attributed to the differential availability of water in these two landscapes. Low-effect size between the capture numbers of the honey badger and other carnivore reflect that there is no spatial segregation in the area use. This finding was in contrast to the studies from Africa, where the species detection was negatively affected by the presence of leopard (Kheswa et al., 2018).

Activity Pattern

This is the first study of the activity pattern of the species from the Indian subcontinent. We found the activity pattern of Honey badger was significantly different from the other carnivores present in the reserve. This finding supported our hypothesis that the species would avoid other large carnivores to minimize agonistic interactions. The finding also corroborates the affinity of the species toward densely forested areas as that mechanism can reduce interference competition. Similar patterns have also been reported from Sariska tiger reserve (Nigam et al., 2018) where the activity peak was at 00:00 h (95% CI 22:56–01:03) and Cauvery Wildlife Sanctuary (Gubbi et al., 2014). This nocturnal activity pattern was different from studies in Africa (Begg et al., 2016). The pattern may arise because of the different carnivore community present in these areas. Studies from Africa (Ramesh et al., 2017; Allen et al., 2018) reported high temporal overlap between the honey badger, spotted hyaena and leopard whereas our study reported high temporal overlap of the honey badger with only small cat species and avoidance from large carnivores (tiger, leopard, and dhole). This can be attributed to the difference in the carnivore community in our study area which results in interspecific interaction among those species shaping the particular activity pattern. It also shows the different mechanism (e.g., spatial in Africa, temporal in this study) used by the species to avoid large carnivore. Further, studies are required to ascertain the principal driver behind the difference in activity between these two populations. Future studies should also cover multiple seasons to ascertain the alteration in the annual activity pattern of the species.

Caveats and Limitations

Similar to other field studies, our study had some limitations. We carried out the camera-trapping exercise in the dry season whereas camera-trapping in monsoon season would reveal any differences in the activity pattern as reported from studies from Africa. Also, camera traps were deployed on trails, and roads to maximize detection of other carnivores along with this species. As the focal species is a burrower, efforts aimed to maximize detection of the honey badger in camera traps would require a different strategy. Micro-scale habitat variables collected from the sampling sites can also be incorporated along with the remotely sensed environmental covariates in habitat preference analysis. Although, we used the recently developed model with proper assumptions but applying the model for multiple years along with simulation studies may reveal further insights of the species demography.

Conservation Implications

Although distributed widely, in-depth ecological understanding of honey badger is still lacking from most of its range. We hope our habitat-use analysis and population density estimates would add to the existing knowledge for better management and conservation. Habitat preference analysis using a regression framework has identified dense forest cover and well-vegetated areas as key factors of the species' niche. Hence, habitat fragmentation and land-use change would affect the species occupancy and survival adversely. Also, affinity toward pristine habitat makes the species more prone to interact with other large carnivores (e.g., tiger, dhole). This can lead to lower survival rate although we postulate that such interactions are minimized by honey badger by shifting to more nocturnal activity. Unlike the African population, the species in the Indian subcontinent is not known to have a negative interaction with the beekeepers and hardly any raiding of poultry farms was observed. The species' range is also majorly understudied in the Indian subcontinent and it has been hardly encountered beyond protected areas in India. Knowledge of the existence of the species outside protected area would reveal the tolerance level of the species in modified habitats and human-dominated landscapes. The difference in ecology between the African and Indian population needs to be further quantified based on the habitat, resource and species interaction. Nonetheless, there is almost no information available about food-habits of the species and that can provide a critical link between the spatio-temporal niche of the species. Future studies should focus on diet, movement, sociality and home-range use of the species to generate an in-depth understanding of the ecology of this population.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

This animal study was carried out under the permit number D-22(8)/WL/Research/CT-722/(12-13)/2934/2013 issued by the principal chief conservator of forests (Wildlife) office of Maharashtra state.

AUTHOR CONTRIBUTIONS

BH and NC conceived the study. NC collected all data, ran the analysis, and wrote the first draft of the manuscript. BH and PN supervised the project and edited the final versions of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.585256/full#supplementary-material

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