SPATIAL ABUNDANCE OF UNGULATES AND ROLE OF PREDATION ON CHITAL DEMOGRAPHY AND BEHAVIOUR IN CORBETT TIGER RESERVE, UTTARAKHAND

A THESIS

Submitted by

SUDIP BANERJEE

For the award of the Degree of

DOCTOR OF PHILOSOPHY
IN
WILDLIFE SCIENCE

Under the guidance of

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February – 2022

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I declare that the thesis entitled "**Spatial abundance of ungulates and role of predation on chital demography and behaviour in Corbett Tiger Reserve, Uttarakhand**" submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2012 to 2019** under the guidance and supervision of Dr. Y.V. Jhala and Prof. Q. Qureshi. The work 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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This is to certify that the thesis titled "Spatial abundance of ungulates and role of predation on chital demography and behaviour in Corbett Tiger Reserve, Uttarakhand" submitted for the award of the Doctor of Philosophy in Wildlife Science to Saurashtra University, Rajkot is a record of original and independent research work carried out by Mr. Sudip Banerjee under our guidance. No part of this thesis has been submitted to any other university or institution for the award of any degree and it fulfills all the requirements laid down by Saurashtra University.

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I also certify that the research work was appreciated by all who were present, and the comments made by the faculty and researchers have been appropriately included in the thesis.

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Dr. Y. V. JHALA Mr . Q. **QURESHI WILDLIFE INSTITUTE OF INDIA Dehradun**

, Uttarakhand, India Saurashtra University Rajkot – 360 005 February – 2022 CHAPTER I – INTRODUCTION AND LITERATURE REVIEW Ungulates are the hoofed mammals represented largely by one of its even-toed families, the cervidae or the deer. Deer exhibit a wide spectrum of body sizes and feeding habits, and inhabit a broad range of habitats, generally attaining a high abundance wherever they are found. However, pervasive report of their populations dwindling almost everywhere, especially in the tropics, owing to reasons such as habitat loss, illegal hunting and habitat degradation, excites serious concern and thereby necessitates long-term scientific monitoring of the populations, supported by a thorough understanding of their biology and ecology, which is largely lacking in India. In a country like India, where deer is legally protected from being hunted or harvested periodically as trophy or as meat, with the exception of a small number of tribal communities hunting them for food, monitoring and conservation of deer populations is aimed primarily towards the broad scale management of the ecosystem they inhabit, as, they play pivotal ecological roles such as indicator of the ecosystem's health by serving as a crucial link in the food web and through their

ACKNOWLEDGEMENT

My doctoral research under the guidance of Y.V. Jhala was certainly the most academically rewarding experience of my life, for which I am ever grateful to him. A trip down the memory lane, when I joined the Wildlife Institute of India (WII) in 2010 in a project under his supervision, fills me with delightful reminiscences of how he would always make field works and technical training sessions most exciting and informative by sharing his vast natural history knowledge of the Shivalik landscape and wildlife in general. Such an experience was overwhelming and had already instilled in me a strong interest of pursuing further research under his mentorship, and eventually succeeding in that seems like a dream coming true. The long association with him as his student not only provided me with academic enrichment, but helped grow mentally as well to deal with various difficulties in life. I feel extremely lucky to have him as a teacher from the very beginning. Effort of penning down his contribution in this manner will probably be never enough. I would like to thank you for bearing with all my drawbacks throughout these years.

I also feel very fortunate to have been mentored by Qamar Qureshi since joining WII, as project supervisor, and later as my PhD guide. His insights on varied ecological theories and different techniques was motivating and helped me in developing my research ideas. He was always there not only for academic help but for any personal assistance.

I am highly grateful to Dr. Sutirtha, for helping me in conceptualizing the research ideas with his significant insights and helping me later with analytical issues.

I am particularly thankful to Chris Carbone for providing me the opportunity of internship at ZSL and work closely with Marcus Rowcliffe who has always taken out his valuable time to teach me the theory and analysis of Random Encounter Model, which comprises a significant part of my research.

I sincerely thank Lex Hiby for extensively helping with his EXTRACT COMPARE software in identifying the chital individuals.

I thank V.P.Uniyal for dealing with my registration process and subsequent extension and urging me to finish the thesis within time.

I thank the field director, deputy director and divisional officers of Corbett Tiger Reserve for allowing the field work, and, specially G.S.Karki ji for his interest and support in the research.

This work would not have been possible without the help of my efficient field assistants. I whole heartedly thank Jagat, Sajid, Sonu, Sabbu and many others for creating a convivial atmosphere which made my field days most convenient and memorable.

Life at WII started by meeting few amazing people, with whom I certainly have become friends for life. I largely owe my PhD to these people, because their presence has always provided me with the much needed mental support. I will forever cherish numerous outing, eating, learning and few fighting memories with Manjari, who is one of the best individuals I have met in my life. Beyond just friendly associations, it was a significant learning process for me under her intellectual capacity and her critical outlook on several important socio-economic aspects. I feel lucky to have shared my field days in Corbett with Shikha, whose field work and planning skills motivated me a lot. It was since then we became very good friends. She not only helped me in shaping my research ideas, but has also assisted in dealing with personal difficulties for which I am forever grateful. From the time of joining WII till this date and always, I will feel lucky to have Anant, one of the most charming and kind person, as my friend. Occasional excursions near and far of Dehradun with Anant, accompanied by two other great friends Srinivas and Ashok would help release mental stress in the most exciting ways possible. My friend circle in WII is incomplete without Indranil, with whom I had many amusing memories during my stay in WII hostel as well as roommate outside hostel. His level-headed, caring nature had helped me numerous times to overcome both academic and personal stress. I am grateful to him for helping me with important geo-spatial modelling of my research. I thank Ayan and Bidyut, two of my very close friends, who has made my daily office time enjoyable. Moreover, research related discussions with Ayan were always very productive. Sharing a short span of field work with Bidyut was exciting.

I thank all the researchers, volunteers and interns of All India Tiger Project of 2010, 2014 and 2018 who had worked in Corbett Tiger Reserve and helped in data collection.

I thank Swaroop, Sagarika, Ritu, Surbhi, Ronit and Mouli for helping me in processing the large amount of camera trap data.

I thank Swati for being a very nice friend and always helping me with all the GIS related stuffs.

I thank Ujjwal and Neha for providing me analytical assistance at any time.

I thank my parents and my sister for being patient and always provide the love and support till the very end. This would not have been possible without them.

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SUMMARY

Monitoring and conservation of the ungulate population carry paramount importance in the conservation of the habitat as well as the carnivores of an area. Corbett Tiger Reserve (CTR), which harbors the single largest tiger population in the world, inevitably entails the need for such initiatives. In addition to the annual monitoring of CTR's prey population dynamics, gaining i resolution spatial distribution along with the population structure is critical for the long-term conservation of the ungulate population. My study attempts to address a few such issues and builds a foundation for further research and management.

To address the first objective which was to estimate the abundance of ungulates in different habitats of CTR, I have used line transect-based distance sampling approach to estimate the density of four major ungulate species (chital, sambar deer, barking deer, and wild pig) of CTR in ~520 sq. km of the Corbett National Park (CNP) region. Density was estimated using 156 spatial transects replicated 1 to 4 times over four sampling years. Both year-wise and pooled (weighted average of four years) density estimates were highest for chital followed by sambar. Barking deer had the lowest density. Chital density has remained stable over the years. Post-stratifying the densities of the four ungulates by three major habitat types of CNP (grassland, sal-dominated, and mixed deciduous) exhibited the highest density of chital in the grassland and lowest in the sal-dominated forest. Sambar density on the other hand was highest in the mixed deciduous and lowest in the grassland. Barking deer also exhibited a similar trend of habitat-wise density.

Additionally, I used the density surface modelling approach to model the line transect-based spatial observations with remotely sensed ecologically significant covariates in order to obtain a fine-resolution understanding of dispersion and the relationship of the ungulates with different significant environmental correlates in the study area. Chital abundance was highest (approx. 60771) in CNP. Chital abundance decreased with higher Normalized Differential Vegetation Index (NDVI) and Digital Elevation Model (DEM) values. However, both sambar (abundance ~ 6797) and barking deer (abundance ~ 4730) abundance increased with an increase in NDVI value

showing a preference for dense forest type. The lower number of wild pig observations on transects rendered the modelling insignificant for the species.

A significant part of my thesis was focused on the objective of evaluating the precision and cost-effectiveness of three different density estimation techniques. The diverse ungulate assemblage and complex terrain of CNP provided an excellent environment to conduct this experiment. The evaluation was done in two parts, 1) a cost-effective comparison of the line transect-based distance sampling, and the relatively recent camera trap-based Random Encounter Model (REM) on four ungulate species, the chital, sambar deer, barking deer, and wild pig in a 100 sq. km area of CNP and, 2) using chital as an individually identifiable study subject, I assessed the efficacy between capture-mark-recapture (CMR) technique, REM and line transect based distance sampling. The first evaluation yielded similar density estimates of chital, barking deer, and wild pig by both methods, while REM estimated a significantly lower density of sambar than distance sampling. Distance sampling produced more precise estimates than REM. REM turned out to be both economically costly (initially) and required more data processing time than distance sampling. However, REM's non-invasiveness and easy implementation gave it a sampling advantage over distance sampling in an area like Corbett Tiger Reserve. The second evaluation of techniques was done in four sampling blocks of varied sizes. All three techniques produced comparable chital density estimates in three blocks, except for one where REM produced a significantly lower chital density than CMR and distance sampling. However, the average density estimate of all four blocks was comparable across three techniques. CMR produced the most precise density estimate while REM yielded the least precise estimate. Such comparison of techniques will prove valuable for both managers and researchers in formulating future studies based on the trade-off between available logistics and statistical rigour.

In addition to density and spatial distribution of ungulate abundance, my research also reports a few important population demographic parameters and body conditions of the key prey species of tiger in CNP, the chital. To meet this objective, I have used camera trap-based captures of chital from two different sampling areas of CNP, which significantly varied by tiger density, thereby possibly establishing the

effect of predation on prey population structure and health status. Population structure was characterised by the adult male-to-female ratio and fawn-to-adult female ratio identified from the photographs. Population composition was evaluated by measuring the percentage contribution of each age-sex class to the total population. In order to deal with the possibility of camera traps capturing the same animal multiple times, I used the single sampling with replacement approach to estimate the ratio and variance of adult female to male and fawn to adult female. The overall number of females per male for CNP was 1.66 (± 0.06) and the number of fawns per female for CNP was 0.25 (0.01). Comparing areas of high and low tiger density it was observed that chital body condition was poorer in areas with high tiger density.

Overall, my thesis highlights how remote camera traps can be extensively applied to simultaneously address several ecologically important aspects of species population in a comparatively invasive and cost-efficient way. I believe, my study in an area like CNP, provides a robust scientific premise and highlights the challenges of addressing some significant conservation aspects of the ungulate prey population, albeit with few shortcomings, which will aid largely in the future management of species as well as ecosystems

CHAPTER I INTRODUCTION AND LITERATURE REVIEW

Ungulates are hoofed mammals represented largely by one of its even-toed families, the Cervidae or the deer. Deer exhibit a wide spectrum of body sizes and feeding habits. They inhabit a broad range of habitats, generally attaining a high abundance wherever they are found. However, pervasive reports of their populations dwindling almost everywhere, especially in the tropics excite serious concern and thereby necessitate long-term scientific monitoring. Such monitoring should be supported by a thorough understanding of their biology and ecology, which is largely lacking in India. Habitat loss, illegal hunting and habitat degradation have played the most important role in the dwindling ungulate population. In a country like India, where deer are legally protected from being hunted or harvested periodically as a trophy or as meat, monitoring and conservation of deer populations are aimed primarily towards the broad-scale management of the ecosystem they inhabit. Deer play pivotal ecological roles such as indicators of the ecosystem’s health link in the food web and through their interactions with different local environmental parameters. Deer are not only incredibly elegant and majestic, but their population dynamics, behaviour and integral role in the environment make them species of great aesthetic and conservation value. Moreover, with the gradually increased inclusion of wildlife as a core component of environmental assessment for infrastructure development, it is also imperative to monitor large mammals such as deer, particularly for outside protected areas where deer are often reported in substantial numbers.

Studying ungulates in an ecosystem is generally driven by the inquisitiveness to examine how they interact with habitats and predators in the area. In the simplest food chain of an ecosystem their position makes them one of the most critical organisms in maintaining the ecosystem integrity. For, their abundance can regulate or limit, the producers via herbivory, the consumers as their resource, and the conspecifics as competitors, therefore driving the important ecosystem processes, such as the bottom-up and the top-down control mechanisms. However, despite such an ecological value ungulates have remained largely underrepresented in scientific investigations about their population biology in India (Jathanna et al., 2006; Johnsingh, 1983; Karanth & Sunquist, 1992; Khan et al., 1996; Kumar, 2010). Lack of information particularly from the part of the Terai landscape of the country, which harbours a huge variety of habitats, large herbivores and carnivores (Bisht et al., 2019; Jhala & Qureshi, 2015), is a matter of conservation concern. Ecological knowledge of ungulates from this important landscape however is limited to few significant studies from Nepal (Dinerstein, 1980; Seidensticker, 1976; Shrestha, 2004; Wegge et al., 2009). Hence, to fill this knowledge gap about ungulate dynamics I have primarily focussed on addressing their population abundance and distribution in relation to local habitat and various environmental correlates and predators in Corbett Tiger Reserve. I believe the study will significantly contribute both from an ecological and management aspect.

Conceivably, the most fundamental objective of any wildlife population monitoring is to obtain a reliable understanding of population abundance over time and space. Abundance is one of the most significant metrics which aids in detecting spatio-temporal patterns of variation in sev

as its distribution, or, fluctuations in any demographic parameter (Skalski et al., 2005). Multi-species large mammalian systems particularly necessitate such attention because conservation and management of such system is often difficult and generally contributes towards the preservation of the entire ecosystem. Beside abundance, it is also important to monitor the demography and behaviour of such species. These parameters help us in predicting popul well as its response to different management interventions in case of unexpected events such as poaching or developmental activities. They also assist us to understand the interaction of the species with different environmental variables. This study was conceptualized to address some of these aforementioned crucial ecological processes in one of the most significant ecosystems of the country, the Terai ecosystem. The study deals with an ungulate assemblage, with a focus on a particularly important ungulate species of the Indian sub-continent the spotted deer or chital (*Axis axis*), at a background of predation (with the tiger as the primary predator). Through this study, we compare different techniques, which involve direct as well as remote camera trap-based observation methods to estimate the abundance of a diverse range of ungulates. I believe the study will contribute significantly to addressing a range of ungulate ecology and behaviour and aid in formulating management decisions in the study area as well as in areas of similar habitat and environment.

In this introductory chapter I will first try to emphasize on the several significant roles of deer in the environment and ecosystems, moving gradually to review our understanding of how predator can affect prey population status and health. Following which, I elaborate on traditional and recent techniques of assessing deer population, and, finally concentrating on the importance of spotted deer/chital, the subject species I had chosen to study these components, albeit within a limited period of time.

Second chapter will give a detailed perspective of the study area, stating its historical importance, its physiography, its flora and fauna and its conservation value in terms of ecology and management within the larger landscape.

In the third chapter, I will focus exclusively on estimating density of four species of ungulates in relation to different habitats. The chapter also highlights the spatial distribution pattern of the species in the landscape under different environmental correlates using spatial analysis.

Fourth chapter builds a comparison between two well-established abundance estimation technique and a relatively recent technique by measuring their efficacy and cost-effectiveness in estimating density of a) different ungulate species, and, b) spotted deer as an individually identifiable species.

In the fifth chapter I attempt to understand the population dynamics of spotted deer, focussing mainly on age-sex ratio, fawn-female ratio and individual health condition (as a surrogate of population performance) under a gradient of predation risk.

Together these chapters will address the following objectives;

1. To estimate the abundance of ungulates (chital, sambar, barking deer and wild pig) in different habitats in Corbett National Park (CNP).
2. Evaluate the cost-effectiveness of three density estimation techniques for estimating the density of ungulates.
3. To access the effect of predation on demography and nutritional health of the chital population in CNP.

Why monitoring deer population is important?

Role in environment and ecosystem

Deer generally exhibit a generalist feeding style with a broad range of plant species within their dietary regime (Freeland & Janzen, 1974). They occupy several habitats of an area, which often encompass the habitat needs of other associated animal and plant species, and therefore in turn invariably serves as an ecological indicator of the ecosystem (Hanley, 1996). Owing to the convenience of studying deer than any other threatened species, which mostly remain undetected, deer often act as more important indicator in an area to understand conservation and management interventions whenever required (Hanley, 1996). Being the primary consumer in an ecosystem, they also function as a link between the lower (the producers) and the higher (secondary and tertiary consumers) trophic levels of a food chain. They play a vital role in ecosystem nutrient cycling and energy flux (Pletscher et al., 1989) and is often considered as potential initiators of interaction chains (Pringle et al., 2007). Deer might influence vegetation community and forest dynamics in various ways, such as, directly through grazing and browsing (Adler et al., 2001; Chase et al., 2000) both positively and negatively (due to overabundance), or indirectly through seed dispersal (Danell et al., 2006; Paine, 2000). Cote et al., 2004 has presented an extensive account of how deer overabundance had affected human health, forestry and agriculture. How it can alter interaction between plants, affect the local population of insects, birds and mammals, and, how it can impact the ecosystem processes and overall community structure.

Apart from the aforementioned roles, another very significant ecological role of deer, is as driver of trophic cascades by functioning as prey for the mammalian carnivores inhabiting the ecosystem. Plant-herbivore interaction has drawn the major attention for studying trophic cascades, due to the effect herbivores can have on plants affecting both the strength and scale of cascades (Polis et al., 2000). However, it is the predator and its interaction with the prey which mediates the trophic cascade eventually (Terborgh & Estes, 2010). Instances, where uncontrolled herbivory have resulted following the removal of an apex predator in a simple three-trophic-level cascades (Terborgh & Estes, 2010), are such pieces of evidence. A classic example is the dramatic effect of herbivory by the elk population on the vegetation structure of Yellowstone National Park following the removal of the wolves, the topmost predator, from the area (Eisenberg et al., 2013). Long term ecological monitoring of the herbivore population in the area aided the park managers to understand the entire ecosystem dynamics within the park and later formulate scientific management approaches in order to restore the ecological balance of Yellowstone National Park.

In addition to the previously mentioned species-evolution based ecological functions, several recent studies have reported how human induced climate change and global warming is affecting several aspects of deer biology. Change in breeding time and duration being one of the most important of all. Bonnet et al., 2019 using 45 years of field records and genetic data of red deer in Isle of Rum in Scotland, has reported how adaptive evolution over few decades, owing to climate change effects, can lead to an observed phenotypic change, in this case through advancement in parturition date and subsequently population structure of red deer. Moreover, a review of studies (Weiskopf et al., 2019) on projected climate change effect on white-tailed deer and moose in the Midwest has highlighted that, while white-tailed deer population might increase due to favourable warm temperatures and decreasing snow, but moose population might decrease due to physiological stress in response to warming conditions. Such contrasting effects are concerning and highlights the importance of continuous long term monitoring of deer populations across the world in order to observe how different climatic fluctuations in different regions might affect various ecosystems with which the deer are associated.

A review of prey-predator dynamics, with focus on mammalian herbivore-carnivore system

Probably the commonest death for many animals is to be eaten by something else

Charles Elton, 1927

Every species in a community of more than one species, interacts interspecifically either as a competitor or mutualist or commensal or at some point in their lives as a prey, predator or both. While mutualists and commensals share a beneficial association, competitors and prey-predator share a negative interaction. Such negative interaction is much stronger between the prey and the predator because, it directly affects the survival of both the species, where one is the resource (prey) and the other is a consumer of that resource (predator). In the animal kingdom, a predator not only harms the prey but most often kills it c

ra (Dawkins & Krebs, 1979) where predators are constantly trying to evolve better predation strategies and prey is evolving predator avoidance strategies. From the prey perspective, predation is a strong selection force and development of memory and adaptation to predation pressure at local scales can be particularly favoured. P

effect on its prey can be manifested in

success and survival) (Messier, 1991; Miller et al., 2006) and behavioural processes (foraging vs. vigilance and micro-habitat choice) (Connell, 1975; Sih et al., 1985), while productivity of the area can additionally influence this relationship.

Examining the mechanism of how predator regulates prey is however extremely complex, and is further compounded by several interrelated factors, such as habitat heterogeneity, occurrence of prey refuges, temporal or spatial availability of prey, the diversity of prey species and prey body size in a multi predator-prey system (Sinclair et al., 2003), presence of alternative more preferred prey in the area (Sinclair, 2006), vulnerability of different age and sex classes of the prey species (Sinclair, 2006). Skogland (1991) presents an exhaustive summary of the various factors which have been known to affect predation. Predation either as a limiting factor or as a regulatory factor, affect the prey population abundance or demography predominately through direct consumption (Messier, 1991; Robinson et al., 2002; Sinclair, 2003). Selective predation of certain age class of prey can have a dramatic effect on the demography of prey populations (Gervasi et al., 2012; Jackson & Ditchkoff, 2013). Messier (1994) through his classic review of studies of moderately diverse community of large herbivore and carnivore systems, has pointed out that predation as a limiting factor of ungulates can be density- dependent, density-independent and inversely density-dependent. Ballard et al., 2001 in another extensive review on deer-predator relationship has highlighted how prey density as well as habitat carrying capacity of deer populations is crucial to understand the impact of predation. Additionally, presence of alternative prey in multi prey-predator systems of large mammals, has been accounted as another confounding but critical factor shaping predation effect. An alternative prey can influence predator-prey interaction by either diluting or intensifying the effects of a predator on its primary prey (Hamlin et al., 1984; Kunkel

& Pletscher, 1999; Stoddart et al., 2001). In a recently published study Frenette et al., 2020 using 30-year monitoring dataset of moose-caribou-coyote-bear system investigated how habitat modification has led to an exacerbated predation pressure on less productive prey (caribou) by the predators that are generally supported by most productive prey (moose and deer) which remained in an apparent competition, eventually leading to a decline of caribou. Hence, despite of several studies (Forrester & Wittmer, 2019; Gese & Knowlton, 2001; Messier, 1994; Robinson et al., 2002; Skogland, 1991) reporting predation as the major factor limiting and regulating prey population, it is vital to address the effect of several other confounding variables, such as habitat change, weather, diseases and competition, all of which might operate in conjunction often leading to confusing conclusions (Conolly, 1978; Gese & Knowlton, 2001). In relation to prey size as another important factor, Sinclair et al 2003, through an extensive long-term study of highly diverse predator-prey community of herbivores and carnivores in Serengeti, showcased how smaller ungulates particularly experience much greater mortality from both preferential as well as opportunistic predation by predators of different body size range and predict that their population is more prone to be severely affected by predation than the larger bodied ungulates in the prey guild. Moreover, for the smaller ungulates, this impact can become more pronounced with predation at the juvenile stage particularly (Sinclair et al., 2003). (Monteith et al., 2014) reported decline in some mule deer populations due to predation on juveniles. Contrarily, maternal condition plays a significant role in juvenile survival when examined from a bottom-up regulatory dimension. Such nutritional effects on juvenile survival via mother is often masked by predation effect.

Predator not only regulate prey population through direct consumption, but also through a suite of non-consumptive or risk effects which lead to changes in prey behaviour and physiology that help in predator avoidance (Hermann & Landis, 2017). Such non-lethal risk effects therefore play a major role in the co-evolutionary prey-predator arms race. Behavioural adaptati

been observed in prey’s decisions (Lima about

& Bednekoff, 1999; Sönnichsen et al., 2013). Studies have shown that predation risk can affect various life history and behavioural strategies of prey such as vigilance (Skinner & Hunter, 1998), habitat selection (Creel et al., 2005), diet selection (Edwards, 1983), physiological stress (Clinchy et al., 2013), and fecundity (Creel et al., 2007). A prevalent measure of anti-predatory behaviour is the time budget trade-off between vigilance and foraging, which has a direct implication on prey fitness and impaction on lower trophic level (Childress & Lung, 2003; Laundré et al., 2011), a phenomenon popularly known as *ecology of fear* (Brown et al., 1999). In case of gregarious ungulates, adjustment in grouping plays an anti-predatory role where it has been reported as a governing factor behind such trading off between vigilance and foraging, exhibiting sex specific effect at individual as well as group level (Cherry et al., 2015; Lagory, 1986). Such non consumptive effects not only involve the predator and the prey tier but can also have a cascading effect through the trophic levels due to variable influence on distribution and intensity of herbivore pressure (Peckarsky et al., 2008; Ripple & Beschta, 2004; Valeix et al., 2009). Consideration of such predator induced non-consumptive effects, which can affect the scale and degree of prey response to predation similarly as consumptive effects, might have significant management of conservation implications (Peckarsky et al., 2008).

Chital

Spotted deer or locally known as chital is a native species of the India subcontinent. It is one of the most abundant and ubiquitous deer species of India, and forms the major bulk of the wild ungulate guild (Bagchi et al., 2004; Karanth & Sunquist, 1992; Khan et al., 1996; Sankar, 1994). Chital plays a critical role of keystone species in most of the Indian forests owing to its high densities and as one of the most preferred preys of the large carnivores. Chital is a plastic species exhibiting considerable adaptive response (Ables, 1974) evident from its wide ranging distribution across different habitats (Kumar et al., 2021).

Chital are principally gregarious though overt interaction between individuals are rare (Schaller, 1967). It exhibits a matriarchal family unit, comprising generally of an adult female, her fawn and a yearling from the previous litter. Much often a herd is mostly composed of two or more of such family units only, occasionally accompanied by individuals of mixed sex and age class, owning to other wise loose aggregation in the herd (Fuchs, 1997). In India average monthly herd size varies from 5-38 individuals (Schaller, 1967, Khan & Vohra, 1992; Ramesh et al., 2012). The species exhibits a fluid 'fission-fusion' group (Barrette, 1991) which is influenced by the interactive effect of different factors such as animal density, rainfall, habitat structure, breeding seasonality (Barrette, 1991; Raman, 1997). Group size variation in chital has been studied with respect to seasonality, feeding periods (Schaller, 1967), predator presence (Dinerstein, 1980), and openness of habitat (Barrette, 1991). A comprehensive study on ecology of chital in Gir National Park by Dave (2008), demonstrated that group size variation was overwhelmingly corresponded to habitat structure and role of predation and not with density or rainfall (Raman, 1997). Herd stability is poor in chital, evident from observation of frequent change of association between male and female, often at a daily rate (Schaller, 1967; Fuchs, 1997; Miura, 1981).

Although, extensive studies on forest ungulates have shown a broad spectrum of habitat use by chital (Schaller, 1967; Berwick, 1974; Eisenberg, 1981; Khan, 1993; Mishra, 1982; Tak & Lamba, 1984), but they are frequently observed in open forests and forest edges, grassland-forest interface and other ecotones (Graff and Nichols, 1966; Schaller, 1967; Krishnan, 1971). However, according to Eisenberg & Seidensticker (1976) dry deciduous habitat with scrub is the favoured habitat, while Karanth & Sunquist (1992) found mixed forest with teak plantation, moist deciduous patches and swampy grassland to support high abundance of chital. Chital occurs in both hilly and flat terrain, with a preference for flat terrain, in the Terai region of India (Johnsing et al., 2004). In the Siwalik hills, Bhat & Rawat (1995) report chita preference for moderate slopes, while high to steep slopes were mostly avoided.

Chital has been classified as a generalist feeder by Rodgers (1988), feeding on grass, forbs and woody plants. However, Hofmann (1985) on the basis of morphologically ruminant type of feeding, classified the species as an intermediate/mixed feeder. It has been reported to feed on both grass and browser items by Schaller (1967) and Chaudhary (1972), with grass comprising the major portion of their diet in all the seasons. Dave (2008) reports chital feeding on 68 plant species in Gir which varied across seasons. 160-190 plant species have been recorded in the dietary regime of chital (Schaller, 1967; Johnsingh & Sankar, 1991). Chital has been considered predominately a grazer (Ables, 1974; Schaller, 1967; Mishra, 1982; Sankar, 1994). Sex ratio is chital is biased towards female. Schaller (1967) reported sex ratio of 0.6 male: 1 female in Corbett National Park and 0.7 male: 1 female in Kanha National Park. In Royal-Karnali Bardia, Dinerstein (1980) reported a sex ratio of 0.5 male: 1 female, and 1: 05 female to fawn ratio. Very similar estimates were reported by Johnsingh (1983) from Bandipur National Park. In Sariska, Sankar (1994) reported an average male to female ratio of 0.4: 1 and the average fawn to female ratio 0.2:1. Dave (2008) reported an adult sex ratio of 1 male: 1.8 female and a ratio of 1 fawn: 2.43 adult female.

Camera trap as a wildlife research tool

Surveying or monitoring of wildlife primarily entails direct observation of the animals either, opportunistically for a short period spanning from few days to few months, or in a systematic manner for a longer duration covering several years. In both these scenarios, however, the task of observing is usually hard, and becomes notoriously difficult when it involves rare and elusive species. Apart from observation, counting animals for the purpose of understanding their population status would often involve physical capture and marking of individuals and releasing them back. Ages of such painstaking activities has built our foundation of understanding the performance of various wildlife. All of these activities however carry a magnitude of invasiveness which can potentially affect the biology of the species or can produce a bias in our understanding. Invention and gradual imbibition of automatic remote camera trap (cameras that are remotely trigger via an active or passive sensor upon a passage of an animal in front) in wildlife research has helped in dealing with such difficulties and influences in a cost effective manner, in compare to radio telemetry which is also an effective but costly alternative. Although, the invention of the first trip wired camera trap by George Siras III in 1890s was for his pleasure to photograph animals at night, later usage by F.M. Chapman to survey animals of Barro Colorado Island (Chapman, 1927) is well known to us as possibly the first ever scientific use of camera traps. After about sixty years since then, camera trap gradually started gaining a wide application in investigation of almost all important aspects of wildlife (particularly mammals), be it for capturing various behaviours, or for understanding different population and demographic parameters, or, presence and absence of a species in an area or as a tool to assess species diversity and richness in a community. This gradual inclusion of camera trap as a tool in wildlife was largely due to its ease of implementation, relative non-invasiveness and fiscal benefit when compared against the greater collective cost of manual labour and disturbance of the natural environment by the observer. However, few limitations of camera trap as has been highlighted by Kays & Slauson (2008) include initial cost of implementation, equipment malfunction, limitations of batteries and films. Although camera traps can be used to achieve numerous objectives of wildlife research (Rovero et al., 2013), here, I briefly review its applicability pertaining to the objectives of the current study.

Abundance and density

One of the few earlier applications of camera trap technology was to measure animal abundance and density for those species in which each individual has unique natural body marking, by using the statistically robust mark-recapture technique. Karanth, (1995) was the first to apply this technique using camera traps on tigers in India. Camera trap based capture-recapture analysis has since become a prevalent option to estimate density of elusive terrestrial mammals, comprising mostly of felids and more recently on other carnivore families (Harihar et al., 2010; R. Jackson et al., 2006; Trolle et al., 2006; Trolle & Kéry, 2005; Wallace et al., 2003.; Wang & Macdonald, 2009). Camera trap has mostly been used in the application of conventional capture-recapture technique (all of the afore mentioned studies), although mark-resight methods have also been used (Fuller et al., 2001; Watts et al., 2008), and more recently spatially explicit capture recapture (SECR) has become a popular camera trap based methodological choice for small as well as large scale abundance estimation exercises (Jhala & Qureshi, 2015; Royle et al., 2008; Royle & Gardner, 2011). More recent novel application of camera trap has been observed in successful estimation of absolute abundance of non-individually identifiable species also (Howe et al., 2017; Keever et al., 2017; Rowcliffe et al., 2008) which enhances the potentiality of camera trap by a great extent.

Demography

Camera trap generated data not only holds information about abundance of species, but can also be used in understanding the demographic parameters of different species. Using baited or non-baited camera traps several studies have estimated age sex ratio of deer, an information which is crucial for management and conservation but otherwise difficult to collect without experienced observer or can be influenced by deer activity and habitat use (Brommer et al., 2021; Ikeda et al., 2013; Macaulay et al., 2020; Peres et al., 2017; Zaumyslova & Bondarchuk, 2015). Such camera trap based demographic study however is limited in mammalian carnivores and has been confined mostly to large felids (Bisht et al., 2019; Harmsen et al., 2017; Joubert et al., 2020).

Behaviour

One of the earliest (Carthew & Slater, 1991; Schaik & Griffiths, 1996) and still a predominant application of camera trap in wildlife research is to study animal behaviours, primarily owing to benefits such as, a) relatively non-intrusive, b) enable behavioural data collection of both target and other species at the same time, c) application over a large area in short time and, d) easy geo-archiving of data without being physically present (Rovero et al., 2013). A large body of camera trap based behavioural study revolves around understanding activity patterns of different species in relation to different environmental parameters and other conspecifics and predators (Bridges et al., 2004; Dillon & Kelly, 2007; Lashley et al., 2018; Maffei et al., 2005; Rowcliffe et al., 2014). Besides activity, quite a number of studies have also reported the application of camera trap in investigating foraging and vigilance behaviour of deer (Altendorf et al., 2001; Cherry et al., 2015; Lashley et al., 2014; Popova et al., 2016; Prugh et al., 2019) thereby extending the potentiality of camera traps in exploring the vast premise of animal ecology not only through their behavioural responses as well.

CHAPTER II STUDY AREA

2.1 LOCATION AND HISTORY

Established as Hailey’s National Park in

as Asia, earned the name Corbett National Park (CNP) in 1956 after the renowned hunter-naturalist-conservationist, Sir Edward James Corbett. Popular for man-eating tigers and leopards during that time, vivid national history descriptions of the area and its surrounding can be found in great details in the hunting stories of Corbett. Such a presence of both the carnivores in large numbers since then fairly reflected the suitability and the importance of the area in conservation of tigers and its various wildlife, which later led to the launch of Project Tiger in CNP in 1973, already boasting a population of more than 150 tigers, and remains to be the single largest tiger population in the world and one of the highest density in the country till date. Located in the Pauri Garhwal district of Uttarakhand at the foothills of the Himalayas, known as Shivalik Hills, CNP encompasses the 520.82 sq.km of core and buffer areas of the larger Corbett Tiger Reserve. Together with a 301.18 sq.km of Sonanadi Wildlife Sanctuary, 466.32 sq.km of buffer and the CNP, Corbett Tiger Reserve comprises a protected area of 1288.32 sq.km (Figure 2.1). Due to its high tiger density and connectivity with other adjoining protected areas CTR acts a critical source population of tigers in the larger Terai-Arc landscape, a critical tiger conservation landscape (TCL) aimed towards global conservation of tigers. Tiger conservation in an area however requires a holistic approach of conserving the habitat and its prey, as prey population reflects the tiger- carrying capacity of an area and also indicates the overall habitat suitability. It is in this context pertinent to elaborate on the geo-physical, climatic and vegetative characteristics of this important conservation area.

2.2 PHYSIOGRAPHY

CTR spans varied habitats like the Terai (characterized by tall grasslands, interspersed with dense moist deciduous forests), the Bhabar (a gently-sloping coarse gravely region with large trees), the foothills of the Himalayas, also known as Shivalik Hills (characterized by moderate to highly undulating terrain with deciduous forests, which forms the northern part of the reserve). CNP falls majorly within the bhabar region. Altitude of CNP ranges from 250 to 1100 meters (Singh et al., 1995). The terrain of the reserve is predominately hilly, with a series of almost parallel ridges running from north-west to south-east gradually decreasing in height towards the plain in the southern part. CNP is interspersed with large river beds and riverine stabilized islands and floodplains formed by network of monsoonal and perennial first, second and third order streams (Babu et al., 2009). These streams, which remain dry in the hot season due to porous boulders, re-emerges with the rainfall. The overall topography is interspersed with riverine valleys forming plateaus and temporary marshlands (Babu et al., 2009). The geology of the park is a composition of sand stone, sand rock, conglomerates and bhabar deposits. River Ramganga flows from the north eastern part of the park towards northwest and emerge out of the park from the south west boundary. Ramganga acts as a major perennial source of water in the area. A reservoir was formed on the river which submerged an area of nearly 80 sq.km. About 42 sq.km of the reservoir falls within the CNP boundary. Kosi river flows along the eastern boundary of the park and is an important water source for the wildlife.

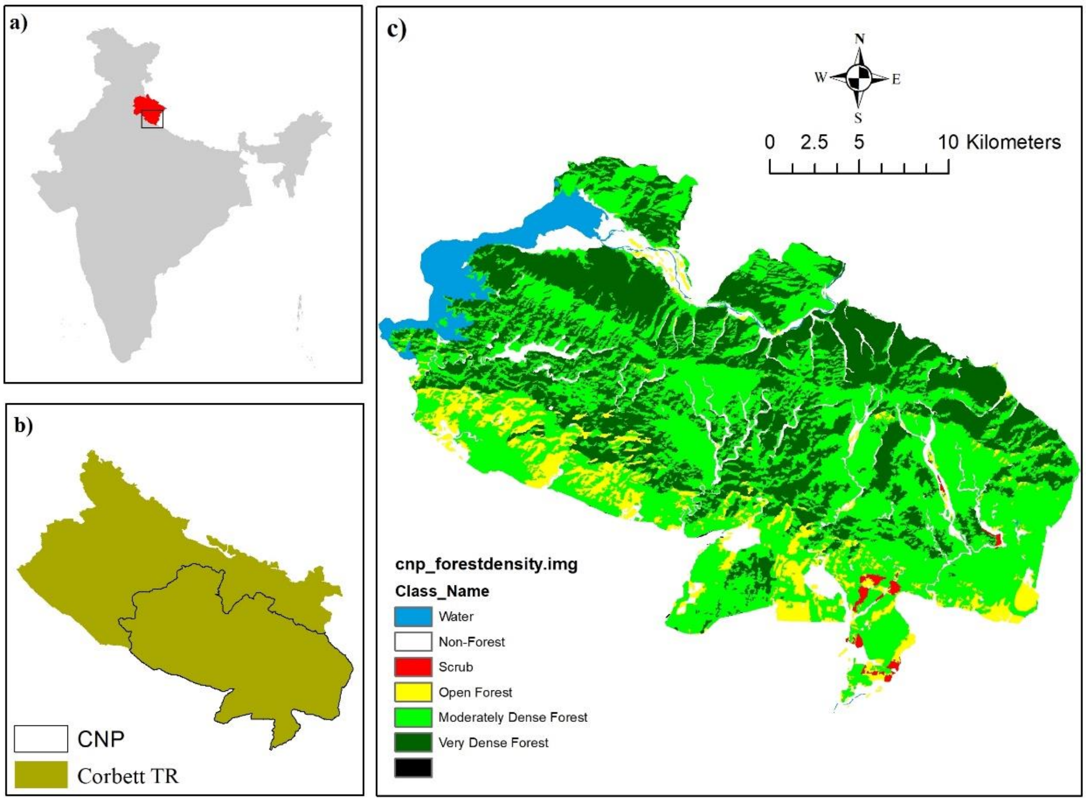


Figure 2.1: a) Map of India (in grey) showing the state of Uttarakhand (in red) and the general locality of Corbett Tiger Reserve, b) Map of Corbett Tiger Reserve with the boundary of Corbett National (in black), c) Forest density map of Corbett National Park (study area).

2.3 CLIMATE

The climate is subtropical with three prominent seasons *viz*. summer (March to June), monsoon (July to October) and season (November to February). Temperature in summer can reach as high as 42º C (between May - June) while in winter it plummets to as low as 3ºC (between January –February). The area receives moderate to high rainfall in the monsoon ranging from 1400mm to 2800mm (Fauna of Corbett Tiger Reserve, Uttarakhand, 2008). Maximum rainfall occurs between June to September from the South-West monsoon. Owing to its location in the Himalayan foothills and dense forest, the area remains moderately humid throughout.

2.4 VEGETATION

Vegetation of the area is formed of forest, riparian and grassland habitats. Champion and Seth (1968) classified the forests of CTR into three major types: Northern moist deciduous (3C), Northern tropical dry deciduous (5B) and Himalayan sub-tropical pine forest (9). The area harbours a phenomenal diversity of 617 species of plants (Pant, 1986), with 132 species of monocots and 462 species of dicots, 1 species of gymnosperm and 22 species of ferns and fern allies. The forests of CTR are dominated by sal (*Shorea robusta*) (approximately 73%, Fauna of Corbett Tiger Reserve Uttarakhand, 2008) often mixed with *Terminalia* spp, and a frequent associate *Adina cordifolia* (Haldu). Among other deciduous tall tress which are frequently found and form the upper canopy are *Terminalia alata, Terminalia chebula, Anogeissus latifolia, Bombax ceiba*. A significant portion of the vegetation is of miscellaneous forest type comprised of evergreen species such as *Mallotus phillippinensis, Litsea monopetala, L.glutinosa, Murraya panniculata and M. koenigii* etc. which often forms a dense middle story. Riparian forests comprise primarily of *Syzygium cuminii, Phyllanthus emblica* and *Acacia spp*. Grasslands (both in low-lying and elevated areas) locally known as 'chaurs' are dominated by species such as *Imperata* spp, *Cynodon* spp, *Saccharum* spp etc.) (Rawat et al.,1997, Badola et al., 2010). Besides, species such *as Vitiveria ziznoides, Themeda arundinacea, Arundo donax, Apluda mutica and Heteropogon contortus* are also found in several grassland patches. *Eulaliopsis binata* and *Thysanolena maxima* are found on the cliffs. Lining the grassland edges are found *Dalbergia sissoo, Kydia calycina* and *Holoptelia integrifolia*. Few important large grassland patches are in Dhikala and Bijrani areas of CNP. The overall forest cover of

CTR ranges from very dense to moderately dense forest (Forest Survey of India, 2014). *Clerodendron viscosum, Colebrookea oppositifolia, Glycosmis arborea* and *Murraya koenigii* are the few most commonly occurring shrub species of the area. The southern and eastern boundaries of the park also comprise of few plantation patches of *Tectona grandis* and *Eucalyptus spp*. This amalgamation of both Himalayan and peninsular flora in CNP, due to its location, harbours a very rich diversity of fauna.

2.5 FAUNA

The wide array of habitats together with perennial streams support a diverse thriving population of ungulates such as chital (*Axis axis*), sambar deer (*Rusa unicolor*), barking deer (*Muntiacus vaginalis*), wild pig (*Sus scrofa*), nilgai (*Boselaphus tragocamelus*), elephant (*Elephus maximus*), hog deer (*Axis porcinus*), serow (*Capricornis thar*) and goral (*Naemorhedus goral*). This ungulate assemblage serves as food for large carnivores such as the tiger (*Panthera tigris*) and leopard (*Panthera pardus*). The area is also home to other large to small carnivores such as Himalayan black bear *(Ursus thibetanus*), sloth bear (*Melursus ursinus*), golden jackal (*Canis aureus*), leopard cat (*Prionailurus bengalensis)*, jungle cat (*Felis chaus*). Among the mustelids and viverrids, yellow throated marten (*Martes flavigula*), smooth coated otter (*Lutrogale perspicillata*), Indian grey mongoose (*Herpestes edwardsii*), palm civet (*Paradoxurus hermaphroditus*), large Indian civet (*Viverr azibetha*) and small Indian civet (*Viverricula indica*) are found in good numbers. Two primate species found in the park are *Rhesus macaque* and *Semnopithecus ajax* (*Himalayan gray langur).* An association between chital and Himalayan gray langur is frequently observed near fruiting trees in the park.

Ramganga river is one of the largest breeding grounds of gharial (*Gavialis gangeticus*). Good number of mugger crocodile (*Crocodilus palustris*) is also found in both the Ramganga river and the reservoir. Among other reptiles, snakes like King cobra (*Ophiophagus Hannah*), Indian cobra (*Naja naja*) and Indian python (*Python molurus*) are found.

CNP also harbours an amazing avifaunal diversity of both resident and migratory species comprising nearly 550 species.

2.6 ANTHROPOGENIC ACTIVITIES

The critical core area of CNP although is devoid of any human activities, but several small to medium sized villages along the southern and eastern boundary of the park such as Kalagarh, Dhara, Laldhang, Dhela and Sunderkhal exert a certain level of pressure on the peripheral areas of the park, where the villagers often venture inside the park under the legal right, for NTFP and fodder collection, however often crossing the permissible boundary limit in search of more productive resources. Cattles and goats are also found to forage quite inside in such areas. Such movements bring both human and domestic animals to close encounter with tiger and leopard as well as elephants posing immense risk to their lives. Sporadic occurrences of such fatal encounters is not uncommon in these areas. Extraction of high quality forage for fodder and grazing by cattle and goats can affect the local wild ungulate populations also. Being a prime tiger reserve of the country CNP draws a large number of tourists annually, catering to which numerous private resorts have come up in these park-adjoining areas.

2.7 CONSERVATION CONCERNS

Decline in hog deer population

Hog deer which was once found in large numbers in the grasslands of CNP, particularly in the grassland patches of Dhikala, has severely declined from these areas. While hog deer can still be observed in low numbers in Dhikala, but is almost entirely absent from other grassland areas where it was earlier found. Such a disappearance of a grassland obligate species might reflect deterioration of the grassland habitat or any other limiting factor such as disease which could have affected the confined populations in fewer grassland areas. Conserving such an important indicator species of habitat health and as prey to the carnivores in the area, should be a conservation priority of the management.

Lantana camara invasion

Few forested areas of CNP is severely invaded by profuse growth of *Lantana camara*, the dominant weed species. Lantana grows by copious seed production and is known to affect the reproductive vigour of native species via allelopathic effect (Gentle & Duggin, 1997). Lantana can therefore potentially inhibit the regeneration of sal, the dominant plant species of the area. Lantana is reported to grow more in disturbed forests, which conversely can indicate the condition of the habitat patches with higher infestation. Although lantana eradication and habitat restoration efforts have been successful in few instances in CNP (Babu et al., 2009), however this notorious weed still remains a serious threat to the habitats as well as various wildlife of CNP.

CHAPTER III SPATIAL ABUNDANCE OF UNGULATES IN CORBETT NATIONAL PARK (CNP)

3.1 INTRODUCTION

Abundance or density as state parameter is the keystone metric of any population because, a) the species abundance pattern in an area essentially describes the species-habitat relationship, b) it is associated directly with almost all the population processes, and, c) a sudden variation or change in abundance/density can help guide the management in identifying the problem and undertake necessary interventions in an informed and timely manner (Skalski et al., 2005). Therefore, obtaining a reliable estimation of abundance or density over space and time is the most pervasive objective of any ecological monitoring of species.

Accurate estimation of species density ideally requires a count of all the individual animals and the measurement of the area within which the counting is done. Such ideal complete count of animal however is seldom possible, with exception of large species in open areas (Talbot & Stewart, 1964). Counting in such cases is generally done via incomplete or index-based or mark-recapture-based sampling approaches. While mark-recapture method and incomplete-count-based sampling techniques have the ability to yield absolute density estimate, index-based-indirect methods produce relative density indices. Such indices do not reflect the actual population size as it fails to capture the underlying variability of abundance, which is otherwise the principle aim of any population monitoring techniques. However, obtaining accurate and precise estimate of density using different count based approaches are dealt with methodological challenges. One such major challenge the sampling techniques try to model, is the species observation processes or the probability of detection, because detection probability of a species can vary with species size, colouration, behaviour, habitat, weather conditions during sampling, and interaction among these (Buckland et al., 2011; Zimmerman & Gutiérrez, 2007). Reliable estimation of density is thus critically dependent on obtaining unbiased estimates of species detection probabil (Yoccoz et al., 2001). Techniques such as capture-mark-recapture (CMR) (White & Burnham, 1999), mark-resight (White and Shenk, 2001) and distance sampling (Burnham et al., 1981; Buckland et al., 1993) have been developed to address species detectability issue and traditionally applied to estimate density/abundance of several large mammalian species. CMR and mark-resight techniques have conventionally remained restricted to carnivores, particularly felids, owing to individually identifiable body marking and had very limited application on large herbivores (Bartmann et al., 1987; Bear et al., 1989; Bowden & Kufeld, 1995; Wingard et al., 2011). Distance sampling on the other hand has been a method of choice for monitoring ungulate population density, primarily because it does not require individuals to be identified, which is the case for majority of the ungulate species and also because of its applicability in different habitat types and its cost effectiveness (Barraclough, 2000; Kumar et al., 2021). Among the suite of methods available for applying distance sampling (Buckland et al., 1993; Burnham et al., 1981; Hayne, 1949), line transect and point transect are two most adopted approaches. While point transect based distance sampling is mostly appropriate for avian sampling, line transect based sampling has been applied for both ungulates density estimation and avian monitoring (Burnham et al., 1981; Cassey et al., 2007; Wilson et al., 2000).

Apart from the well-established line transect based distance sampling method, recent advancement in sensor technology has led to the development of other absolute density estimation methods, such as those using remote camera traps, which can be similarly applied on non-individually identifiable species and has the extra potential of largely reducing the need of observer’s physical presenc Two such techniques named random encounter model (REM) and camera trap based distance sampling (CTDS) is gradually becoming popular alternative choices of density estimation methods and requires evaluation of their applicability across different species and habitats. In this study, I have used line transect based distance method, as a more established sampling technique, to estimate density of four major ungulate prey species (chital, sambar, barking deer and wild pig) of CNP across years which I report in this chapter. I have also estimated densities of the four ungulates using REM (in two different sampling surveys), which I compare with line transect distance sampling based density of these species, as well as with mark-recapture based density of only chital, in the next chapter.

Beside just density, as stated above, knowledge about spatial abundance pattern of species in an area carries enhanced ecological importance for conservation and management. Density surface modelling (DSM) provides an efficient way of generating precise abundance estimates of a species in any spatial resolution within the study area by modelling distance sampling based detection corrected counts with ecologically meaningful environmental covariates. Here I have used line transect-based spatially referenced detections and DSM to predict density of ungulates in Corbett National Park. I generate density surface maps of ungulates in order to visually depict the relationship between population distribution and different environmental covariates in CNP, which I believe will be significant for any future management interventions.

Since each of the above mentioned methods differ by their modelling approach and relies on different preconditions and assumptions, I believe it is pertinent to briefly discuss the fundamental concept and highlight the important assumptions and their possible violations for each of these methods. Here I discuss the same about distance sampling with focus on line transect method, while I elaborate on the theory and assumptions of REM in my next chapter where I compare different density estimation techniques.

Line Transect Distance Sampling

Fundamental concept

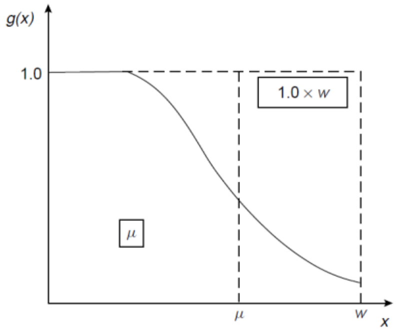
Distance sampling is a significant methodological advancement over quadrat sampling, developed to deal with the predominant problem of counting all animals within a plot of known area, to estimate density of animals. Fundamental to distance sampling is the usage of information contained in distances of animals from the observer to model the imperfect detection within an effective area (Buckland et al., 1993). Among the class of distance sampling methods, line transect is the most pervasively applied technique and is a dominant sampling choice for estimating the abundance of forest ungulates (Focardi et al., 2002; Gray et al., 2012; Kumar, 2000). The technique employs surveying a number of randomly or systematically (with random start point) placed trails of kn

animals sighted. Given the usual non-random distribution of animals in an area, lines are ideally placed following a random but representative design thus ensuring a uniform distribution of animals around the lines which allows an equal chance of detection therefore enabling an unbiased sampling of the population. Detections on both the sides of the line but only in the front of the observer are recorded. Although it might seem logical that frequency of observation will remain same throughout the line, but due to several factors such as animal body size or group size, vegetation density, terrain and animal behaviour, number of detection decreases with increasing distance from the line, which is modelled and is known as the monotonic decreasing function in distance sampling. This function technically relaxes the strip-transect assumption of detecting all animals within a pre-determined distance w, the half width of the strip. Distance sampling models the distribution of observed perpendicular distances of animals to estimate the proportion of animals that is detected (P_a) in compare to the proportion missed, together which comprise the effective area of observation within the strip. Density estimation takes the form;

$$D = n/2wLP_a$$

Where, D is density, n is number of observations from both side of the strip ($2w$) and L is transect length.

Critical to distance sampling analyses is to fit a *detection function* $g(x)$ to the observed perpendicular distances from the line (0) till a distance w (known as truncation distance) that describes how detectability decreases with increasing distance from the transect. $g(x)$ is defined as the probability of detecting an animal at distance x from the line, only after assuming that probability of detection on



the line is certain or g(0) =1. Integration of *g(x)* between 0 and *w*, produces the crucial parameter called effective strip (half) width (μ) which is essentially the distance from the line for which as many objects are detected beyond μ as are missed within μ. It is also the area under the detection function curve, *g(x)*, which when expressed as a proportion of the area bounded by the rectangle between *g(x)* and *w* (figure above), signifies the probability that an object within the surveyed area is detected. An estimate of μ is critical for density calculation as, P_a or the expected proportion of animals counted is a ratio of μ and *w*, denoted as $P_{a} = \mu/w$. Finally, with estimates of μ and *g(x)*, derived from the probability density function of perpendicular distances, density estimator takes the form;

$$D = n / 2\mu L$$

For animals occurring in group, the above equation gives an estimate of the density of clusters. In order to obtain individual density an estimate of mean cluster size, *E(s)* is multiplied to the equation;

$$D = n^{*}E(s) / 2\mu L$$

Size of cluster can bias detection probability as larger clusters are easy to detect and can be over represented in the sample. Distance sampling uses different methods to estimate the average population cluster size and deal with this size biasness. One which is commonly used is to regress the logarithm of mean size of detected clusters (s) against estimated probability of detection or g(x), ignoring the effect of cluster size, to predict log (s) when detection is certain i.e. g(x)=1. This negates any size bias in that condition.

Fitting a detection function by choosing an appropriate model (or curve) to estimate g(x) is integral to distance analysis. Model selection is based on four main criteria, a) model robustness (flexibility of fitting a wide variety of shape for g(x), b) shape criterion (shoulder near the line), c) pooling robustness (robust to data pooled over several factors affecting detectability), d) efficiency (yielding precise estimation of density).

Assumptions

Three important assumptions are critical for a reliable estimation of density using the standard line transect method, but are prone to violation under different scenarios.

Objects on the line are detected with certainty

Certainty in detection of object on or near the line is one of the most crucial assumptions of distance sampling and is of paramount importance in designing surveys (Buckland et al., 1993). Violation of this assumption is quite widespread (Marques, 2007). Density estimate is biased low, if objects on or near the line is missed. Because this bias is a function of g (0), ensuring g (0) =1 will result in zero bias, hence should be of prime consideration in sampling. Sampling burrowing animals, or marine mammals or, birds are few of the scenarios where this assumption can be violated (Applegate et al., 2011; BÄCHLER & Liechti, 2007; Murray et al., 2011). Slow consistent movement along lines, use of video cameras in aerial or underwater surveys, are some of the attempts to ensure g (0) =1. Using mark-recapture approach in distance sampling can be another way of dealing with this issue, which however is not possible most often.

Objects are detected at their initial location

In undisturbed dense forested habitat or in hunted populations, evasive movement of animals due to observer’s presence often initial positions (Southwell, 1994), while some species remain unavailable for observation (Fragoso et al., 2016) leading to violation of this crucial assumption of distance sampling (Buckland et al., 2001). Undetected responsive movements can lead to upward or downward bias in density estimate. Proper field methods and appropriate survey design can only help in dealing with this issue (Barraclough, 2000).

Measurements are exact

Distance and angle measurement using laser range finder and compass although is one of the preferred ways of collecting these data, but can often be difficult to use effectively in dense forested habitat, where visibility is often blocked by vegetation. Although reliable density estimation is possible even if this assumption is violated but tendency of overestimating or rounding of distance and angle values in case of ocular judgement can lead to unreliable density estimation (Buckland et al., 1993). Accurate measurement of object distance near the line is however important.

Density Surface Modelling (DSM) using Line Transect Data

DSM is a model-based approach of estimating species abundance using spatially referenced count data, unlike CDS which depends on the study design to validate density estimate over the entire area by scaling up from the effectively sampled region (Miller et al., 2013). DSM can be applied using either a two-step approach (accounting for imperfect detection followed by spatial modelling) or a one-step approach (where all the relevant parameters are jointly modelled) (Miller et al., 2013). In my study I used the two-stage approach. Following this approach, firstly a detection function is fitted to the observed distances to derive detection probability for individuals or clusters. Transects are divided into segments of ecologically meaningful length (producing contiguous segments along the transects), within which counts are summarised. Lastly, detection adjusted counts or estimated abundance per segment is modelled as response to different environmental covariates. This is achieved by modelling the count as a sum of smooth functions of covariates using a generalised additive model (GAM) (Miller et al., 2013). GAMs include a flexible class of generalized linear models (GLMs) which is used to generate the smooth functions of covariates. The modelled abundance per segment is finally used to predict species abundance over the entire area of interest which was divided into segments similar to the dimension of the ecologically meaningful segments of line transects. In my study I report DSM based density of three ungulates, chital, sambar and barking deer using line transect based sampling.

3.2 METHODS

3.2.1 Field methods

Line transect Distance sampling

(for conventional distance sampling and density surface modelling)

Line transect sampling was mostly done in summer. Owing to limited accessibility inside the park, for some duration of winter (November-December), affected from the preceding monsoon would generally interrupt an early sampling commencement. Also few important grassland patches on river beds would remain submerged till December.

However, in 2011 and 2019 I could sample few transects during the winter months as well. Line transects of length 1-2 km were laid with a random start point and at a random bearing, preferably avoiding east-wise orientation in order to avoid the rising sun while walking the transects early morning. After a transect was laid, it was sampled only after a period of 2-3 days in order to avoid bias resulting from change in animal movement due to the habitat alteration while laying the transect. Besides a reachable starting point (important to start sampling early morning), transects were random with respect to animal distributions (Buckland et al., 2001). Although every attempt was made to maintain the same bearing throughout the entire length of transect, but given the undulating terrain of the area transects deviated from the original bearing, but not to any large extent which will violate the basic survey principle. Transects were mostly habitat specific, however in few cases transects have traversed different habitats. Transects were sampled over four years (2010, 2011, 2014 and 2018). Each transect was walked 1-4 times per year. Sampling was done early in the morning when ungulates remain most active. The observer maintained a stable speed while walking transects in order to reduce the risk of missing animals. For each sighting, data on species, cluster size, distance of observer to the animal cluster, bearing to the animal and transect bearing were recorded using a sighting compass (Sunnto KB-20/360R, Finland) and a laser range finder (Bushnell Scout 1000 ARC, USA). GPS locations of the point from where the observation occurred was also recorded. In case of large clusters of spotted deer, distance and bearing of the centre of the cluster was recorded. Clusters separated by a minimum of 30 meters from each other were considered as two different clusters. Along with observation data, habitat and terrain characteristics were also recorded at the beginning of transect as well as for each animal sighting.

3.2.2 Analytical methods

Conventional distance sampling

Line transect data was analysed using the conventional distance sampling (CDS) engine of Distance software version 7.3. I used global detection function and cluster size estimates by pooling observations across all four years to account for any large variability in these parameters in any single sampling year. I stratified the analysis into four survey periods (as samples 2010, 2011, 2014 and 2018) and obtained densities for each year. I also report pooled density estimates of all the four ungulates, which is an average of the four-year (stratum) densities weighted by total effort in each year. I used combinations of half-normal, hazard rate, and uniform models with cosine and polynomial adjustments and selected the best model based on minimum Akaike Information Criteria (AIC) values. Five percent of the largest distance observations were truncated. Cluster size was estimated using size biased regression after testing if the regression of cluster size vs. distance was statistically significant. Simple one-way ANOVA was used on distance sampling summary data to see if the ungulate densities varied significantly over years. Analysis as done using Conventional Distance Sampling (CDS) engine of Distance software version 7.3.

Besides year-wise density, I also estimated habitat-wise density of the ungulates using the CDS engine of Distance software. For this, I classified the transects into habitat and types recorded during transect sampling. Habitat classes were, mixed deciduous, sal dominated, grassland, plantation, riverine, scrub and teak forest. Among these classes, I report the ungulate densities for mixed deciduous, sal dominated, and, grassland habitat, as these were the major habitat types of the area. For the few transects which traversed through two or more habitats, I based my attribution considering the habitat type which was represented more in a transect. Broad habitat classes recorded for each sighting helped me in classifying such transects. In this case, I post-stratified the analysis by the habitat types and obtained densities for each stratum. Detection function and cluster size were estimated for each stratum. I used the same combination of key functions and adjustment terms as mentioned in the above paragraph. Best model was selected based on the minimum AIC values. I used as simple one-way ANOVA on distance sampling summary data to test whether densities between the different habitat types were significantly different or not.

Density Surface Modelling (DSM)

I used the 2019 line transect-based (n= 78) observation data to estimate DSM-based spatial abundance of chital, sambar, and barking deer in CNP. DSM was not appropriate to model wild pig abundance as the number of wild pig observations was low (n=16) in the sampling year. For DSM, I used the two-stage approach, which is essentially the ‘count model’ of Hedley and Buckland (Hedley & Buckland, 2004). I used conventional distance sampling to determine the truncation distance (w) for chital, sambar, and barking deer, which was used to slice the transects into species-specific meaningful segments of dimension 2w. A square area of dimension 2w x 2w was then generated separately for each species using their respective w. This area of each segment was later used in the model as the offset (effort). DSM analysis using the two-stage approach on line transect data required four data sets to be prepared, viz. distance data, segment data, observation data, and prediction data. *Distance data* had the distance information of each observation. Along with distance, cluster size, effort

(2w), and GPS coordinates during the observation are also provided in the distance data. This distance data was used to fit the detection function. I used the Distance package in R to fit the detection function and estimate detection probability. A combination of half-normal and hazard-rate function with cosine and polynomial adjustments as well as without any adjustment terms were used. The best model was selected based on the lowest AIC value. The relationship between cluster size and observed distances was explored. The *segment data* comprised of the species-specific transect segments which were generated by splitting the transects. I used ArcMap version 10.5 to generate this data which created unique ids for each segment. Ecologically significant remotely sensed covariates (Table 3.6) were extracted for these segments which were used in fitting DSMs. This was done using QGIS 3.2. A crucial step in data analysis was to attribute each observation (as object id) to the correct segment (using the unique id of each segment generated). This was accomplished by the *observation data*, which comprised of the observation ids and the segment ids together with the cluster size and effort information, thereby essentially linking the distance data to the segment data. This was done in ArcMap. The *prediction data* contained the prediction grid laid over the study area with all the remotely sensed covariates extracted for each grid. Prediction grids were of similar size to that of the segment area, specific to each species, and hence were different for the three ungulate species. For fitting DSMs I used the package *dsm* in R which entails a generalized additive model-based approach of calculating spatially explicit animal abundances from distance sampling data (Miller et al., 2021). *dsm* requires the family of response distribution and the method for smoothing parameter estimation to be provided. I used a quasipoisson distribution, assuming that the counts of individuals within each segment were distributed following an overdispersed Poisson distribution. Since, there were very less transects with no sighting, I did not use the tweedie distribution. I used the default Restricted Maximum Likelihood (REML) method for smoothing, as REML can produce unbiased variance and co-variance parameter estimates in compare to maximum likelihood estimation (MLE) method. I started by fitting a DSM on the count data assuming that the counts are a smooth function of their locations. Following this simple model, I build various models by plugging the covariates separately as well as by combining them with the spatial location of the counts. I used percentage deviance explained as the measure to compare between models. Plotting the DSMs generated response curves which allows to understand the effect of a covariate on species abundance. Selection of covariates was based on percentage deviance explained and the response curves. It was also important to check the model fitting, which was easily done using a function included with the *dsm* package. The function generated Q-Q plots and plot of residual vs linear predictor to diagnose whether the models were reasonable. A final DSM is built by combining the selected covariates. The DSM was used to predict abundance over the entire study area (prediction region) using the prediction data which contained all the covariates extracted for the prediction region at a grid size similar to the transect segment dimensions. Abundance was predicted for each cell, which was then plotted to obtain species specific abundance surface maps for the entire study area. Overall estimate of species abundance was easily calculated by summing the abundance of each cell. I used delta method to estimate uncertainties in model prediction and detection function. The analysis was done in R studio version 4.0.3.

3.3 RESULTS

Conventional distance sampling

I sampled 156 spatial transects over 2010, 2011, 2014 and, 2019 (Figure 3.1). Transect effort ranged from 150 km in 2010 to 386 km in 2018. Line transect sampling amounted to a ~1027 km of combined effort over all the four years. Total number of observations over all four years was highest for chital (n=628) followed by sambar (n=223), barking deer (n=134) and wild pig (n=58). Hazard rate with polynomial adjustment was the best selected model for chital and wild pig (Figure 3.2 and 3.5). For Sambar and barking deer half normal with cosine adjustment was selected as the best model (Figure 3.3 and 3.4). Effective strip width was highest for chital (33.69m, SE= 1.56) and was lowest for sambar (27.44m, SE = 1.82) (Table 3.1). Detection probability was however highest for sambar (0.377, SE = 0.02) and was lowest for chital (0.16, SE = 0.07). Chital had the highest year wise as well as global (average of four years) density estimate followed by sambar (Table 3.1). Barking deer had the lowest global density estimate (Table 3.1) among all. Year-wise density estimates for chital, sambar and barking deer were within an acceptable level of precision (Table 3.1) while estimates were comparatively imprecise for wild pig (Table 3.1). Test statistics of ANOVA on year-wise distance sampling summary data show that chital densities did not vary significantly between the four sampling years (Table 3.3) and had overlapping confidence interval (Figure 3.6). Densities of sambar, barking deer and wild pig however varied across years (Table 3.3; Figure 3.7, 3.8 and 3.9). Barking deer densities remained similar between 2014 and 2019 (Table 3.3) with overlapping confidence interval (Figure 3.8).

Post stratifying the line transects into mixed deciduous, sal dominated and grassland resulted into an effort of respectively 701 km, 209 km and, 74 km over four years.

Chital

The encounter rate of chital was highest in the grassland (1.14, SE = 0.21) and lowest in sal dominated habitat (0.40, SE = 0.06) (Table 3.2). Detection probability and effective strip width was also highest in the grassland (p = 0.28, SE = 0.02; ESW = 58.2 meters, SE = 2.06 meters) (Table 3.2). Mean group size was nearly similar in sal dominated habitat (11.09, SE = 1.52) and grassland (10.52, SE = 2.06). Group density was higher in mixed deciduous habitat (12.11, SE = 1.35) followed by grassland (9.83, SE = 2.02) (Table 3.2). Individual density of chital was highest in the grassland (103.46, SE = 29.41) and lowest in sal dominated habitat (50.08, SE = 12.51). Chital density in grassland was significantly different from densities in mixed deciduous and sal dominated habitat using (Table 3.4). Densities were however not significantly different between mixed deciduous and sal dominated habitat (Table 3.4).

Sambar

Encounter rate of sambar was highest is sal dominated habitat (0.23, SE = 0.04) and was lowest in grassland (0.14, SE = 0.04) (Table 3.2). Detection probability and effective strip width was highest in grassland (p = 0.24, SE = 41.58; ESW = 41.58, SE = 15.98) followed by in sal dominated forest (p = 0.2, SE = 36.25, ESW = 36.25, SE = 3.61). Mean group size was fairly similar in the three habitat types (Table 3.2). Group density was highest in mixed deciduous habitat (3.97, SE = 0.54) and lowest in grassland (1.78, SE = 0.82). Individual density of sambar was highest in mixed deciduous habitat (8.94/km^2, SE = 1.31) and lowest in the grassland (2.83/km^2, SE = 1.4) (Table 3.2) and was significantly different (Table 3.4). Densities between mixed deciduous and sal dominated habitat was however not significantly different (Table 3.4).

Barking deer

Encounter rate of barking deer was almost similar across the habitat types, with highest in mixed deciduous (0.14, SE = 0.02). Number of observations in grassland was considerably low (n=7) than in mixed deciduous and sal dominated habitat. Group density was highest in mixed deciduous habitat (2.4, SE = 0.37), while mean group size was slightly higher in the sal dominated habitat (1.36, SE = 0.09). Mean group size in mixed deciduous habitat was 1.21 (SE = 0.03). Individual barking deer density was highest in mixed deciduous forest (2.4/km^2, SE = 0.37) and was lowest in grassland (0.88, SE = 0.42). Density in grassland was imprecise (Table 3.2.). Individual barking deer density in grassland was significantly different than densities in mixed deciduous and sal dominated habitat, while densities between mixed deciduous and sal dominated did not vary significantly (Table 3.4).

Wild pig

Encounter rate of wild pig was similar between mixed deciduous and sal dominated habitat (Table 3.2). Only 2 observations of wild pig occurred in the grassland and hence was not considered for comparison. Detection probability was same in mixed deciduous and sal dominated habitat (Table 3.2). ESW was also almost similar between these two habitat types (Table 3.2). Mean group size and group density was higher in sal dominated habitat (Table 3.2). Individual density was higher in sal dominated habitat than in mixed deciduous, but was not significantly different (Table 3.4).

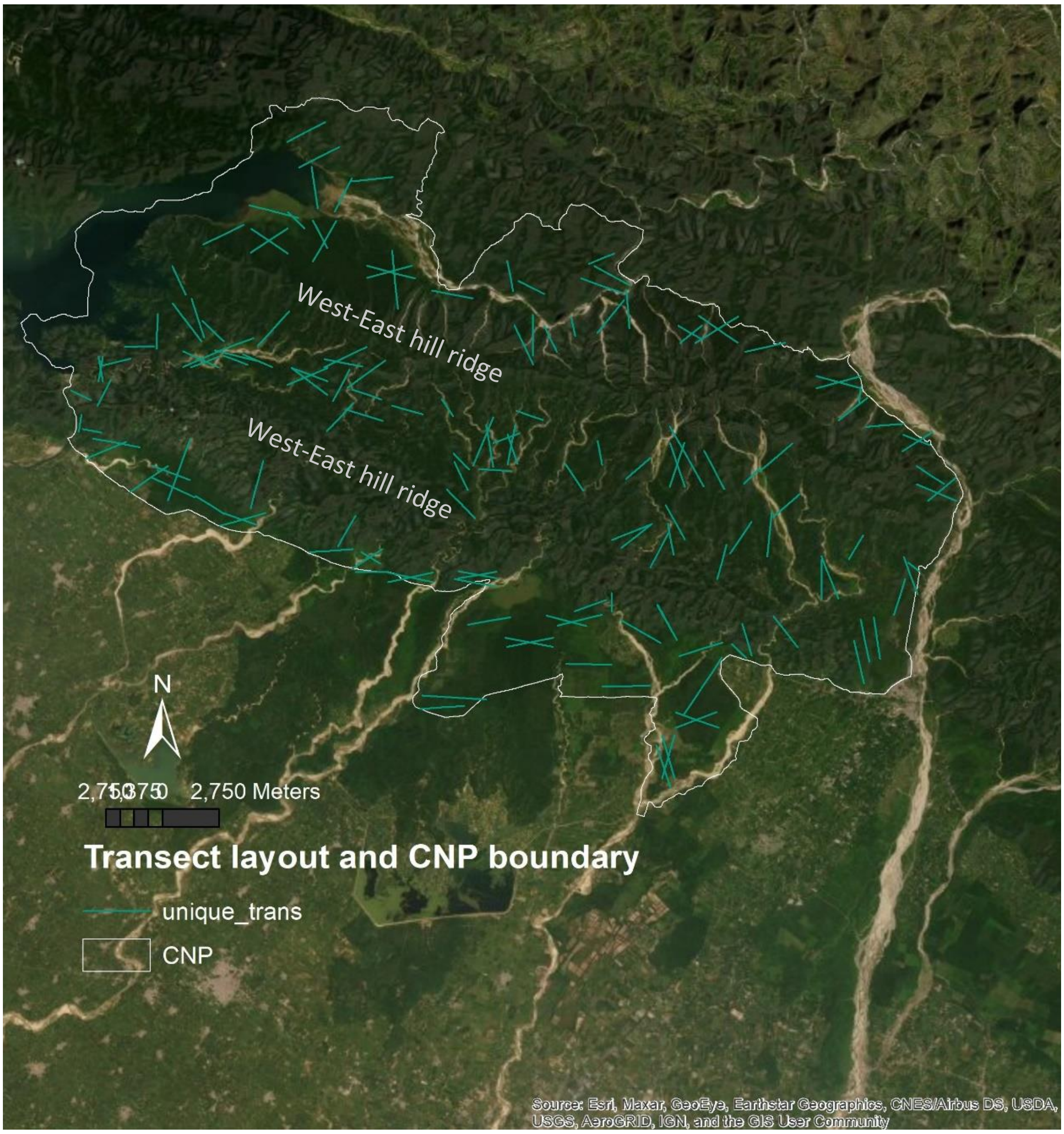


Figure 3.1: Map of the study are showing layout of spatial transects (green lines) over 2010, 2011, 2014 and 2019 survey years. The unsampled steep hill ridge is labelled.

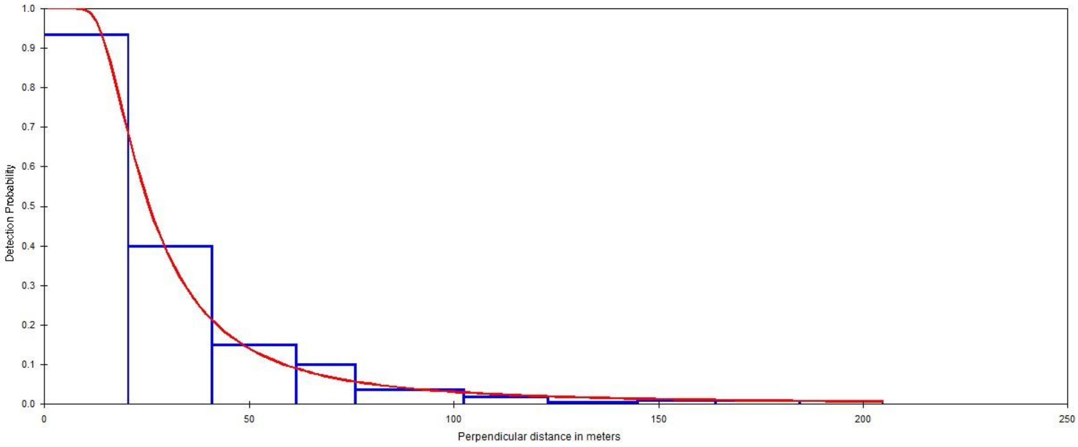


Figure 3.2: Hazard-rate detection function plot of chital.

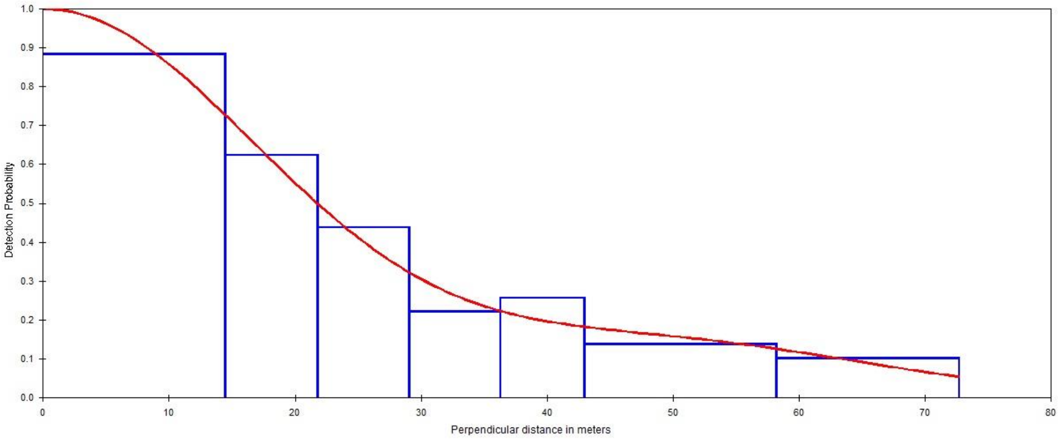


Figure 3.3: Half-normal detection function plot of sambar

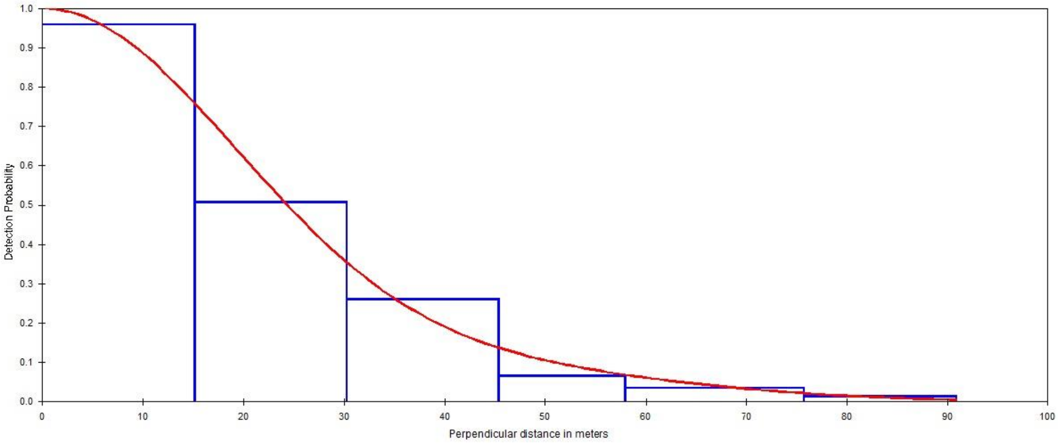


Figure 3.4: Half-normal detection function plot of barking deer

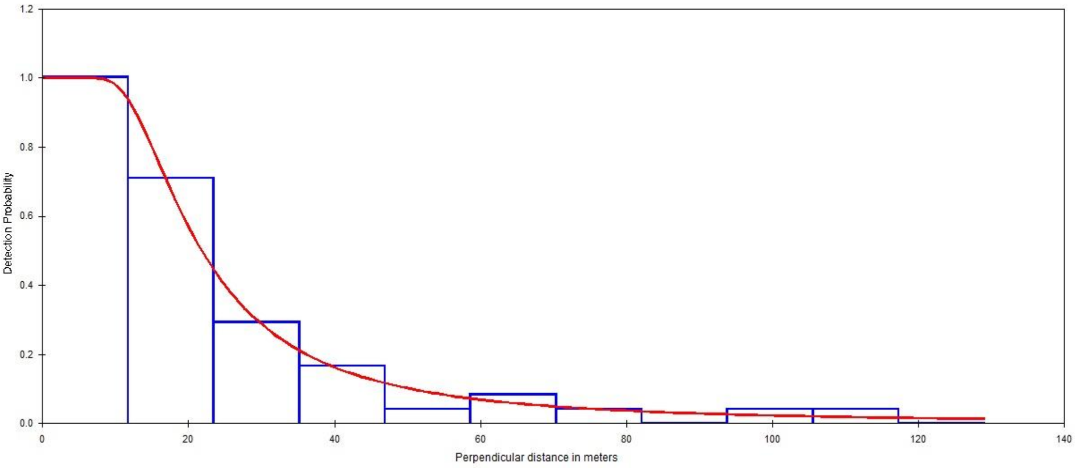


Figure 3.5: Hazard-rate detection function plot of Wild pig

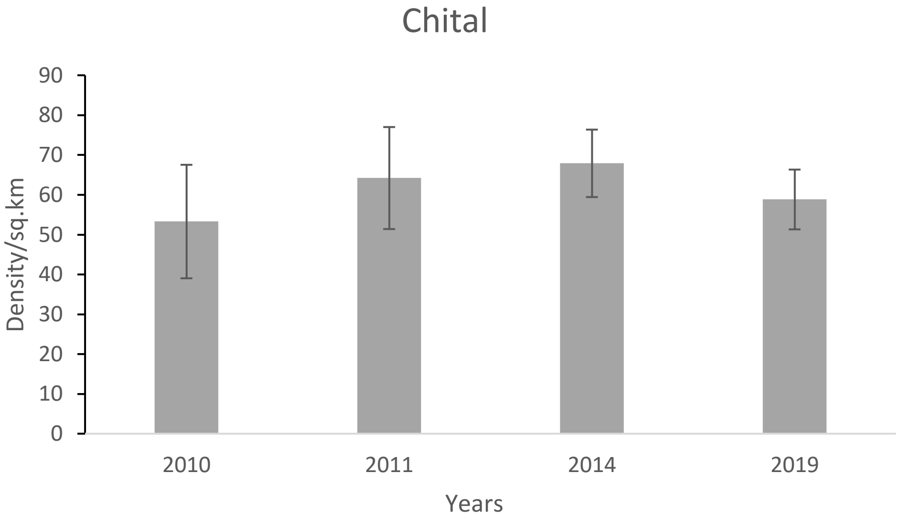


Figure 3.6: Distance sampling based individual density of chital per km^2 for each sampling years (2010, 2011, 2014 and 2019) with 95% confidence intervals

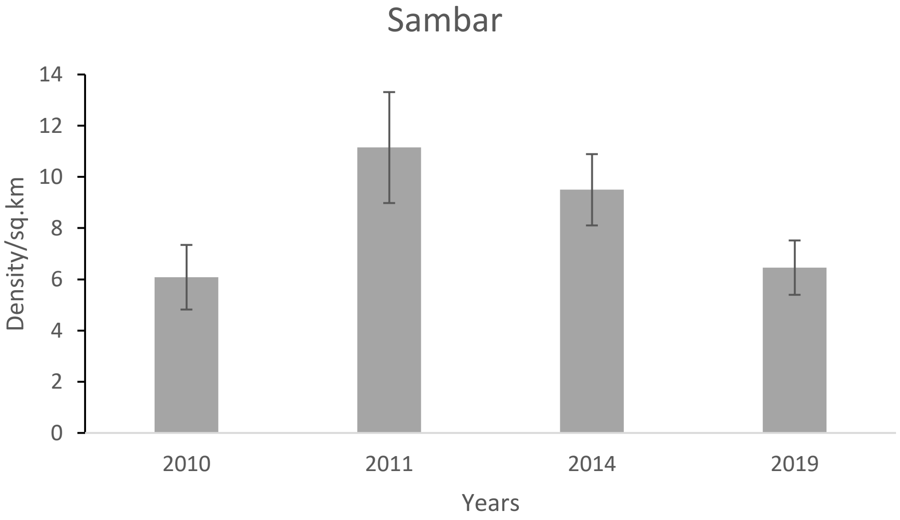


Figure 3.7: Distance sampling based individual density of sambar per km^2 for each sampling years (2010, 2011, 2014 and 2019) with 95% confidence intervals

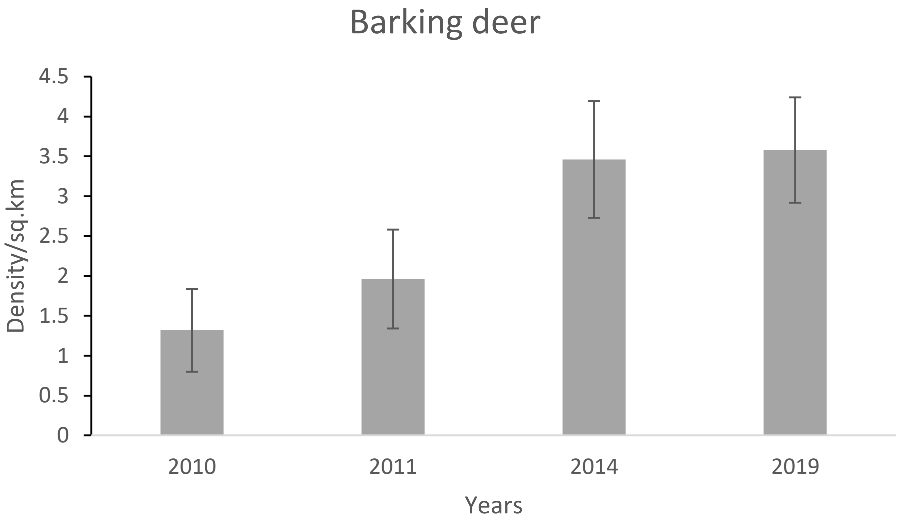


Figure 3.8: Distance sampling based individual density of barking deer per km^2 for each sampling years (2010, 2011, 2014 and 2019) with 95% confidence intervals.

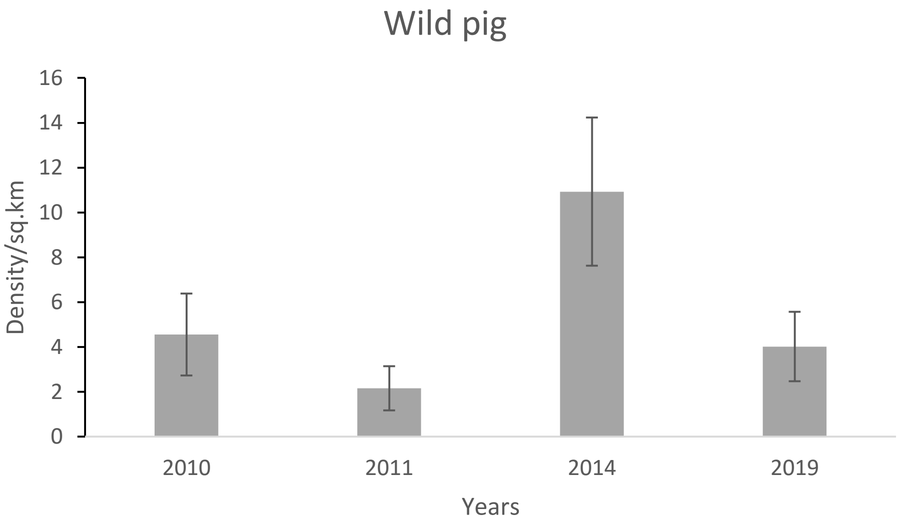


Figure 3.9: Distance sampling based individual density of wild pig per km^2 for each sampling years (2010, 2011, 2014 and 2019) with 95% confidence intervals

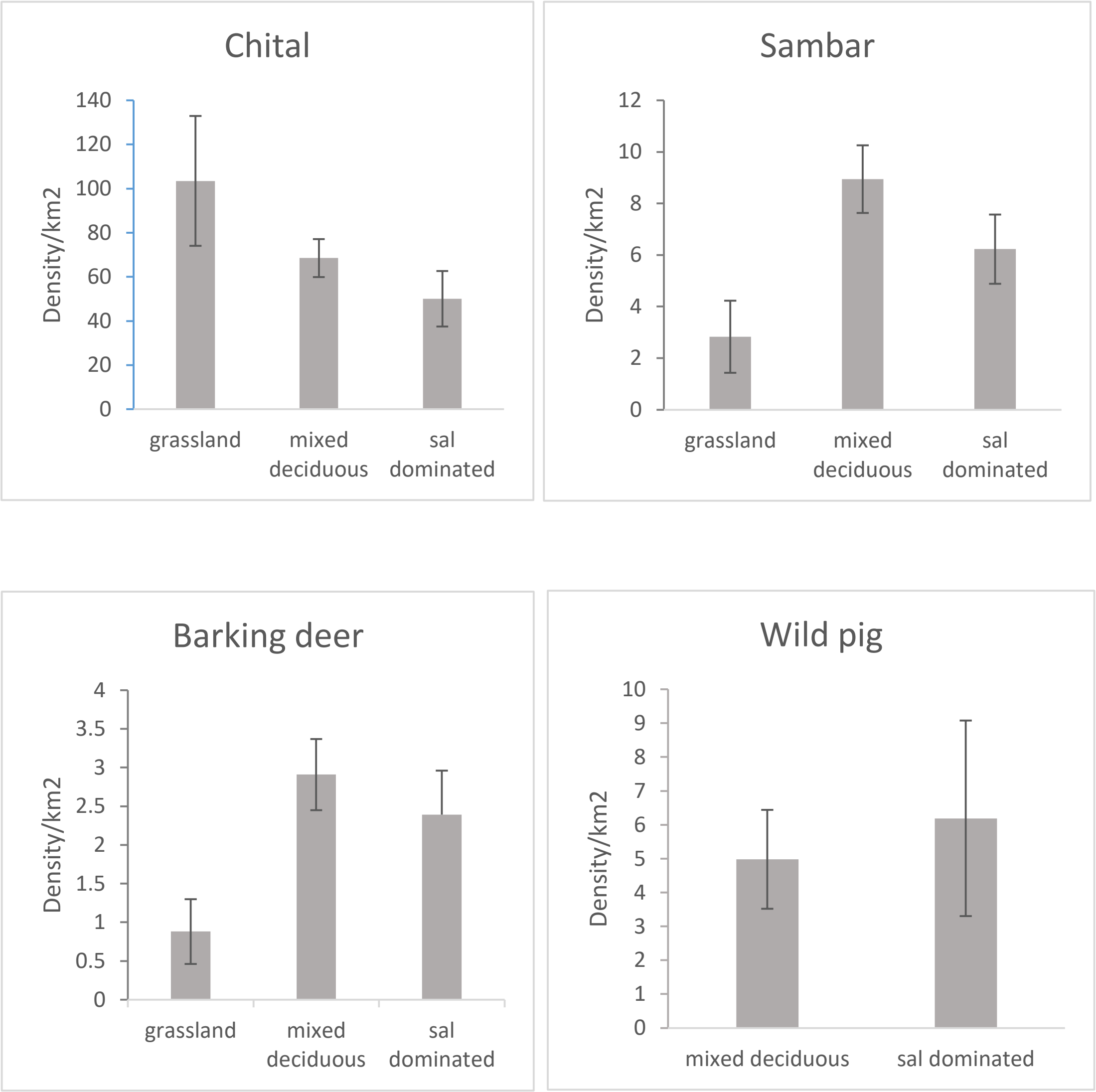


Figure 3.10: Habitat wise density of chital, sambar, barking deer and wild pig in CNP from post-stratified line transect based distance sampling data over 2010, 2011, 2014 and 2019.

Table 3.1: Line-transect distance sampling density estimates of chital, sambar, barking deer and wild pig reported for each sampling year (strata) and as mean of stratum estimates weighted by total effort in stratum (global). Standard errors of the model parameters and density estimates are provided in brackets. Percent coefficient of variation of the global density estimates are also provided.

Species	$\hat{p}$	*ESW*	$\hat{D}$ *2010*	$\hat{D}$ *2011*	$\hat{D}$ *2014*	$\hat{D}$ *2019*	$\hat{D}$ *global*	*%CV global*
Chital	0.16 (0.01)	33.69 (1.56)	53.3 (14.25) *n*=79	64.24 (12.81) *n*=143	67.92 (8.49) *n*=180	58.87 (7.51) *n*=226	61.58 (6.14)	9.97
Sambar	0.37 (0.02)	27.44 (1.82)	6.08 (1.26) *n*=24	11.15 (2.17) *n*=66	9.5 (1.39) *n*=67	6.46 (1.06) *n*=66	8.22 (0.92)	11.3
Barking deer	0.30 (0.02)	27.79 (2.08)	1.32 (0.52) *n*=9	1.96 (0.62) *n*=20	3.46 (0.73) *n*=42	3.58 (0.66) *n*=63	2.87 (0.39)	13.91
Wild pig	0.22 (0.03)	28.42 (4.48)	4.56 (1.83) *n*=7	2.16 (0.99) *n*=5	10.93 (3.31) *n*=30	4.02 (1.55) *n*=16	5.49 (1.48)	26.99

p = detection probability; ESW = effective strip width; D = density/km^2; n=number of observations of species

Table 3.2: Distance sampling based habitat-wise densities and important modelling parameters for chital, sambar, barking deer and wild pig in CNP. Standard errors are provided in brackets.

Species	Habitat	n/l	p	ESW	E(S)	D(S)	D/km^2
Chital	Grassland	1.14 (0.21)	0.28 (0.02)	58.2 (4.85)	10.52 (2.06)	9.83 (2.02)	103.46 (29.41)
	Mixed deciduous	0.62 (0.05)	0.12 (0.01)	25.65 (1.83)	5.66 (0.31)	12.11 (1.35)	68.53 (8.55)
	Sal dominated	0.39 (0.06)	0.21 (0.02)	43.98 (5.36)	11.09 (1.52)	4.51 (0.94)	50.08 (12.51)
Sambar	Grassland	0.14 (0.03)	0.24 (0.09)	41.58 (15.98)	1.58 (0.27)	1.78 (0.82)	2.83 (1.4)
	Mixed deciduous	0.22 (0.02)	0.16 (0.01)	28.66 (2.56)	2.24 (0.12)	3.97 (0.54)	8.94 (1.31)
	Sal dominated	0.23 (0.04)	0.2 (0.02)	36.25 (3.61)	1.92 (0.17)	3.23 (0.63)	6.23 (1.34)
Barking deer	Grassland	0.1 (0.04)	0.5 (0.15)	53.12 (16.28)	1.00	0.88 (0.42)	0.88 (0.42)
	Mixed deciduous	0.14 (0.02)	0.27 (0.02)	29.65 (2.07)	1.21 (0.03)	2.4 (0.37)	2.91 (0.46)
	Sal dominated	0.12 (0.02)	0.33 (0.04)	35.41 (4.83)	1.36 (0.09)	1.75 (0.4)	2.39 (0.57)
Wild pig	Mixed deciduous	0.06 (0.01)	0.17 (0.02)	35.31 (4.4)	5.88 (1.16)	0.84 (0.18)	4.98 (1.46)
	Sal dominated	0.06 (0.02)	0.17 (0.03)	35.87 (7.86)	6.62 (1.98)	0.93 (0.33)	6.19 (2.89)

n/l = Encounter rate; p = detection probability; ESW = Effective Strip Width, E(S) = Mean group size; D(S) = Group density, D/km^2 = Individual density per square kilometre

Table 3.3: Results of one-way ANOVA on summary line transect based year wise densities of chital, sambar barking deer and wild pig between sampling years to test for equality.

Species	*F statistic*	*df1*	*df2*	*p*
Chital(all years)	0.30	3	215	0.82
Sambar(all years)	2.35	3	215	0.07
Barking deer (all years)	2.15	3	215	0.1
Wild pig(all years)	3.21	3	215	0.02
Barking deer (2014,2019)	0.01	1	134	0.90

Table 3.4: Results of one-way ANOVA on summary line transect based habitat wise densities of chital, sambar, barking deer and wild pig to test for equality.

Species	Habitats	Grassland	Mixed deciduous	Sal dominated
Chital	Grassland	------	F = 1.81 P = 0.17	F = 3.89 P = 0.05
	Mixed deciduous	------	------	F = 1.15 P = 0.28
Sambar	Grassland	------	F = 2.76 P = 0.09	F = 2.33 P = 0.13
	Mixed deciduous	------	------	F = 1.15 P = 0.28
Barking deer	Grassland	------	F = 2.48 P = 0.11	F = 2.78 P = 0.1
	Mixed deciduous	------	------	F = 0.33 P = 0.56
Wild pig	Mixed deciduous	------	------	F = 0.15 P = 0.69

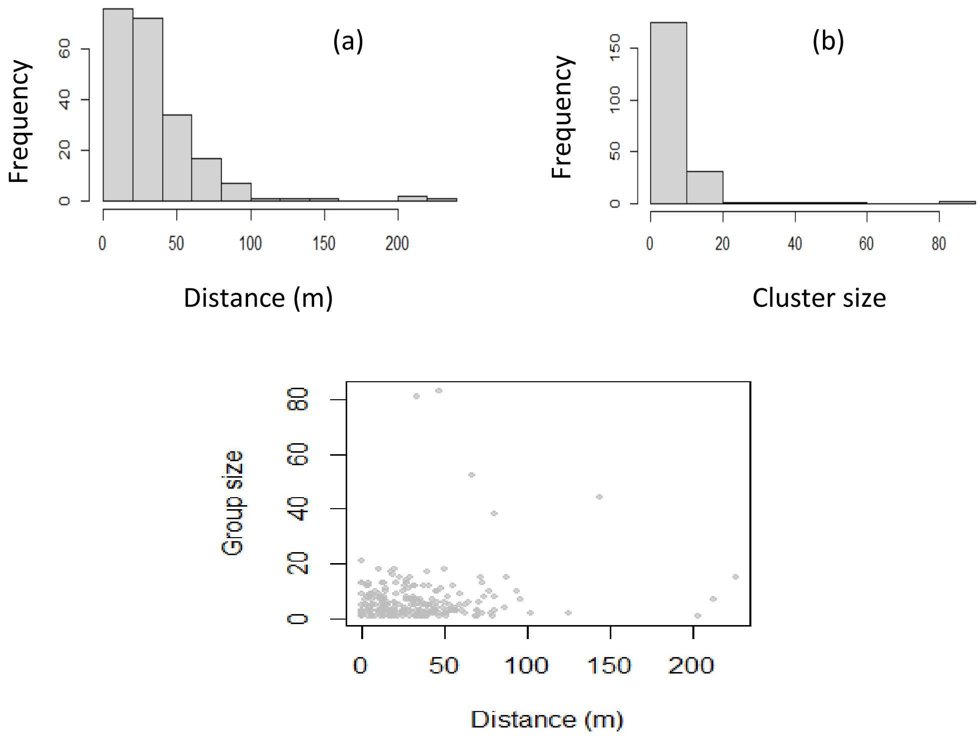
Density surface modelling

Chital

A total of 226 chital observations occurred on the 78 line transects of 2019. Analysing these distance observations of chital in the CDS engine resulted in a truncation distance of 86 meters, beyond which very few observations occurred and were needless for fitting detection functions. We used twice this truncation distance (172m) to subdivide the transects into equal lengths of 172m. This generated 778 total segments. Buffer area of 172m*172m was generated around each of these segments. This segment area was used as offset in the analysis. Out of the total 226 spatially referenced chital observations, 14 observations were outside the buffer area and hence were excluded from the analysis. Plotting the observed distances and cluster size shows few smaller clusters were observed in larger distances (Figure 3.11c). For detection function estimation of chital hazard rate function was selected over half normal using the chi-square goodness of fit test (Table 3.5; Figure 3.12). Detection probability was 0.32 (SE = 0.02).

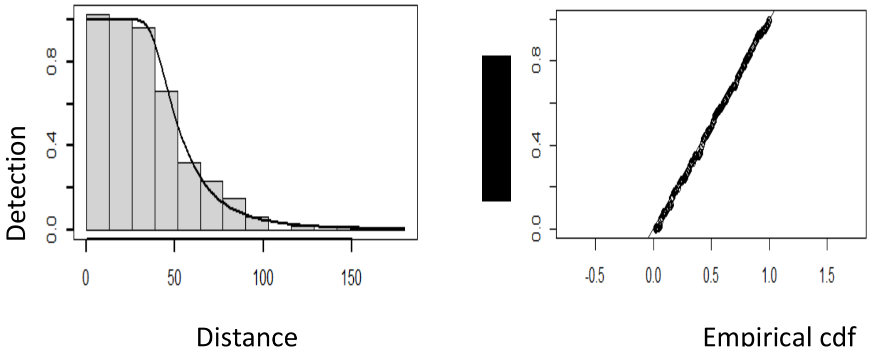
Modelling counts as function of their spatial co-ordinates explained 16% of the deviance. Among the covariates used NDVI and DEM explained most of the deviance as respectively, 20.5% (K = 14) and 18.7 % (K = 16). However, combining these covariates with the spatial co-ordinates of the counts in GAM increased the deviance explained to 25.7 % and 21.4% for NDVI and DEM respectively. Therefore, the final GAM was built by combining these three covariates. The overall deviance explained by the final GAM was 28.5% (Table 3.5). Checking the DSM using functions inbuilt in the dsm package generated diagnostic plots (Figure 3.14). The Q-Q plot shows that there was some level of deviation (Figure 3.14). The residual plot shows considerable number of zeros in the data (Figure 3.14).

The NDVI response curve shows that with higher NDVI value, reflecting dense vegetation, chital abundance decreased (Figure 3.13). The response curve of the DEM highlights the declining chital abundance with higher elevation (Figure 3.13). Chital abundance was predicted to be ~ 60771. Dividing this abundance by the total area of the predicted cells gives a density of 97.15 chital/km^2 (SE = 13.3). Figure 3.15 shows the density surface map for chital in CNP. Using the delta method co-efficient of variation (CV) of detection function was estimated to be 5.4 % and for GAM the CV was 12.6 %. Total co-efficient of variation was 13.7%.



(c)

Figure 3.11: Exploratory plot of chital distance data. Histograms of distance (a) and cluster size (b). Plot of distance against cluster size (c)



(a) (b)

Figure 3.12: Fitted hazard rate detection function (a) and goodness of fit (b) plot for chital

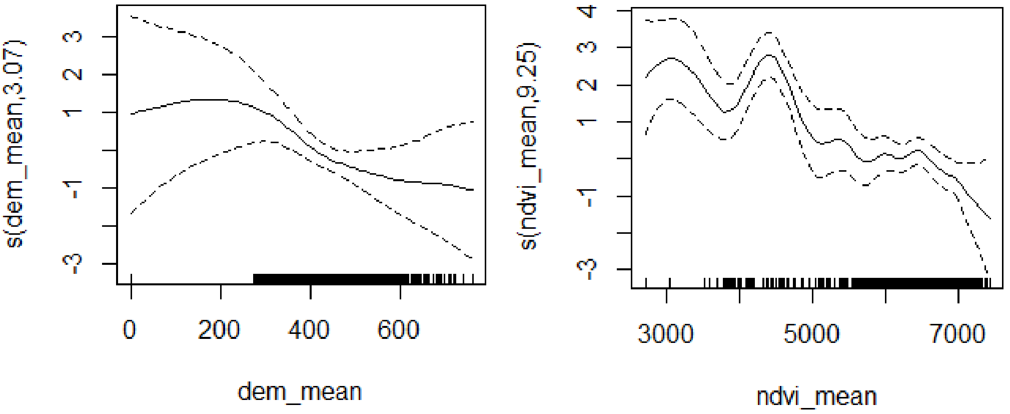
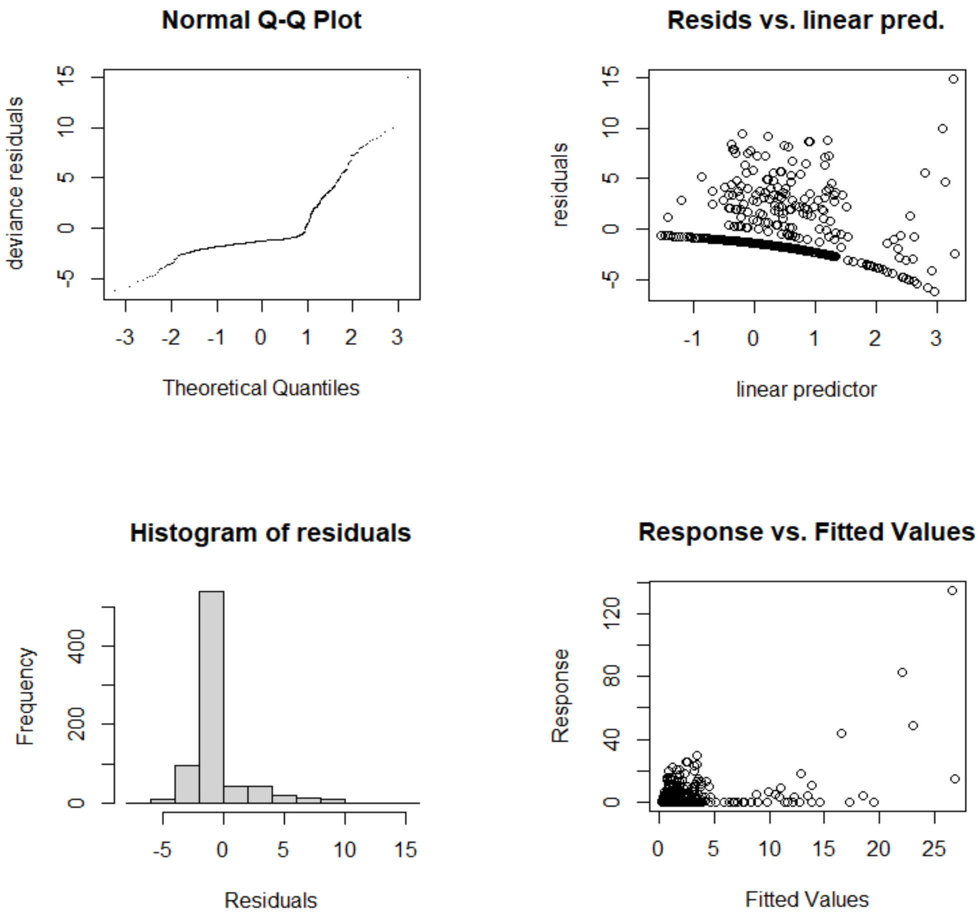


Figure 3.13: Response curves of mean of DEM and NDVI, the two covariates which explained most of the deviance for chital abundance.



Normal Q-Q Plot

Resids vs. linear pred.

Histogram of residuals

Response vs. Fitted Values

Figure 3.14: Diagnostics plot for the final DSM model for chital.

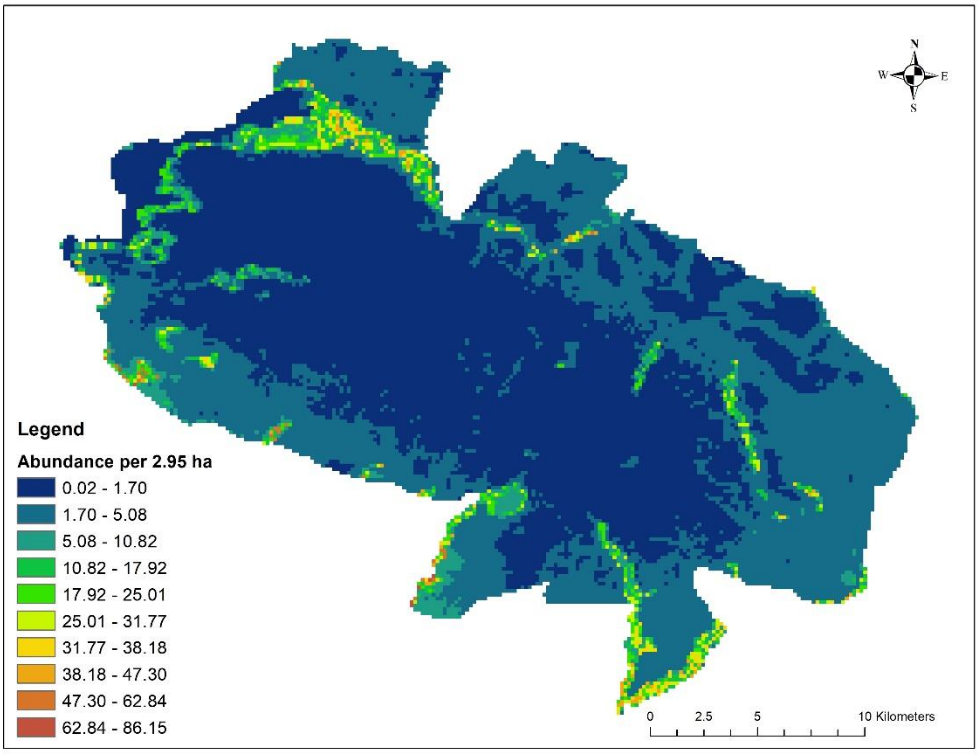
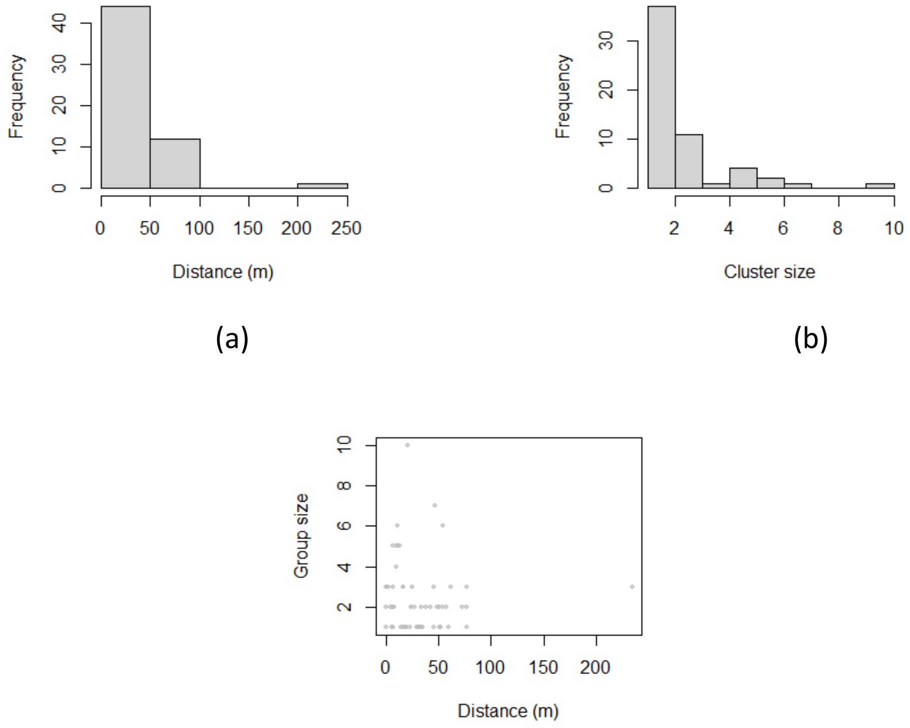


Figure 3.15: Density surface map of chital abundance in Corbett National Park

Sambar

68 sambar observations occurred on the 78 line transects. I truncated observations beyond 72m to fit detection function models in CDS. Transects were chopped into segments of 144m (2*72m) and buffer of 144m*144m was created around this chopped segments. A total of 922 segments were generated. Out of the 68 sambar observations, 11 observations were outside the segment area and hence were excluded from the analysis. Plotting the observed distances with cluster size showed only one small cluster size detected at a larger distance (Figure 3.16). Half-normal was the selected model with a higher chi-square goodness of fit P value than hazard rate (Table 3.5). Figure 3.17a and Figure 3.17b shows the detection function plot and the goodness of fit plot respectively. Detection probability was estimated to be 0.46 (SE = 0.05).

Modelling counts as a smooth function of their spatial co-ordinates as GAM explained 17.4% deviance. For Sambar, NDVI and mean of ruggedness explained most of the deviance as respectively, 9.8% and 12.4%. Combining spatial co-ordinates of counts as a covariate with these two parameters increased the respective deviance explained to 22.7% and 26.8%. The overall deviance explained by the combined model, using spatial co-ordinates of counts, NDVI and ruggedness was 36% (Table 3.5). The Q-Q diagnostic plot highlighted deviation and the residual plot showed high frequency of zeros in the data (Figure 3.19). Although the ruggedness response curve did not reflect much relationship of abundance with the parameter, but the NDVI response curve shows that sambar presence increased with dense vegetation (reflected by higher NDVI value) initially and becomes nearly stable after a certain extent (Figure 3.18). The combined DSM predicted an abundance of ~ 6797 sambar in CNP, which yielded a density of 10.86 sambar/km^2 (SE = 1.86). Density surface map of sambar was generated (Figure 3.20). Using delta method percentage CV of detection function and GAM was 10.8% and 13.3% respectively. Overall CV was 17.14%.

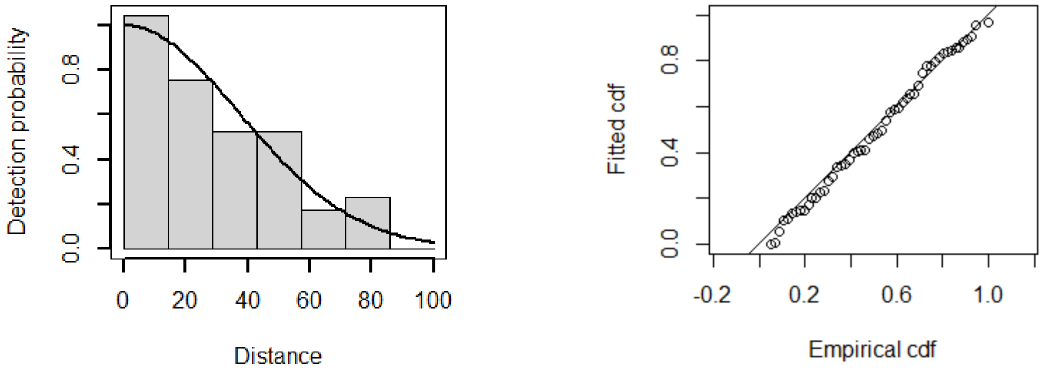


(a)

(b)

(c)

Figure 3.16: Exploratory plot of sambar distance data. Histograms of distance (a) and cluster size (b). Plot of distance against cluster size (c).



(a)

(b)

Figure 3.17: Fitted half normal detection function (a) and goodness of fit (b) plot for sambar.

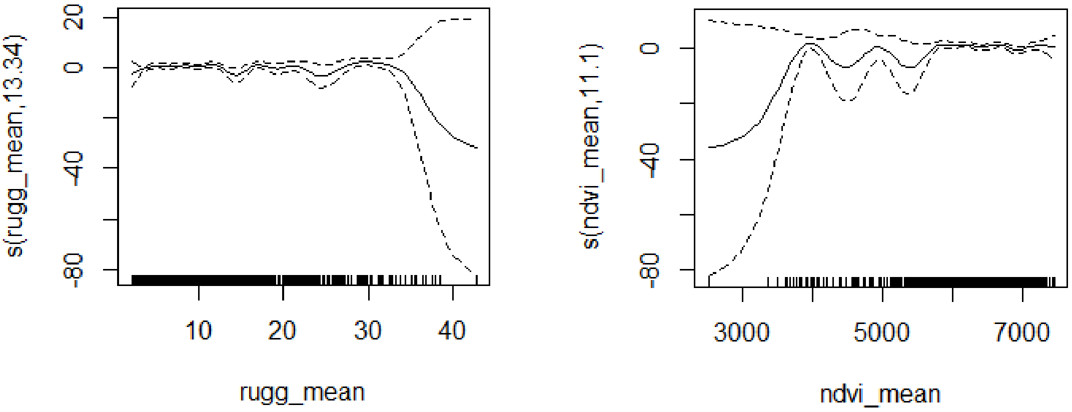


Figure 3.18: Response curves of mean of ruggedness and NDVI, the two covariates which explained most of the deviance for sambar abundance.

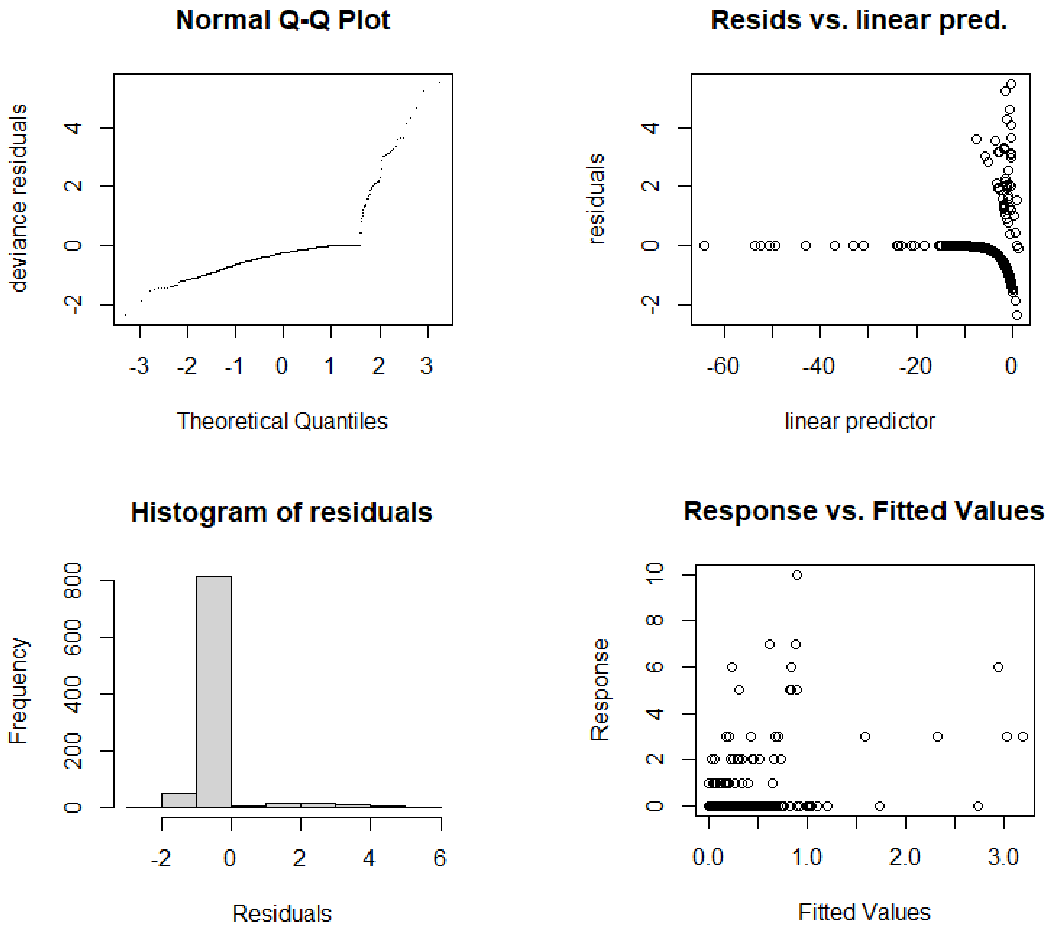


Figure 3.19: Diagnostics plot for the final DSM model for sambar. The Q-Q plot shows that there was deviation in the data. The residual plot shows considerable number of zeros in the data.

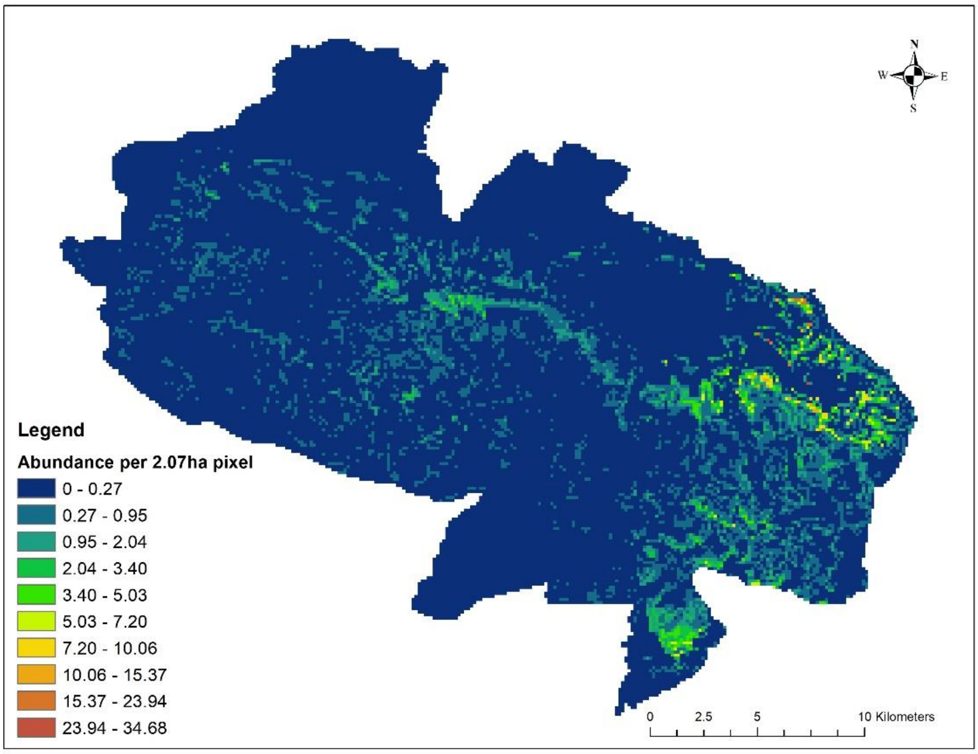
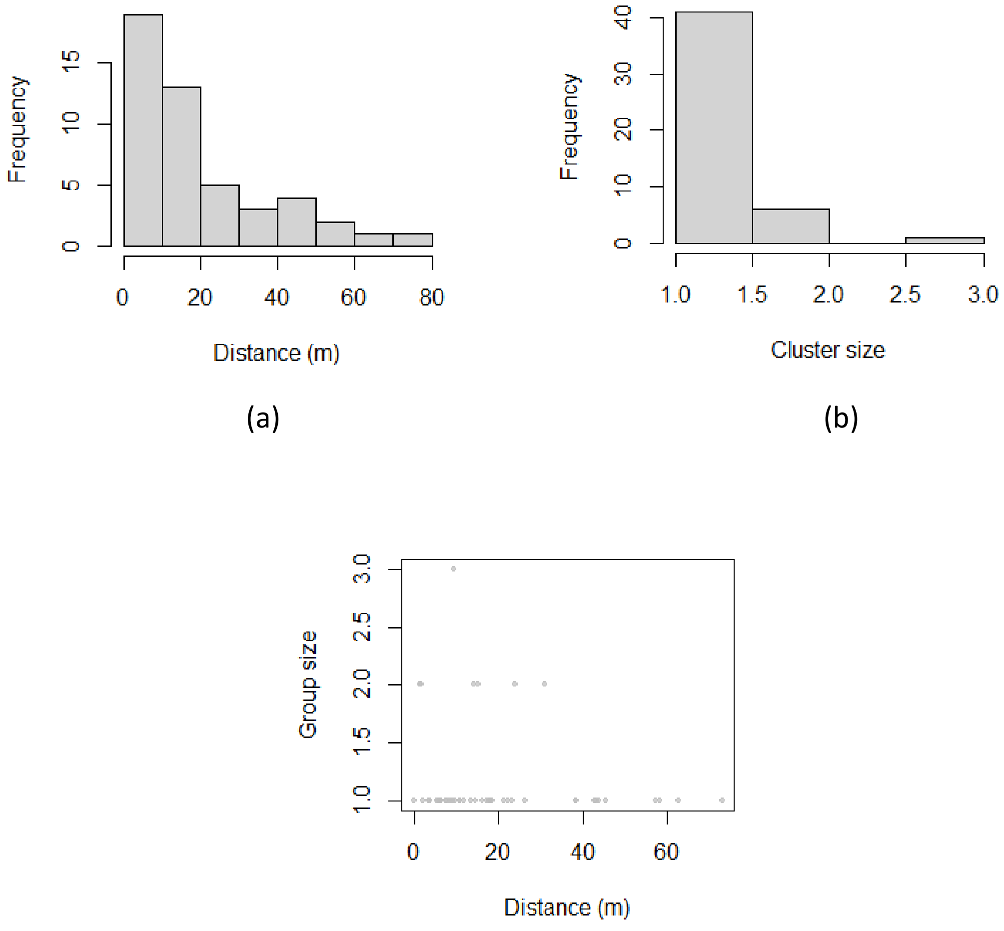


Figure 3.20: Density surface map of sambar abundance in Corbett National Park

Barking deer

Barking deer observations were 63 on the 78 line transects. Truncation distance was 50m for fitting detection function models in CDS engine. Using twice this truncation distance (2*50m) transects were subdivided into segments of 100m and buffer of 100m*100m was created around each of these segments. Chopping the transects into 100m segment generated a total of 1307 segments. Out of the 63 barking deer observations, 15 observations were outside the segment area and hence were excluded from the analysis. Plotting the observed distances with cluster size showed that few smaller clusters were sighted at larger distances (Figure 3.21c). Hazard rate detection function was selected giving a detection probability estimate of 0.26 (SE = 0.05). Figure 3.22a and Figure 3.22b shows the detection function plot and goodness of fit plot respectively.

GAM modelling of counts as a function of spatial co-ordinates explained 14% of the deviance. NDVI mean and mean of slope explained most of the deviance of barking deer abundance, as respectively 5.5% and 7.98% respectively. Modelling spatial co-ordinates of counts with these two parameters increased the respective deviance explained to 17.3% and 21%. Therefore, the final DSM was built by combining spatial co-ordinates of counts, mean of NDVI and mean of slope, which explained 19.4% of the overall deviance. Model checking using Q-Q diagnostic plot and histogram of residuals exhibited deviation and random high frequency of zero in the data (Figure 3.24). Response curve of mean NDVI shows that barking deer abundance increased with increase in vegetation density, however decreasing after a certain level (Figure 3.23). Response curve of mean of slope indicates a decreasing abundance trend with increase in slope (Figure 3.23). The combined DSM predicated an abundance of ~ 4730 barking deer in CNP, which resulted into a density of 7.5/km^2 (SE = 1.92). Density surface map of barking deer was generated (Figure 3.25). Using delta method percentage CV of detection function and GAM was 18% and 18.1% respectively. Overall CV was 25.6%.



(a) (b)

(c)

Figure 3.21: Exploratory plot of barking deer distance data. Histograms of distance (a) and cluster size (b). Plot of distance against cluster size (c).

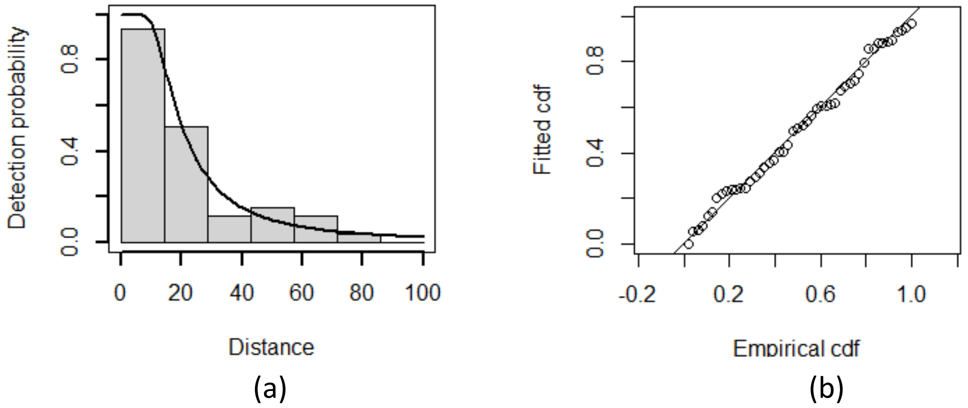


Figure 3.22: Fitted hazard rate detection function (a) and goodness of fit (b) plot for barking deer

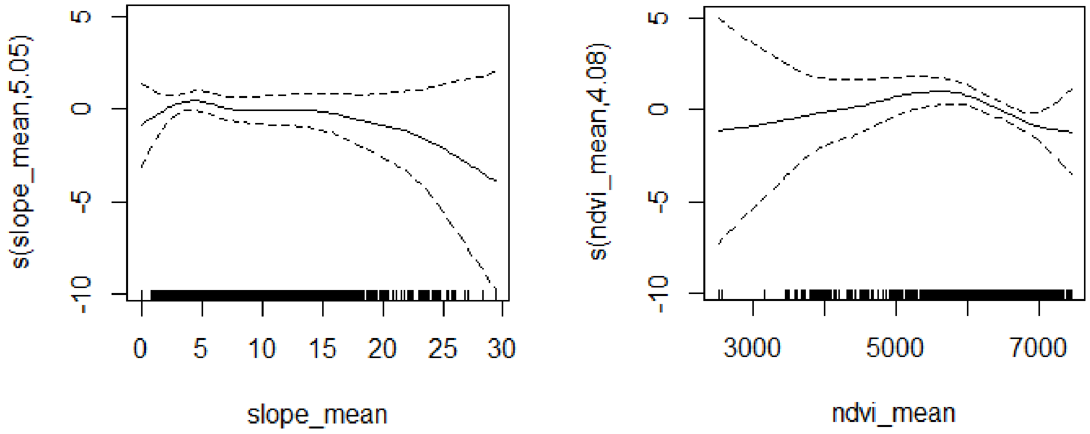


Figure 3.23: Response curves of mean of slope and NDVI, the two covariates which explained most of the deviance for barking deer abundance.

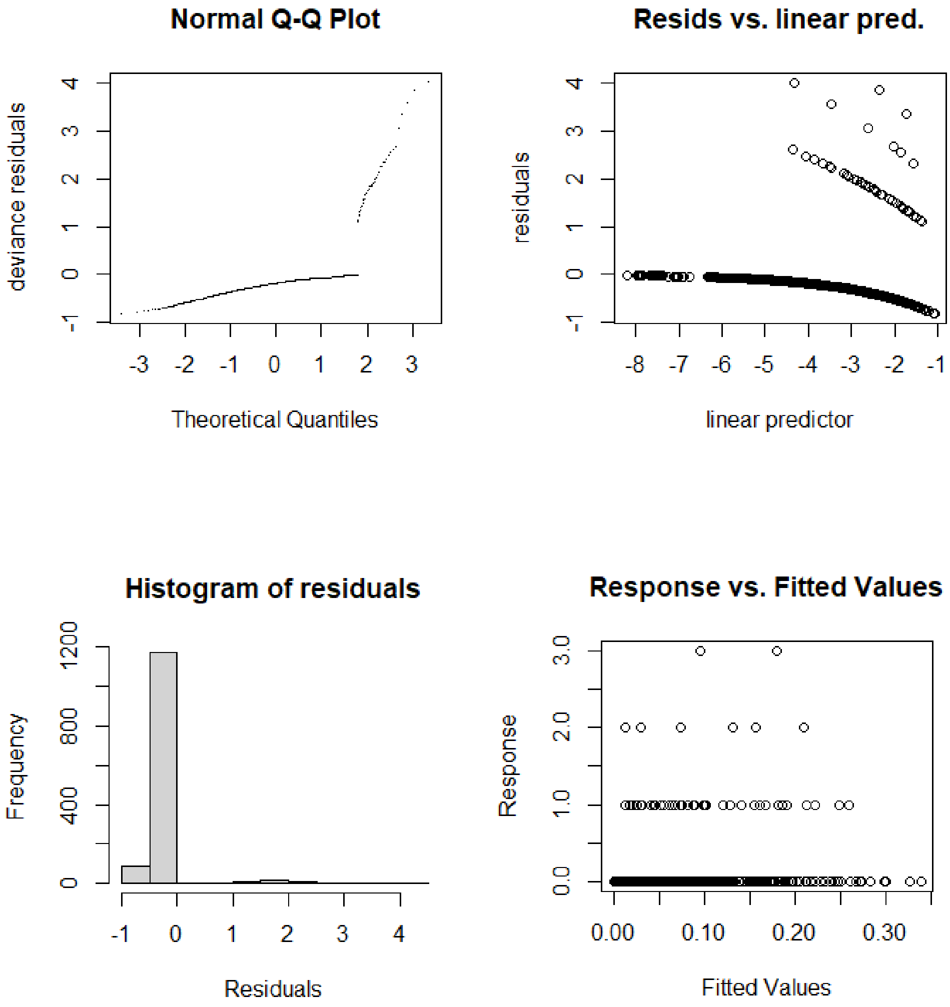


Figure 3.24: Diagnostics plot for the final DSM model for barking deer. The Q-Q plot shows that there was a considerable deviation in the data. The residual plot shows considerable number of zeros in the data.

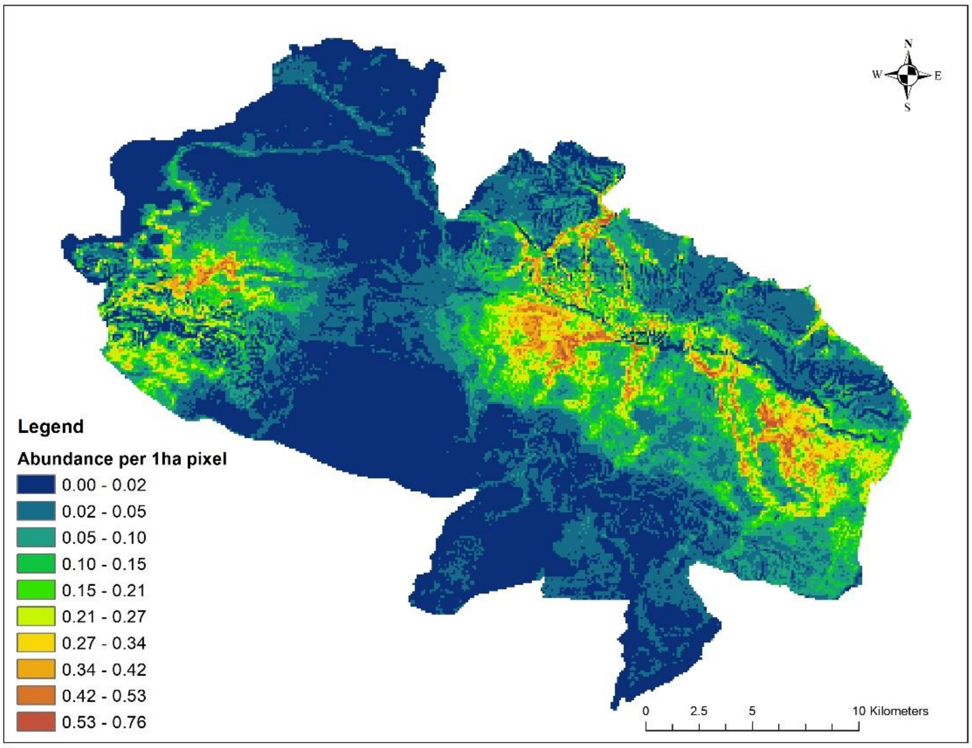


Figure 3.25: Density surface map of barking deer in Corbett National Park

Table 3.5: Best selected models for each species are presented. Reported number of detections (n) for each species, selected detections models with goodness-of-fit statistics [GOF-p (d.f.)], the significant smooth functions of the covariates * (estimated degrees of freedom), percentage deviance explained by the final DSMs† a
of each species (individual per km^2) with associated standard errors.

Species (n)	Chital (226)	Sambar (68)	Barking deer (63)
Detection model	Hazard-rate	Half-normal	Hazard-rate
GOF-p (d.f.)	0.89 (11)	0.5 (5)	0.43 (4)
GAMs			
Intercept	-9.6	-13.59	-12.45
s (NDVI-mean)	0.48*(9.04)	0.04*(11.1)	0.3*(4.08)
s (DEM-mean)	0.97*(3.07)	-----	-----
s (rugg-mean)	-----	0.7*(14.1)	-----
s (slope-mean)	-----	-----	0.22*(5.05)
s (x,y)	0.02*(9.44)	0.06*(10.2)	0.29*(14.4)
s(x,y) + s (NDVI-mean) + s(DEM-mean)	28.5†	-----	-----
s(x,y) + s (NDVI-mean) + s(rugg-mean)	-----	36†	-----
s(x,y) + s(NDVI-mean) + s (slope-mean)	-----	-----	19.4†
Overall individual density (per km^2) ± SE	97.1 ± 13.3	10.86 ± 1.86	7.5 ± 1.92

Table 3.6: Predictor variables used to estimate spatially explicit densities of ungulates using DSM.

Remotely sensed covariates	Description
NDVI-mean	Mean of Normalized Differential Vegetation Index
DEM-mean	Mean of Digital Elevation Model derived from ground elevation data at 30-m resolution from the Shuttle Radar Topographic Mission dataset (SRTM); SRTM GL3_NC.003
slope-mean	Mean of slope of the area extracted at a resolution of 30m*30m cell size
rugg-mean	Mean ruggedness of the area extracted at a resolution of 30m*30m
wh_mean	Mean of distance to waterhole
lc_puresal, lc_misc, lc_grslnd	Landcover map of pure sal forest, miscellaneous and grassland habitats

3.4 DISCUSSION

CNP encompasses heterogeneous habitats with predominately undulating terrain. It was crucial but challenging to capture the habitat heterogeneity using line transects. Logistical constraints initially (2010) meant limited transect sampling coverage. However, number of spatial transect samples and effort increased substantially over years allowing me to account for the habitat heterogeneity which can significantly affect species movement and detectability. Although almost all the habitat types were sampled by transects, but a substantial portion of steep hilly terrain (ridges running from west to east) remained largely unsampled (Figure 3.1). This was primarily due to the difficulty in laying and maintaining random straight line transects in such steep terrain. Transects were laid from a random start point using a random bearing but were carefully oriented to avoid placing them parallel to any river streams, a major characteristic of the area, therefore, a) negating any bias in species sightability arising from species’ preferential usage of partic

the transects were random in respect to animal distribution (Buckland et al., 1993). Each transect was walked 1- 4 times each year in order to obtain the recommended number of species observations required for modelling detection function. I believe that detections across these replicates were independent as the replicates were walked in different days. Moreover, density estimators in distance sampling are quite robust with respect to independence issue (Buckland et al., 1993). The number of independent transects (n=156) together with the temporal replicates were sufficient enough to account for the variance due to species encounter rate. Although, ideally sampling should have occurred in each year, but owing to administrative matters, sampling was not possible between the year 2014 and 2019. However, comparing the species density between 2014 and 2019 using distance sampling summary data revealed that, except for wild pig, density of all the other three ungulate species did not differ significantly (chital, F = 0.63, p = 0.42; sambar, F = 3.13, p = 0.08; barking deer, F = 0.01, p = 0.9, wild pig, F = 4.3, p = 0.04).

It was important to assess whether the assumptions of distance sampling were valid during sampling. Histograms of perpendicular distances of the species show that chital, barking deer and wild pig showed evasive movement prior to detection hence detections were less on or till some distance from the line (Figure 3.26). Such evasive movement however was relatively less for sambar (Figure 3.26). Distance and angle measurements were accurate as these were collected using laser range-finder and see through compass. Comparing the detection probability plots of the four ungulates, it seems that detection of sambar and barking deer falls relatively more sharply than chital and wild pig (Figure 3.3 and 3.4) as evident from the peaked probability plot, while for chital and wild pig the plots were shouldered (Figure 3.2 and 3.5) meeting the shape criterion (Buckland et al., 1993). Lower number of transect samples in the year 2010, led to very less observation of barking deer and wild pig, however detection function modelling was possible but density estimates were highly imprecise. Particularly for wild pig, observations did not however increase significantly with increase in sampling effort in the subsequent years and estimates were very imprecise, probably hinting that line transect is not a suitable technique for estimating density of the species, or a better different design with much larger sampling effort will be required.

Habitat wise density estimation by post stratification of the transects demonstrated the usual occurrence of the species in these habitats as similarly reported in different studies (Awasthi et al., 2016; Bagchi et al., 2004; Dave, 2008; Khan et al., 1996). However, I acknowledge that systematic and comparable sampling effort at each of the habitat types would have been more robust, which is largely lacking in my study, primarily owing to lack of sampling opportunity and difficulty in appropriately classifying the complex heterogeneous habitats of CNP beforehand. This issue of post stratifying the transect data resulted in fewer than minimum number of sambar observations in grassland, and, barking deer observations in both grassland and sal dominated habitat, which although might also reflect the general low occurrence of these species in these habitat types (Awasthi et al., 2016). Highest density of Chital in the grassland reflects that the species is a predominant grazer and an open forest species, while its lower density in sal dominated forest might reflect that the species avoids dense canopied forest in order to avoid predation by tiger and due to unavailability of sufficient forage. CNP has very high tiger density (Jhala et al., 2020) and chital being the most abundant of the ungulates is presumably the preferred prey species (Bisht, 2019). Sambar on the other hand, is known to be both a browser and grazer and prefers dense forest relatively more. Higher density of sambar in mixed deciduous and sal dominated forest types than in grassland conforms to this general characteristics of the species (Kushwaha et al., 2004; Varman & Sukumar, 1993). Barking deer density estimates in the respective habitats exhibits a similar pattern and is also known to prefer dense vegetation like the sambar (Awasthi et al., 2016; Kushwaha et al., 2004). Although, wild pig is not known to show preference for any particular habitat type and is known to occupy all the habitats wherever found (Keuling and Leus, 2019), only two observations of the species in the grassland in my study, can be attributed to the otherwise elusive behaviour of the species. Higher density of wild pig in sal dominated followed by mixed deciduous habitat is probably due to the availability of food which primarily includes roots, tubers, bulbs, bark, flowers, fruits, seeds and sedges (Spitz, 1986). The general low number of wild pig observations on transects render the technique inappropriate for estimating the species density. Few studies have however suggested nocturnal transect with infrared camera as an effective sampling method (Focardi et al., 2020).

I used the spatially referenced distance sampling data of 2019 for density surface modelling of ungulates because, a) among all the sampling years, 2019 had the highest number of spatial transects, meaning a better spatial coverage of all the available habitats and terrain, except for the very steep hilly ridges (Figure 3.1) and, b) more than recommended number of spatially referenced observations of all the three ungulates. Although, my study lacks seasonal comparison of spatial density of these ungulates, which would have been ecologically more significant, but I believe my study will most definitely act as a reference for future similar investigations and will also be important for management interventions. Modelling the detection function demonstrated the expected shouldered pattern, denoting proper fit, as also observed from the goodness of fit statistics. The significant percentage of deviance explained and low CV of the selected DSMs for all the three ungulate species, suggest strong predictive power of the models. In my case, although Tweedie distribution should have been statistically appropriate for fitting the data than quasipoisson, given the high proportion of zero, however Tweedie distribution was returning erratic abundance estimates and incorrect response curves. Mean NDVI as one of the selected covariates in all the chosen DSMs suggest the significant effect of vegetation density on species abundance pattern, thereby highlighting the importance of seasonal comparison even more. At least one terrain variable was also selected in all the final DSMs, signifying a crucial relationship of species' numb

surprisingly for sambar, which is known to prefer rugged terrain did not however exhibit a strong trend with the terrain type, probably due to the dominating effect of forage availability during the sampling duration. Chital was present throughout the park, although higher abundance was observed in the grasslands and large riverbeds. DSM based chital density was nearly double than the CDS based density of the year 2019. This could be due to over prediction of chital abundance in grassland area by the DSM. However, the DSM density is almost similar with the habitat-wise post-stratified CDS based density of chital in the grassland strata (Table 3.2).

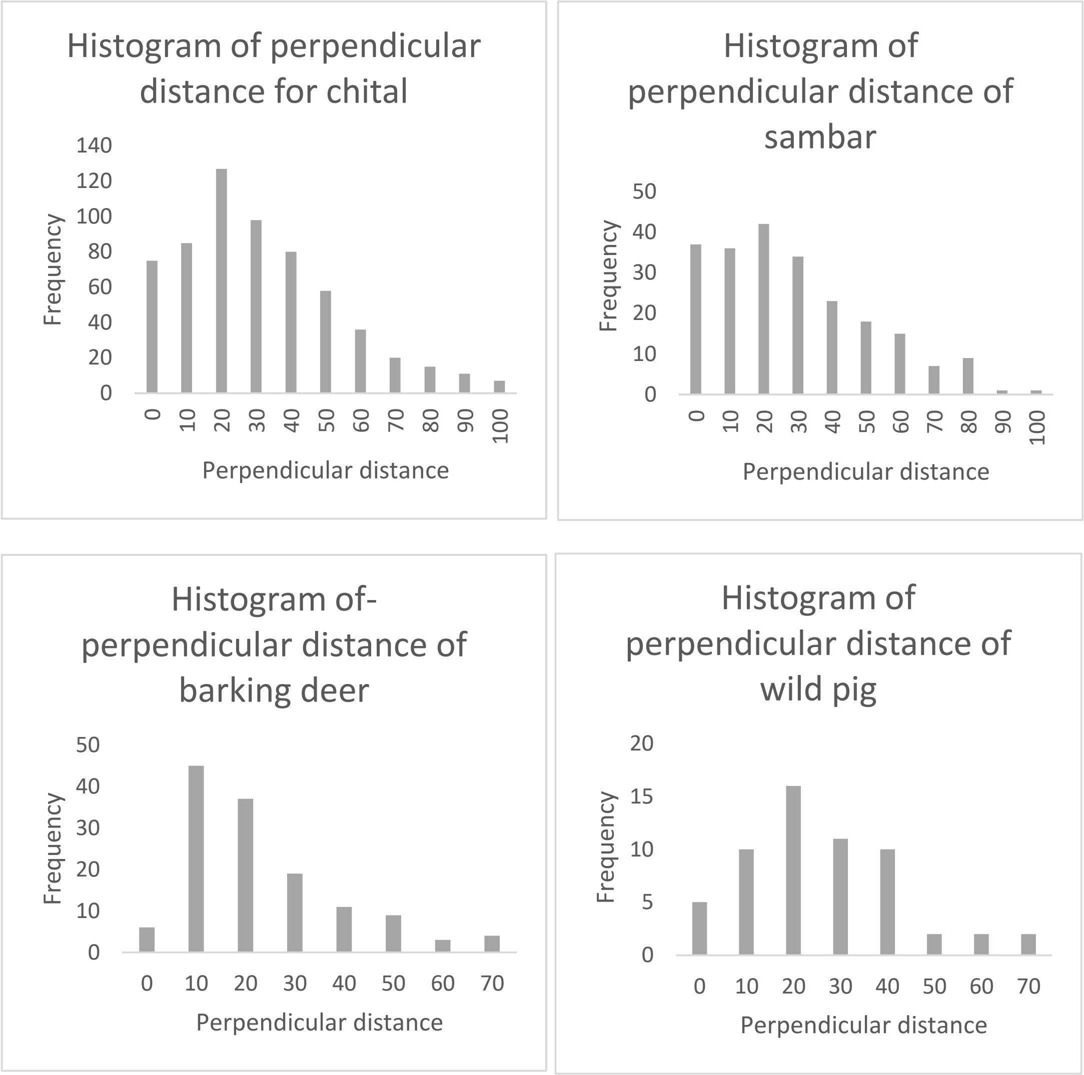


Figure 3.26: Histogram of perpendicular distance plots for chital, sambar, barking deer and wild pig

CHAPTER IV COMPARISON OF ABUNDANCE ESTIMATION TECHNIQUES

4.1 INTRODUCTION

Density and abundance of species are fundamental to our understanding of ecosystems, and a requirement for effective management of populations, be it for sustainable use or conservation (Williams et al., 2002; Andrewartha & Birch, 1954). However, obtaining accurate estimates of density for most wildlife populations is often a daunting task and depends on obtaining probability (Yoccoz et al., 2001). Detection probability can vary with species size, colouration, behaviour, habitat, weather conditions during sampling, and interactions amongst these (Buckland et al., 2011, Zimmerman and Gutierrez, 2007). Therefore, it is vital to use methods that account for detection probability but which are also practical in a range of environmental conditions and species assemblages. In this chapter, I report a cost-effective evaluation of three such methods by comparing density estimates of four ungulate species, chital (*Axis axis*), sambar deer (*Rusa unicolor*), barking deer (*Munitacus vaginalis*) and wild pig (*Sus scrofa*) in Corbett National Park (CNP).

Techniques such as capture-mark-recapture (CMR) (White and Burnham, 1999; Pollock, 2000) and distance sampling (Buckland et al., 1993) have been commonly applied to estimate density/abundance after modelling for imperfect detection. However, since each of these approaches relies on different preconditions and assumptions, each has its advantages and disadvantages in applying for different species, populations, and habitat conditions (Williams et al., 2002, Wearn and Glover-Kapfer, 2017).

Density estimation based on distance sampling does not require individual recognition. Estimates are based on observed distances of animals from a line or point to model species detectability and estimate absolute density (Buckland et al., 1993). With a well-described theoretical framework and comprehensive software, distance sampling has become a widely used technique across a broad spectrum of species and is often used for large-scale monitoring of species that can be visually detected in reasonable numbers (Kumar, 2000; Focardi et al., 2005). However, the method depends on a few critical assumptions (discussed in chapter III) sensitive to species-specific behaviour, habitat, and terrain conditions (Buckland et al., 2001). For example, the assumption of random sampling, critical for any detectability-corrected sampling method, is prone to violation in rugged terrain due to the difficulty in laying and walking random straight line transects. Moreover, in hunted populations evasive movement of animals due to the presence of the observer often makes it difficult to detect initial location of animals (Southwell, 1994), while some species remain unavailable for human observation (Fragoso, 2016) thus violating crucial assumptions of distance sampling (Buckland et al., 2001) which can produce biased density estimates (Waltert et al., 2020).

For species where individuals can be recognized from natural markings (Karanth and Nichols, 1998; Bisht et al., 2019; Harmsen et al., 2020) or by artificial markings (Pine et al., 2003; Sutherland et al., 2016), CMR has been the abundance estimation method of choice. CMR sampling of a population has been done by physically capturing and recapturing individuals, or, more recently using automatic camera traps or by genotyping of DNA samples from scats or tissues (Goode et al., 2014; Keiter et al., 2016; Kubasiewicz et al., 2017). Sampling by any of these forms generates unique capture/recapture histories of individually identified animals over a duration of time, divided into multiple (Otis et al., 1978). Traditional non-spatial CMR (Otis et al., 1978) models probability of initial capture (p) and the probability of recapture (c) from histories of individually marked animals, easily constructed using a matrix comprising of 'X'0 where '0' signifies non-capturing of a particular individual in a particular occasion and, '1' signifies capture in a particular oc (Otis et al., 1978), to estimate population size (N) under the full likelihood parameterization process. Capture history indicates the underlying probability of capture/de an outcome of a binomial or multinomial distribution (Williams et al., 2002). Theoretical basis of CMR is to model the variations of these individual capture probabilities and estimate absolute abundance of species. The foundational two-occasion based Lincoln-Peterson index of estimating population abundance using capture-recapture assumed equal capture probability across animals, however, such equal probability is unrealistic in wild populations which can vary by factors such as time, individual's age, sex, movement of individuals et to 'traps' upon initial capture (e.g. trap-shy or trap-happy). Conventional closed capture-recapture modelling however generalises this restrictive assumption and requires capture probabilities to be appropriately modelled. Various maximum likelihood based models allowing capture-probability to vary singularly by time (Mt), behavioural response of animals to traps (Mb) or individual heterogeneity based on age or sex

(Mh), or, as combination of these factors (Mtb, Mth, Mbh and Mtbh), have been developed to account for the unequal capture probability in order to effectively estimate abundance of species (Otis et al., 1978). Another important assumption for effective CMR modelling is consideration of a population to be geographically and demographically closed, meaning, no immigration/birth and emigration/death, from and within the sampling area and duration. However, this assumption is hardly met for large mobile animals owing to their biological characteristics and under various field conditions (Boulanger & Mclellan, 2001; Dupont et al., 2019; Williams et al., 2002). Kendall (1999) evaluated many scenarios of possible violation of closure and found that complete random movement of individuals in and out of the sampled area does not produce bias in estimates, only affecting the precision. Therefore, designing the survey period of a meaningful short duration can effectively deal with the issue of closure violation (Williams et al., 2002). Sampling a population of uniquely identified individuals (mt+1) within a duration of time (t) following CMR modelling framework yields a population size. Individual density is estimated by dividing this population size by the effective trapping area (ETA) calculated by adding a buffer strip of calculated either from mean of maximum distance moved (MMDM) by all individuals or half of this distance (1/2 MMDM) or home range radius of animals, either obtained from captures of individuals across different traps or from telemetry based estimate (Alonso et al., 2015; Sharma et al., 2010).

However, many mammals cannot be reliably identified by their markings, leaving the need for other methods to estimate the density of these species. With the advancement of sensor technology, heat-and-motion triggered infrared camera traps capable of non-invasively capturing the movement of animals have increasingly become the popular choice in wildlife monitoring studies (O'Connell, 2010). Photographic encounter rates of animals at camera traps are often used to surrogate abundance (Carbone et al., 2001; O'Brien et al., 2003; Rovero and Marshall, 2009). However, at best, these encounter rates are considered to be a biased index of abundance since they do not account for detection probability and variation in detection across species, time, and study sites (Jenelle et al., 2002). Remote camera trap-based random encounter model (REM) (Rowcliffe et al., 2008) and distance sampling (Howe et al., 2017) techniques have successfully modelled detection probability from contacts of animals with the camera traps have demonstrated potential for estimating absolute density of unmarked animals under a wide range of environmental conditions (Corlatti et al., 2020; Cusack et al., 2015; Gray, 2018; Pal et al., 2021).

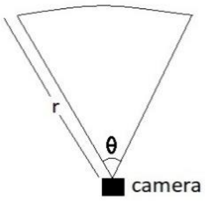


Figure 4.1. A schematic diagram of detection zone dimensions (radius and angle) of camera trap

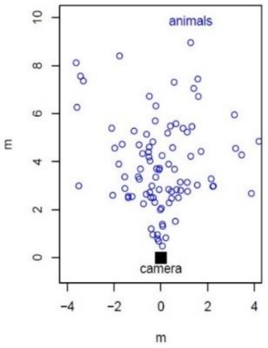


Figure 4.2. Representative image showing animal positions during each initial contact with the camera.

Developed with the concept of two-dimensional ideal gas collision theory, REM requires two biological attributes (speed and activity level of a species) and two camera detection zone (sensor) parameters (radius and angle within which it detects animals) (Figure 4.1) to model the underlying detection probability using contacts of animal with the camera (Rowcliffe et al., 2008). Critical to REM is estimating an effective detection area, inside the camera field of view (FOV), estimated from effective detection radius (EDR) and effective detection angle (EDA) derived from animal positions on first encounter with the camera (Figure 4.2). EDR is the distance at which the number of animals detected further away from the camera equals the number of animals missed nearer by (Hofmeester et al., 2017). Data to estimate these parameters have been derived from time-consuming or relatively invasive means, either by manually measuring animal positions in the field visible from the camera trap photographs or by leaving physical markers within the camera field of view (Rowcliffe et al., 2011, 2016, Hofmeester et al., 2017, Schaus et al., 2020). Such approaches were however not feasible in the study area due to risk from presence of large mammals such as tiger and elephant. In addition to detection zone parameters, REM also requires a measure of animal travel speed or day range to estimate density. Most of the studies applying REM have used movement information available either from radio telemetry data (Zero et al., 2013, Caravaggi et al., 2015) or by observing focal individuals (Rowcliffe et al., 2008, Cusack et al., 2015). In my study, I have used camera trap images to derive all the parameters through digitization of animal positions using an image processing platform, thus augmenting the applicability of the technique. Density was estimated using the following equation;

$$D = \frac{P}{T} \frac{\pi}{v \; p \; r \; (2 + \theta)}$$

(Rowcliffe et al., 2008: equation 4)

Where, P is the number of independent photographic events, T is the total camera survey effort, v is the average speed of animal movement while active, p is the proportion of time the population was active, and r and θ are the radiu

camera detection zone respectively (Figure 4.1).

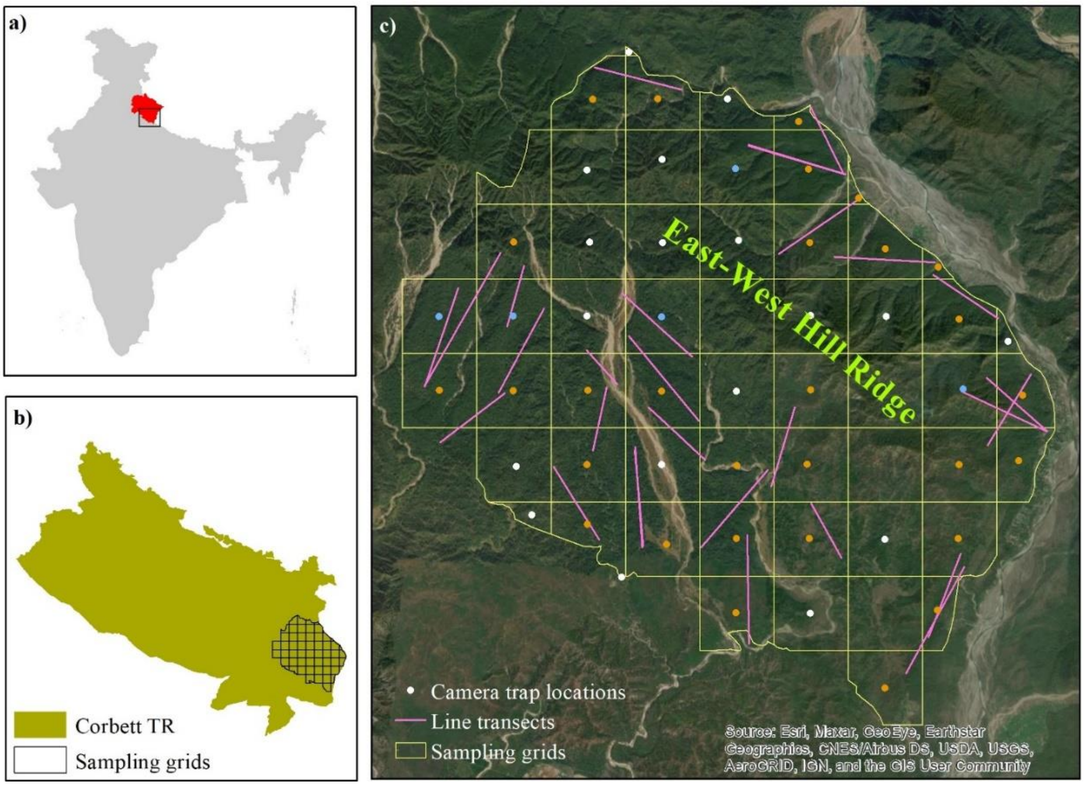
Successful execution of REM requires these critical parameters to be obtained with sufficient precision (Rowcliffe at al., 2008, Cusack et al., 2015). Although REM has been used in quite a few studies to estimate species density (Rovero and Marshall, 2009; Manzo et al., 2012, Zero et al., 2013, Cusack et al., 2015) broader acceptance of the technique depends chiefly upon the validation of its reliability and cost-effectiveness against other available techniques (Cusack, 2015). In India, so far REM has only been applied in one study in Eastern Himalaya (Nijhawan, 2017) and remains to be recognized as a potential density estimation tool across other landscapes of the country. Here I report in detail, REM based estimates of density as well as fine resolution estimates of movement speed for the four species, which I believe will assist future studies for density estimation and on movement ecology of these or similar species.

Hereafter, this chapter is divided into two sections, where, in the first section I evaluate density estimation and cost-effectiveness of REM against line transect-based distance sampling in enumerating density of four ungulate species, and, in the next section I compare line transect-based distance sampling, REM and CMR on density estimation of chital, as CMR could only be applied on this species because of its body marking unique to every individual.

4.2 COMPARING RANDOM ENCOUNTER MODEL AND DISTANCE SAMPLING

4.2.1 STUDY AREA

The study was conducted in a 100 km^2 area of Corbett Tiger Reserve (CTR; 29°25'N to 29°40'N latitude and 79°05'E to 79°05 (Fig. 4.8). My sampling area typically represented the Himalayan foothills. The terrain within the sampling area was mostly undulating, with roughly 30% of the area having steep slopes and hilly ridges (Figure 4.3). The elevation of the sampled area ranged from 450m to 850m. The sampling was carried out during the peak summer months between March and June, when the temperature in CTR ranged between 16˚C and 44˚C (Khan and Thakur, 2008). With its diverse habitats and complex terrain, CTR provided a challenging experimental ground for testing REM.



Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 4.3. a) Map of India (in grey) showing the state of Uttarakhand (in red) and the general locality of Corbett Tiger Reserve, b) Sampled area within Corbett Tiger Reserve, c) Random camera trap locations (circles) and sampled line transects (pink lines) within the sampled area. Orange coloured circles indicate the 29 trap locations used for the comparison of techniques. Blue coloured circles denote lost camera traps.

4.2.2 MATERIAL AND METHODS

4.2.2.1 Field Methods

Camera trap sampling design (REM)

Camera trapping for REM sampling was done from March - June in 2015. The sampling area of 100 km^2 was divided into 2 km^2 grids, and cameras were placed at grid centroids (Figure 4.3c) to adhere to the requirement of random camera placement with respect to animal distribution (Rowcliffe et al., 2008, 2013). The grid size of 2 km^2 was used to systematically distribute the sampling effort across the study area within the budgetary and logistical constraints (Figure 4.3). For the few camera placements where the grid centroid was inaccessible due to topographical features such as cliffs or water bodies, cameras were deployed within a 100m radius of the centroid. I ascribed camera locations as flat or hilly terrain type, based on my judgment of the terrain features not only at the camera location but also on the relief while approaching the location from some distance. Cameras were installed by tightly fixing them to a tree or on a log staked into the ground. The camera field of view (FOV) was adjusted to avoid facing east or west (to avoid the rising and setting sun). In thick vegetation, cameras were oriented to obtain maximum FOV. Other than these adjustments, the FOV was random. At locations where these minimal adjustments were required, I ensured that I did not manipulate site characteristics to attract or repel animals. Cameras were placed at a height of 30-40 cm from the ground but were aligned according to the inclination of the foreground in order to maximize the visible area. I used Reconyx Hyperfire passive infrared heat-and-motion triggered camera traps (HC500, RECONYX Inc., Holmen, WI). At every motion-triggered event, the camera recorded ten continuous images (a sequence) at a frame rate of ~1 per second and was ready to trigger immediately again without delay, thus producing a high-resolution record of animal movement. Each image was automatically tagged with date, time (to the nearest second), and image sequence id (represented as 1/10, 2 in a sequence of 10 images). Out of total 50 camera traps, data from 45 camera traps could be used since two traps were damaged by elephants while two malfunctioned and one was washed away by flash floods. The number of operational days differed between camera traps, with a minimum of 20 and a maximum of 76 functional days. Once deployed, cameras were not checked until the end of the sampling to minimize disturbance to animal movement and to avoid changing camera FOV from its initial calibrated position.

In order to estimate the camera detection zone parameters (radius (r) (meters) and angle (θ) (radians) as well as animal speed (v) (meters/second) from camera trap images of animal encounters, it was necessary to calibrate each camera FOV with an object of known height placed at a range of known distances within the FOV. This was accomplished by photo-recording of a person holding a 1m pole graduated at every 10 cm by black and white bands, standing at 1-meter interval distances in three radial directions from the camera (Figure 4.4 and 4.5) till the maximum visible distance (3-15m, depending on vegetation and terrain). The black and white colouration allowed visibility in the photo-images even through some vegetation. Distance to each pole position from the camera was measured using a measuring tape.

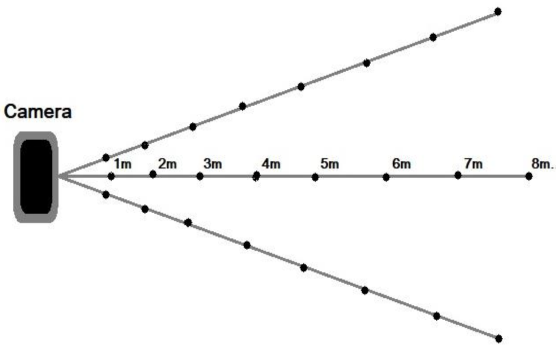


Figure 4.4 (left): A schematic diagram showing the calibration process followed for each camera deployment for REM

Figure 4.5 (right): Field demonstration of calibrating a camera trap site, where the researcher is seen standing at various known distances, as indicated on the white board (in meters), with a pole of known length demarcated by alternate black and white bands each of 10 cm.

Distance sampling

Line transects (n=26) were laid within the study area (Fig. 4.3). Transects had been established for prior studies and were not grid-based. Besides an accessible starting point (essential to commence sampling early morning), transects were random with respect to animal distributions (Buckland et al., 2001). Transects varied in length from 1 to 2 km and were sampled over four years (2010, 2012, 2015, 2018), with one to four visits to each transect per year (Table 4.5). Transects were walked early in the morning when ungulates remain most active. For each sighting, data on species, cluster size, distance of observer to animal cluster, bearing to the animal and transect bearing were recorded using a sighting compass (Sunnto KB-20/360R, Finland) and a laser range finder (Bushnell Scout 1000 ARC, USA).

4.2.2.2 Analytical method

Random Encounter Model parameterization

Detection zone parameters (r, Ɵ)

For estimation of camera detection -wise zone approach was undertaken. Firstly, on calibration pole images, pixel positions (x, y) of two points on the pole, identified by the marked 10 cm bands, were digitized using the 3D computer graphics software Blender (Blender online community, 2018). Using this digitized data with known pole size and distance, a camera-specific model was created describing the relationship between pixel size, pole size and distance (Figure 4.6 (a)). This relationship was then used to predict the distances of poles from cameras at camera deployment sites. These distances were subsequently used to generate site calibration models, mapping image pixel positions to real world positions relative to the camera (distance and angle) for each site (Figure 4.6 (b)). Finally, detection zone parameters were estimated by fitting point and line detection functions to radial distances (Figure 4.7) from camera, and angular distance (Figure 4.8) from camera midline, at the point of first capture (Rowcliffe et al., 2011). I used hazard rate detection function with cosine expansion terms for obtaining the effective detection zone dimensions.

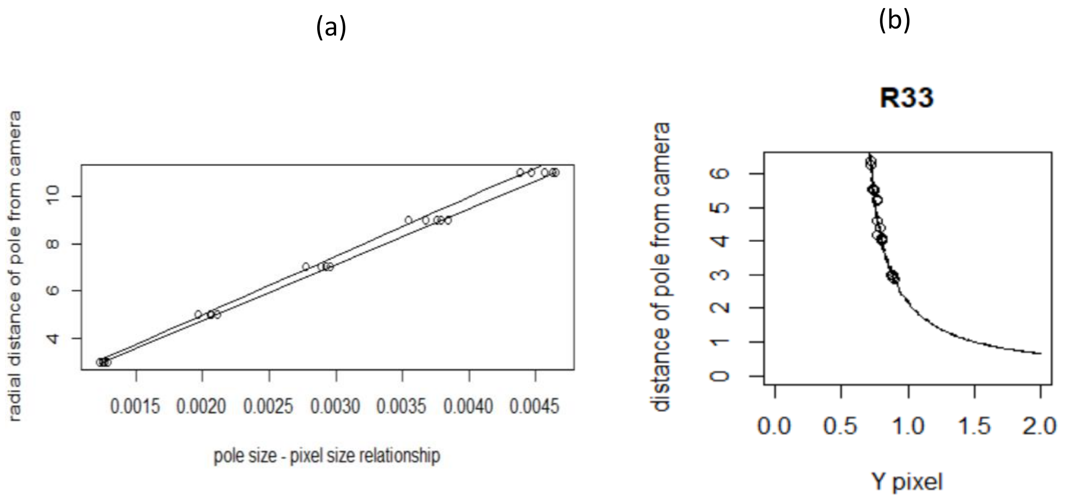
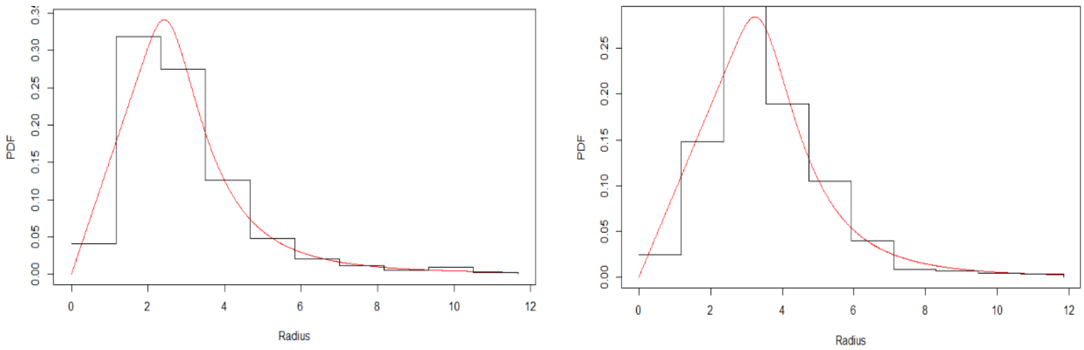
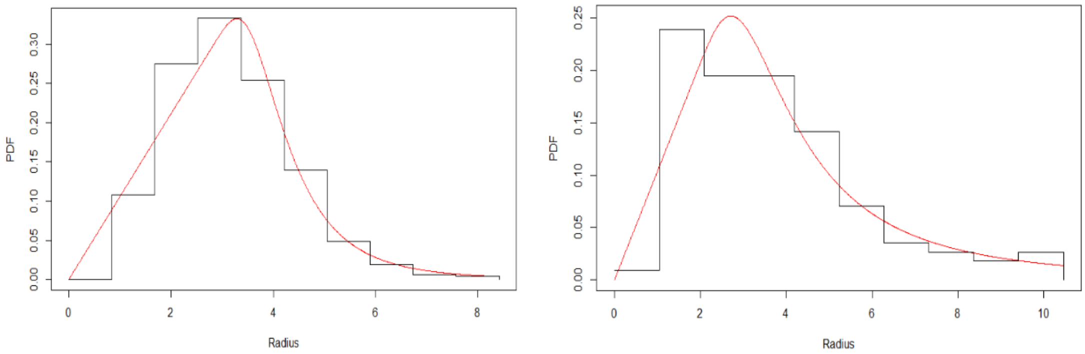


Figure 4.6: Plots showing example camera calibration (a) and site calibration (b) model relationships.

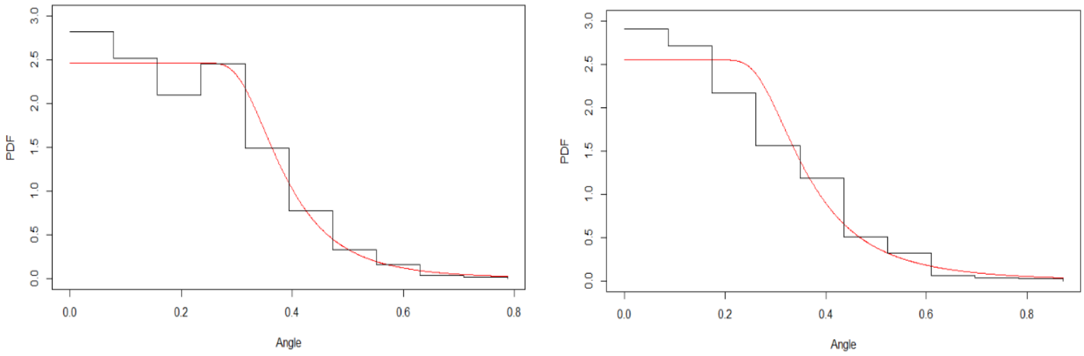


Chital Sambar



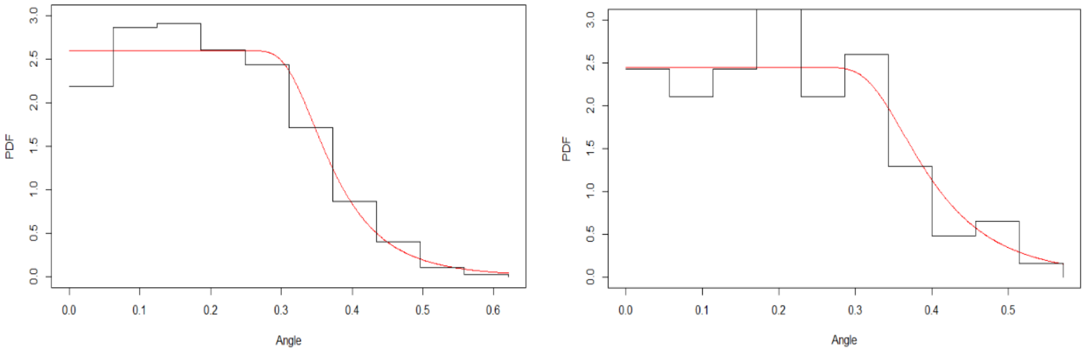
Barking deer Wild pig

Figure 4.7: Probability density functions (PDF) for distance from the camera on detection of a) chital, b) sambar, c) barking deer and d) wild pig in Corbett Tiger Reserve using REM,2015. Bars are density distributions (for PDF) and curves are the fitted hazard-rate model.



Chital

Sambar



Barking deer

Wild pig

Figure 4.8: Probability density functions (PDF) for angle of detection relative to the camera line of sight for a) chital, b) sambar, c) barking deer and d) wild pig in Corbett Tiger Reserve using REM, 2015. Bars are density distributions of the data, and curves are the fitted hazard-rate model

Speed (v)

Speed estimates were obtained from image sequences where an animal passage generated at least two frames with positions between which displacement could be measured from the digitized animal positions. Speed was estimated by dividing distance travelled (meters) by the duration of a movement sequence (seconds). Distance travelled was calculated by summing the linear distances between different positions in a movement sequence. Linear distances (displacements) were obtained trigonometrically from the already estimated radial and angular distance of animal positions obtained from digitized data. Duration of a movement sequence (passage) was obtained from time stamps of the first and the last images of the sequence. Though Reconyx cameras used infra-red flash illumination, which is invisible to animals, I noticed that sometimes animals became aware of the camera and may have potentially moved in response to camera detection. Therefore, I omitted all sequences from speed analysis where I observed that the animal had detected the camera and changed its behaviour in response. To account for possible bias resulting from more frequent captures of faster moving animals, average speed for each species was calculated by fitting three size-biased distributions; gamma, log-normal and Weibull (Rowcliffe et al.; 2016). The best distribution was selected based on minimum Akaike information criterion (AIC) values (Burnham and Anderson, 2002). For overall density to be estimated for a species, a measure of daily distance travelled by the species was required. Mean distance travelled (km) per day was estimated as the product of average speed of movement while active and proportion of time the species was active (activity level, described in the next section). Speed estimates in meters per second were multiplied by 60*60*24 (seconds) and divided by 1000 (meters) to obtain the required measure in km/day.

Activity level (p)

Activity level of a population is defined here as the proportion of time animals are active in a day. This is an important parameter in REM computations as trap rate is dependent on activity level in addition to detection zone parameters and animal speed

(Rowcliffe et al., 2014). Activity level was estimated by fitting circular kernel probability density functions (PDF) to radian times of day of animal detections, in order to obtain the underlying activity pattern and then calculate overall proportion of time active from the distribution (Rowcliffe et al., 2014). For multiple events where a camera was repeatedly triggered by continuous presence of an animal, time of the first event only was used. R package *activity* (Rowcliffe, 2019) was used to analyse the data. Standard error and 95% confidence interval were estimated by bootstrapping the data with 10,000 iterations using the *activity* package.

Trap rate

Camera trap rate or photographic capture rate of a species was calculated as the number of camera contact events at each camera deployment divided by the length of each deployment in days. A capture event was defined as the first photo of an individual entering the camera field of view (Pfeffer et al., 2018; Rowcliffe et al., 2011). An individual re-entering the field of view was considered as a new contact, regardless of the time since it had last been seen. Variance in encounter rates was estimated by bootstrapping, resampling camera locations with replacement 10,000 times (Rowcliffe et al., 2008). I used trap rate of 45 camera deployments to report density of all the four ungulate species from the entire study area using REM.

Density

Overall density (per km^2) was estimated using the total number of contact events, camera deployment time, detection zone dimensions, and average speed and activity level estimates. Density standard errors were calculated using the delta method (Seber, 1982), incorporating the standard errors of encounter rate and model parameters (radius, angle, speed, and activity level). All the analyses were carried out in R version 3.6.1.

Distance sampling

I analysed distance sampling data using the Conventional Distance Sampling (CDS) engine of Distance software version 7.3. Since there were few observations on transects in the focal year of camera trapping (2015), I estimated the detection functions and group sizes by pooling observations across all four years. I stratified the analysis into four survey periods (as samples 2010, 2012, 2015, and 2018) and obtained densities for each year. I used combinations of half-normal, hazard rate, and uniform models with cosine and polynomial adjustments and selected the best model based on minimum AIC values. Five percent of the largest distance observations were truncated. Cluster size was estimated using size biased regression after testing if the regression of cluster size vs. distance was statistically significant. Chital, sambar, and barking deer densities were reported for all survey years as well as an average over these years. I did not analyse wild pig data since there were only 18 detections occurred across all years.

Comparison of REM and line-transect distance sampling

For the purpose of comparing methods, I used trap rate data from 29 cameras that were deployed in grid cells that were also sampled by line transects (Figure 4.3). Some camera trap grid cells in rugged terrain were not sampled with transects as it was not possible to establish a straight line walk in this terrain (Figure 4.3). It would have been ideal to compare REM estimates against estimates based on a single distance survey in the same year, however logistical limitations during 2015 meant that I was not able to sample sufficient transects during this time (number of transects=7, effort=42 km). I used a simple one-way ANOVA on distance sampling summary data to test whether densities estimated by distance sampling remained similar between years. Subsequently, I used average density obtained from 4 years to compare with species density obtained from REM. To evaluate the relative precision of the methods I compared the co-efficient of variation (CV) of the estimates.

Cost comparison

For evaluating cost effectiveness of the two methods I considered the cost associated with equipment, transportation, labour (in person-days) in terms of field work and data processing. Additionally, we also compared the effective area sampled by line transects and camera traps and the associated cost per square kilometre of sampling.

4.2.3 RESULTS

REM

Camera trap sampling resulted in a total of 2202 camera trap days. This effort yielded 3752 capture events of four ungulate species (chital: n = 2547, sambar: n = 460, barking deer: n = 650 and wild pig: n= 95).

Detection zone parameters (r, Ɵ)

The species-specific effective detection radius and angle estimates of the four ungulates were similar, except for chital which had the lowest effective detection radius. Sambar had the highest detection radius (Table 4.1).

Speed (v)

For speed calculation log-normal distribution was the best fitting distribution for all the four species (Figure 4.9). Speed of movement was highest for wild pig and lowest for sambar (Table 4.1).

Activity level (p)

Proportion of time spent active in a day was lowest for wild pig and highest for sambar (Table 4.1). Activity patterns were mostly bimodal for all the ungulate species (Figure 4.10), with two very distinct activity peaks, one during early morning and another during late afternoon or early evening (Figure 4.10).

Trap rate

Photographic capture rate of chital was highest at 1.30 chital/day (SE 0.4) and was lowest for wild pig at 0.04/day (SE 0.01) (Table 4.2).

Density

Overall density estimates were highest for chital, 26.18/km^{-2} (SE 8.07), and lowest for wild pig, at 0.96/km^{2} (SE 0.38). Overall densities of sambar and barking deer were respectively 3.4/km^{2} (SE 0.82) and 7.26/km^{2} (SE 2.85) (Table 4.2). Density estimates were within an acceptable level of precision for chital and sambar, while estimates were imprecise for barking deer and wild pig (Table 4.2).

Variation in trapping rate accounted for the majority of overall variance of density estimates (Table 4.2). Segregating the 45 camera traps broadly by two terrain attributes, viz. flat (n=15) and hilly (n=30) I observed that trap rate of chital and wild pig was higher in flat terrain (3 chital/day SE=1.0 and 0.07 wild pig/day SE=0.03) and was lower in hilly areas (0.43 chital/day SE=0.2 and 0.03 wild pig/day SE=0.01). Trap rate of sambar remained similar between the two terrain types (0.21 sambar/day SE=0.1 in flat and 0.24 sambar/day SE=0.1 in hilly terrain). Trap rate of barking deer was higher in hilly region (0.5 barking deer/day SE=0.25) than in flat area (0.14 barking deer/day SE=0.03).

Distance sampling

Line transect sampling amounted to an effort of ~ 202 km. I used observations of chital (n=105), sambar (n=73) and barking deer (n=45) pooled across 2010, 2012, 2015 and 2018 line transect surveys to model detection function and cluster size estimates, since number of observations of all the three species was inadequate for the focal sampling year 2015 (chital: n = 32, sambar: n = 19 and barking deer: n = 16). The low number of pooled wild pig observations (n = 18) rendered it unsuitable for applying distance sampling. Uniform key function with cosine adjustment term was the best fitted model for chital and barking deer, while for sambar half normal with polynomial adjustment was the best selected model. Chital had the highest density estimate, followed by sambar and barking deer across all the years (Table 4.3).

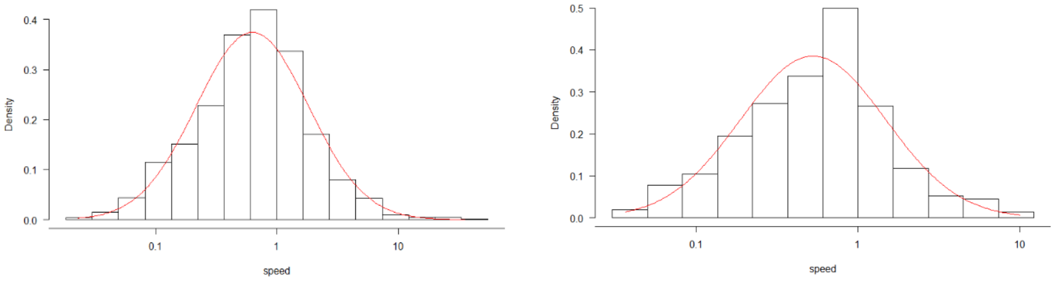
Comparison of methods (REM vs Distance Sampling)

Comparing line transect densities of chital, sambar and barking deer across the four sampling years I observed that chital and sambar densities did not vary significantly between the years, but were significantly different for barking deer (Table 4.6). However, barking deer density was not significantly different between sampling years, 2015 and 2018 (Table 4.6). I therefore used global density estimate of chital and sambar averaged over all the four years, and, global density estimate of barking deer averaged over two years (2015 and 2018) to compare with REM derived densities (Table 4.3; Figure 4.11). Global density estimates, averaged over years, were highest for chital (36.7/km^2, SE = 8.1) followed by sambar (10.27/km^2, SE = 1.96) and barking deer (3/km^2, SE = 0.53) (Table 4.3).

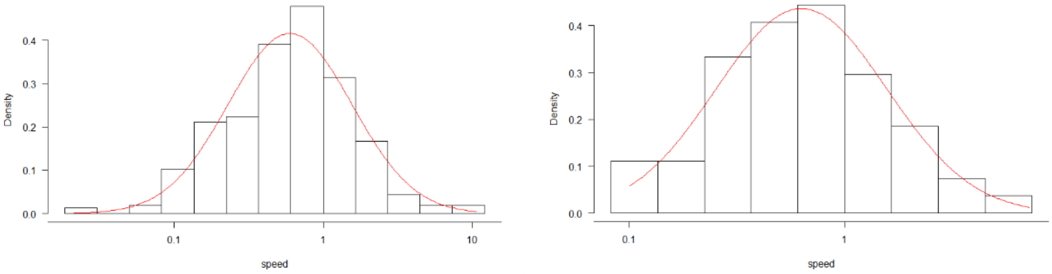
Applying REM on capture data of 29 cameras within grid cells traversed by transects resulted in chital density of 32.68/km^2 (SE = 11.01). REM derived densities of sambar and barking deer were 2.79/km^2 (SE = 0.8) and 3.8/km^2 (SE = 0.81) respectively (Table 4.2). Thus REM estimated lower density of chital and barking deer than distance sampling, but the estimates had broadly overlapping confidence intervals, and were not significantly different (Figure 4.11). However, density of sambar using REM was significantly lower than distance sampling density (Figure 4.11). Distance sampling based density estimates had lower CV than REM based estimates, for all the three species, and hence was the more precise method.

Cost comparison

The initial cost of implementing REM was much higher than line transect due to cost of camera traps. I used a comparatively expensive brand of camera trap (USD 400 per unit) which was already available from an ongoing monitoring project. However, cheaper (ranging between USD 160 to USD 200; www.trailcampro.com) yet effective (fast trigger speed and recovery time) camera traps are available which are suitable for implementing REM. I believe the cost comparison will be more practical and justifiable with these more economical camera traps. Moreover, since camera traps can ideally last for a minimum of five surveys (from experience of scientists and field biologists) it seems justifiable to distribute the cost. Thereby, considering a unit camera price of USD 160 spread over five surveys, and, with camera running cost which includes batteries and memory cards along with other equipment like GPS and iron casing (for elephant proofing) the amount totalled to c. USD 2,368 (Table 4). Equipment such as laser range finder and compass required for surveying line transects can also last for a minimum of five surveys. I therefore calculated the equipment cost by spreading it similarly over five surveys. Besides, laying the transects required other accessory things such as tools for clearing the vegetation and metal plates for marking the transects for repeated surveys. Together, this amounted to USD 581 (Table 4.4). The REM exercise was carried out by a team of one researcher and two field assistants and the line transect exercise was carried out by a team of five researchers and five field assistants. Person-days required for conducting the line transect survey to yield the same amount of effort used in the study across all years (using 108 replicate surveys of 26 transects) was much higher than the person-days required for the REM survey (Table 4.4). Higher person days translated to higher cost as well. However, data processing and analysis was more intensive for REM than for distance sampling (Table 4.4), driven by the need for time-consuming image classification followed by digitization of the animal positions for the final REM analysis. Considering the cost in terms of effective area sampled, camera trapping is a more beneficial sampling investment (both financially and labour wise) than line transect, as the area sampled by camera traps were much larger than by line transects (Table 4.4).

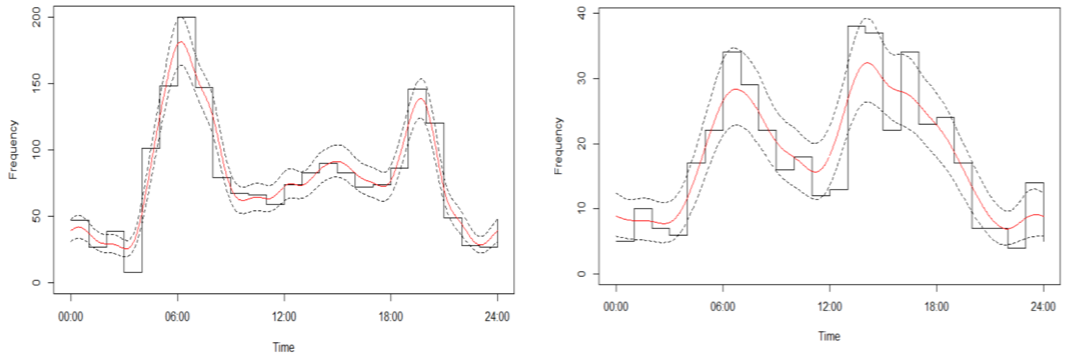


Chital Sambar

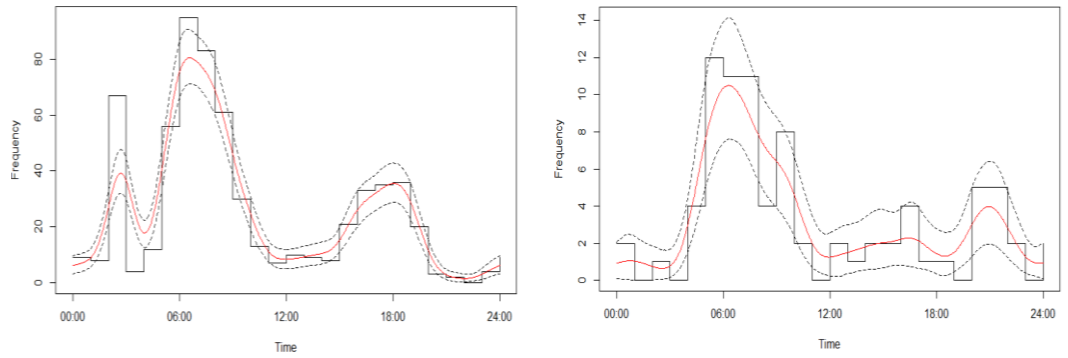


Barking deer Wild pig

Figure 4.9: Distribution of speed observations (bars) and fitted log-normal distribution (indicated by red curve) for a) chital, b) sambar, c) barking deer and d) wild pig in Corbett Tiger Reserve using REM, 2015.



Chital Sambar



Barking deer Wild pig

Figure 4.10: Activity patterns of a) chital (n=2589), b) sambar (n=943), c) barking deer (n=1047) and d) wild pig (n=108) in Corbett Tiger Reserve using REM, 2015. Grey steps represent observed frequencies of detections and red solid curve indicates the fitted circular kernel distribution with 95% confidence bands shown by grey dotted lines.

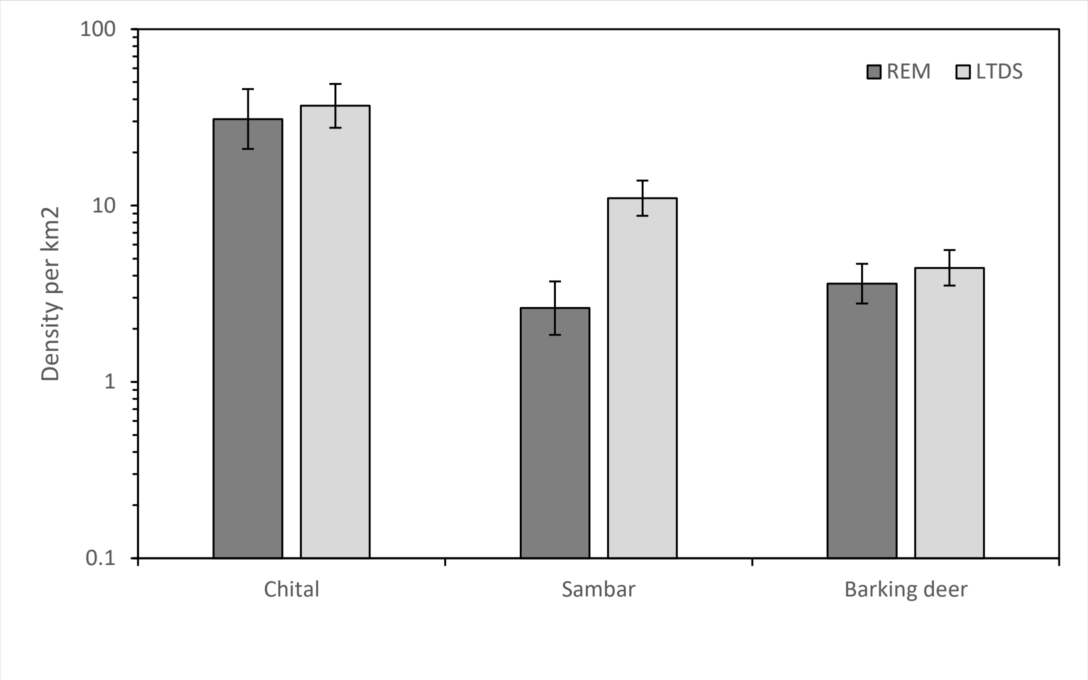


Figure 4.11: Comparison of density estimates of chital, sambar and barking deer using random encounter model (REM) and line transect based distance sampling (LTDS). Figures are provided as individuals per km^2 with 95% confidence intervals.

Table 4.1: Sample sizes (n), distance, angle, speed and activity level estimates for chital, sambar, barking deer and wild pig based on data from all 45 randomly placed camera traps using REM, 2015.

Species	*distance(m)*	*angle (radians)*	*activity level (p)*	*speed (m/s)*
Chital	3.62 (±0.04) n = 2589	0.81(±0.01)	0.44 (±0.02)	0.36 (±0.01) n =1044
Sambar	4.62 (±0.08) n = 943	0.78 (±0.02)	0.56 (±0.04)	0.30 (±0.02) n =308
Barking deer	4.34 (±0.06) n =1047	0.77 (±0.01)	0.32 (±0.02)	0.38 (±0.02) n =313
Wild pig	4.39 (±0.33) n = 108	0.81 (±0.04)	0.32 (±0.05)	0.41 (±0.06) n =54

Table 4.2: Photographic trap rate and REM based density estimates (animals per square kilometre) of chital, sambar, barking deer and wild pig with 95% confidence intervals. Estimates are using data from all 45 camera traps (overall) and 29 camera traps (transect region), in order to compare with distance sampling based density estimates for chital and sambar and barking deer.

Species	*trap rate/ day (P/T)*		*Density(per sq.km)*	*95% CI*	*Density(per sq.km)*	*95% CI*
	Overall (SE)	*transect region(SE)*	*overall(%CV)*		*transect region(%CV)*	
Chital	1.30 (±0.40)	1.72 (±0.55)	26.18 (30.63)	10.46 – 41.41	32.68 (33.69)	12.86 – 52.49
Sambar	0.23 (±0.07)	0.16 (±0.04)	3.4 (23.53)	1.83 – 4.92	2.79 (28.67)	1.30 – 4.27
Barking deer	0.38 (±0.17)	0.15 (±0.03)	7.26 (39.25)	1.67 – 12.67	3.8 (21.31)	2.25 – 5.34
Wild pig	0.04 (±0.01)	0.06 (±0.02)	0.96 (39.58)	0.21 – 1.68	1.32 (43.18)	0.30 – 2.33

SE = Standard error, CI = Confidence interval, CV = Co-efficient of variation

Table 4.3: Line-transect distance sampling density estimates of chital, sambar and barking deer reported for each sampling year (strata) and as mean of stratum estimates weighted by total effort in stratum (global). Barking deer global density estimate averaged over 2015 and 2018 (years between which the species density did not vary significantly) presented separately. Standard errors of the model parameters and density estimates are provided in brackets. Percent coefficient of variation of the global density estimates are also provided.

Species	$\hat{p}$	*ESW*	$\hat{D}$ *2010*	$\hat{D}$ *2012*	$\hat{D}$ *2015*	$\hat{D}$ *2018*	*D (global)*	*%CV (global)*
Chital	0.46 (0.04)	38.24 (3.60)	33.36 (9.78) *n*=13	28.41 (16.88) *n*=23	53.03 (13.32) *n*=33	35.32 (7.97) *n*=36	36.70 (8.19) *(all year)*	22.33
Sambar	0.49 (0.04)	31.41 (2.75)	2.46 (1.42) *n*=2	15.03 (4.57) *n*=30	12.18 (2.55) *n*=19	7.95 (2.41) *n*=22	10.27 (1.96) *(all year)*	19.17
Barking deer	0.60 (0.06)	41.64 (4.53)	0 *n*=0	0.94 (0.50) *n*=4	5.04 (1.11) *n*=16	4.48 (0.98) *n*=25	3.0 (0.52) *(all year)*	18.14
	0.57 (0.05)	47.44 (4.19)			4.84 (1.20)	4.20 (0.94)	4.43 (0.8) *(2015, 2018)*	18.14

p = detection probability; ESW = effective strip width; D = density/km^2; n=number of observations of species

Table 4.4: Comparison of resources for REM and line transect-distance sampling presented in terms of equipment and labour (provided as person and days) and transportation (provided with financial cost).

Distance sampling		REM	
EQUIPMENT			
Rangefinder (5)	$1000/5 surveys =$200 (assuming rangefinder will last for min. 5 years)	Camera traps (50)	$8,000/5 surveys =$1600 (assuming camera traps will last for min. 5 years)
Compass (5)	$390/5 surveys = $78	Batteries (600)	$214
GPS (5)	$1365/5 surveys =$273	memory cards (50)	$357
Accessory for transects	$30	iron cages (50)	$142
		GPS(1)	$ 273/5 surveys =approx. $55
Total cost	*$581*	*Total cost*	*$2,368*
LABOUR			
Laying transects (26)	10 days, 5 researchers, 5 field assistants (100 person-days)	camera deployment and removal	30 days, 1 researcher, 2 field assistants (90 person-days)
Walking transects (total replicates = 108)	22 days, 5 researchers, 5 assistants (220 person-days)		
Total field days (approx.)	320 person-days	Total field days	90 person-days

Data processing	5 days, 5 researchers (25 person-days)	Data processing	90 days (1 researcher)
Total person days	*345*	*Total person days*	*180*
Total labour cost	approx. $3700 (@$16/day for researchers and @$4.5/day for assistants)	*Total labour cost*	approx. $2204 (@$16/day for researchers and @$4.5/day for assistants)
TRANSPORTATION			
Vehicle hiring and running cost (1)	$857/month	Vehicle hiring and running cost (1)	$857/month
TOTAL COST			
Equipment, labour and transportation	$5138	Equipment, labour and transportation	$5429

EFFECTIVE AREA SAMPLED AND COST			
Effective area sampled	19.18 sq.km (calculated using the largest ESW over the total transect effort)	Effective area sampled	1644.95 sq.km (calculated using the largest EDA and EDD over the total camera trap days)
Cost (per sq.km)	$5138/19.18 sq.km =approx. $ 268 (cost is sum of equipment, labour and transportation)	Cost (per sq.km)	$5429/1644.95 sq.km =approx. $3 (cost is sum of equipment, labour and transportation)

Table 4.5: Table showing the number of transects and effort expensed at each of them between sampling years as well as total effort combined.

Transect	**2010**		**2012**		**2015**		**2018**		**Total effort (km)**
	#reps	effort (km)	#reps	effort (km)	#reps	effort (km)	#reps	effort (km)	
1	3	6	3	6	3	6			**18**
2	3	6.48	4	8	3	6			**20.48**
3	3	6	3	6	3	6	3	5.64	**23.64**
4	3	6	4	8	3	6	3	6.01	**26.01**
5			1	2					**2**
6			1	2					**2**
7			1	2					**2**
8			1	2					**2**
9			1	1.5					**1.5**
10			1	2.8					**2.8**
11			3	6					**6**
12			3	6	3	6	3	4.91	**16.91**
13			1	1.8					**1.8**
14			3	6					**6**
15					3	6	3	6.32	**12.32**
16					3	6	3	4.64	**10.64**
17							3	2.63	**2.63**
18							3	5.73	**5.73**
19							3	4.44	**4.44**
20							3	6.08	**6.08**
21							3	4.99	**4.99**
22							3	5.61	**5.61**
23							3	5.27	**5.27**
24							3	4.53	**4.53**
25							3	5.3	**5.3**
26							3	3.57	**3.57**
Total		**24.4**		**60.1**		**42**		**75.6**	**202.2**

#reps: number of replicate visits to each transect

Table 4.6: Results of one-way ANOVA on summary line transect based densities of chital, sambar and barking deer between sampling years to test for equality. The test statistics show that the chital and sambar densities did not vary significantly between the four sampling years. For barking deer, while densities varied significantly between the four sampling years, but were not significantly different between 2015 and 2018.

Species	*F statistic*	*df1*	*df2*	*p*
Chital(all years)	0.466	3	36	0.7
Sambar(all years)	1.49	3	36	0.23
Barking deer(all years)	6.29	3	36	0.001
Barking deer (2015,2018)	0.11	1	20	0.73

4.3 COMPARISON OF CHITAL DENSITY ESTIMATION BY LINE TRANSECT DISTANCE SAMPLING, RANDOM ENCOUNTER MODEL AND CAPTURE-MARK-RECAPTURE

4.3.1 STUDY AREA

Four blocks of varying sizes were selected in four ranges of CNP to carry out the three sampling techniques for comparison (Figure 4.12). The areas together represented the typical habitat and terrain characteristics of CNP as detailed in chapter II and under the study area portion of the earlier section.

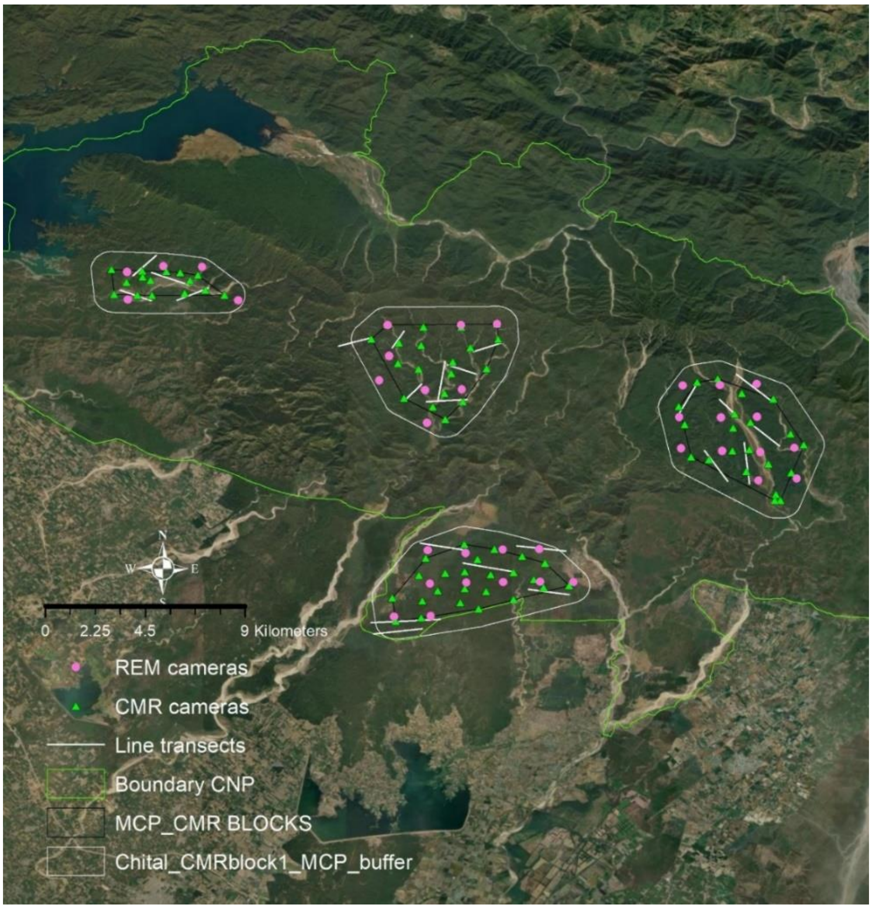


Figure 4.12: Map showing the four sampling blocks inside the Corbett National Park (green line). Camera traps for CMR and REM sampling are indicated by green triangles and pink circles respectively. Line transects are shown as white lines. Minimum convex polygon of the trapping area is highlighted in black line while buffer boundary around the MCP is denoted by white line.

4.3.2 METHODS

4.3.2.1 Field methods

Four blocks (block1, block2, block 3 and block4) of area ranging between approximately 14 sq.km to 32 sq.km were delineated for sampling using the three techniques for this study (Figure 4.12). Together a total of 104.14 sq.km of CNP was sampled in this fashion. The entire area of CNP was however previously being intensively sampled with line transects and randomly placed camera traps for REM (in a 2 sq.km gridded design) under an already ongoing project. Sampling in four blocks instead of a larger block was primarily driven by the aim to effectively sample all the representative habitats and terrains of CNP, by striking a balance between camera availability and fulfilling crucial sampling requirements of CMR as well as for ease of access in placement and post-deployment monitoring of camera traps. As for example, two of the larger blocks were in tourism zones of CNP and were well connected by vehicular roads allowing an easy access. With respect to important sampling requirements for CMR, I believe even the smallest block of ~ 14 sq.km was sufficient enough to hold home ranges of a minimum of 5 chital individuals, as reported by few radio-collared based studies on chital in India and Nepal (Moe & Wegge, 2011; Sankar & Acharya, 2004). For CMR sampling, I divided the blocks into 1 sq.km grids and placed a single Reconyx Hyperfire camera trap in each grid at an optimized location, based on criteria like presence of fresh pellets, higher intensity of chital movement from hoof marks, sudden open areas with grasses etc., in order to increase chital detections by the traps. Number of cameras ranged from a minimum of 15 to a maximum of 27 according to the area of a block (Table 4.7). Cameras were spaced at

700-1000 m from each other on the basis of the home range size. Cameras were placed at a height of 40-50 cm from the ground by tightly fixing it to a tree. This height enabled the cameras to capture images with flanks fully visible. Vegetation obstructing the camera field of view was cleared. Cameras were operated for a period of 20-30 days, which I believe was short enough to adhere to the closure assumption of CMR. Cameras were set to take photographs at a frame rate of ~1 per second, recording ten continuous images at every motion-triggered event. Although this camera setting had generated a large number of repetitive photographs of the same individual, however chances of missing a capture where individuals moved together (generally the case for group living species like chital) was rendered to almost nil. Images were automatically tagged with date and time (to the nearest second). Cameras were checked at a regular interval of five days, or opportunistically whenever possible, for replacement of memory cards or any damage due to elephant. Cameras without any capture of chital within the five-day interval were moved to a nearby preferred location, however within a distance not affecting the spacing between the cameras. Co-ordinates of each initial placement as well as shifted placements were recorded using a hand held GPS device.

For REM sampling the general field methodology detailed in the earlier section was followed. Random cameras placed at a resolution of 2 sq.km grid led to a minimum of 5 placements in the smallest block of 14 sq.km and a maximum of 12 placements in the largest block of 32 sq.km. Duration of deployment ranged between 25 days to 126 days, owing to an early initiation of REM sampling under the ongoing project.

Basic field methodology followed for line transect sampling is elaborated in chapter III and in the earlier section. Number of line transects varied between a minimum of 5 and maximum of 7 transects across the blocks. Transects varied between 1-2 km in length and were replicated three times. Additional line transects with random start points were sampled in blocks where ongoing sampling did not cover the area sufficiently. Yet, I believe few areas still remained unsampled by transects primarily owing to inaccessibility of those areas (Figure 4.12).

4.3.2.2 Analytical methods

CMR

I used the program EXTRACTCOMPARE (Hiby et al., 2009) to identify the chital individuals. The program uses three dimensional modelling to match pattern on the body flanks across multiple captured images for individual attribution, which is generally based on images of both the flanks of a passing animal captured simultaneously by a paired camera trap. However, in my case I have used single sided camera trap and hence individuals were identified based on either the left or the right flank. Subsequent block wise analysis of abundance was based on the flank which was captured more. Individual identification using EXTRACTCOMPARE generated the capture histories of individuals in the standard X-matrix format, where information about captures or non-captures of individuals are res
the rows against each occasion stored in the columns. I plotted the cumulative number of photo-captured individuals against the occasions to check for closure violation. Fawns were excluded from the analysis due to high probability of mortality. I used null (M_0), heterogeneity (M_h), and behaviour (M_b) models to account for the variation in capture probabilities using Huggins version which uses the probability of initial

capture (p) and probability of recapture (c) (Huggins, 1991) to condition out the population size (N) from the likelihood of individual encounter histories. Model selection was based on minimum Akaike Information Criteria (AICc, (Akaike, 1974). The analysis was done in Program MARK v 9.0. The abundance estimate generated for each block was then used to calculate chital density through dividing the abundance estimate by the sampled area of each block, which was the trapping area plus a buffer of home range radius of chital. An average chital density was calculated as a simple mean of the individual block-wise densities which were already weighted by the area of the blocks.

REM

Critical for REM is to model the species specific effective area, estimated using effective detection distance (EDR) and effective detection angle (EDA) (explained in the introduction and earlier section of this chapter), from each randomly placed and calibrated cameras. This area critically relies on precise estimation of effective detection distance of animals from camera traps by fitting detection function models. For this study I used an Artificial Intelligence based Image processing algorithm on camera trap images (currently under development and unpublished) to estimate distances of chital positions in the camera trap images. I used hazard rate detection function on the initial detection distances to estimate EDR for each block separately as well for all blocks combined. For EDA and speed of movement I borrowed the estimates from the earlier REM modelling (earlier section), assuming the estimates would not vary as the sampling was from a similar larger area of CNP. Activity level (proportion of time active) of chital is however estimated for all the blocks together.

Final chital density estimates are calculated using trap rate (explained in the earlier section under REM) in each of the blocks separately as well all as combined for comparison with CMR and line transect based densities.

DISTANCE SAMPLING

Line transect based distance sampling densities of chital was estimated individually for each block by defining the blocks as stratum. I also estimated an average chital density of as mean of the stratum estimates weighted by total effort in each stratum. Due to low number of observations in individual blocks global detection function was used. Cluster size was estimated for each stratum as well as mean of all the blocks. The general modelling process was similar to that explained in chapter II as well as in the earlier section of this chapter.

COMPARISON OF TECHNIQUES

I converted the block wise population size estimates of chital into density by dividing the abundance estimates of each block by the respective ETA. I calculated average CMR based chital density as a simple mean of the estimates of four blocks (individual block wise densities were already scaled by areas). I used percentage co-efficient of variation (% CV) of chital density estimates derived from the three techniques to compare their relative precision across each block as well as for average density combined over the blocks. 95% confidence interval of the density estimates were used to infer whether the density estimates varied significantly between the techniques.

4.3.3 RESULTS

CMR

Two telemetry studies on chital in Royal Chitwan, Nepal estimated annual home range of males at 2.2 sq.km and 2 sq.km (± 38 SD) (Mishra, 1982; Moe & Wegge, 2011). I used this to calculate the home range radius (0.8 km±0.01) and added it as buffer around MCP of trapping grid of each block to obtain ETA of each block (Table 4.7). Sampling effort was lowest in block 4 (29 occasions) and highest in block 1 (39 occasions) (Table 4.7). Plotting the cumulative number of photo-captured individuals against the occasions demonstrated negligible change after 25-30 days in all of the blocks, which in a way explained that the average sampling period of 30 days for each block took care of the closure assumptions (Figure 4.13).

Mt+1 was highest in block2 (887 uniquely identified individuals of chital using left flank) and lowest in block 1 (421 individuals using left flank) (Table 4.8). Abundance was highest in block 2 at 1825 chital (SE = 82) using the M_0 model (Table 4.8, Figure 4.14). Although M_h was the best selected model (based on AICc value), but the model results did not reflect any effect of individual heterogeneity on initial capture probability, therefore I used the next best model which was the null model. Chital abundance was estimated lowest for block 4 (618 individuals, SE = 114) using the behaviour model (M_b) (Table 4.8, Figure 4.14). Block wise estimates of modelling parameters and population size is reported in Table 4.8.

REM

Camera trapping effort varied a lot across the blocks, from as high as 668 trap days in block 1 to a low of 309 trap days in block 4. Trap rate of chital was however highest in block 2 (3.87 chital/day, SE = 1.71) and lowest in block 4 (0.25 chital/day, SE = 0.08) (Table 4.10). Fitting hazard detection function on detection distances, EDR of chital was estimated highest is block 3 at 7.35m (SE = 0.24), while it was lowest in block 4 at 4.04m (SE = 1) (Table 4.9). Overall EDR of chital combining all the blocks was 5.41 (SE = 0.02). Overall proportion of time active was 0.36 (SE = 0.01) (Table 4.9). Density of chital was highest in block 2 at 61.4/km^2 (SE = 24.17) and was lowest in block 4 at 5.47/km^2 (SE = 2) (Table 4.10; Figure 4.14).

DISTANCE SAMPLING

Total number of chital observation was 83 combining all the blocks. Although number of observations were lower than recommended for individual block, however data conformed to the assumptions of model fitting, as evident from the block wise detection function plots and goodness of fit scores (Figure 4.16). Half normal function with cosine adjustment was the selected model for three blocks, while uniform cosine was the selected model for block 4. Mean cluster size remained nearly similar for all the blocks (Table 4.11). Density of chital was highest in block 2 at 89.71/ km^2 (SE = 44.65) and was lowest in block 3 at 26.51/km^2 (SE = 12.08). Global density estimate was 51.91/km^2 (SE = 14.87) (Table 4.11; Figure 4.14).

COMPARISON OF CMR, REM AND DISTANCE SAMPLING

Comparing block wise chital density estimates I observed that, all the three techniques produced comparable density estimates for three blocks (Figure 4.14), while REM derived density was significantly lower than CMR and distance sampling based density estimates for block 4 from non-overlapping confidence interval (Table 4.8, 4.10 and 4.11; Figure 4.14). However, all the three techniques produced comparable average density estimates (Table 4.8, 4.10, 4.11; Figure 4.15). Using percentage co-efficient of variation, CMR yielded the most precise estimates of both block wise as well as average density (Table 4.8). Block wise precision in density estimates varied between REM and distance sampling (Table 4.10 and 4.11). REM produced the least precise average density estimate (Table 4.10).

Table 4.7: Details of camera trap exercises for CMR sampling in four blocks

Blocks	ETA	Number of camera traps	Number of occasions	Trap nights
Block1	31.86	21	39	819
Block2	29.72	25	32	800
Block3	28.27	27	34	918
Block4	14.29	15	29	435

Table 4.8: Block wise CMR based population size estimates and density (derived) of chital using the best fit models with associated standard errors.

Parameters	Block1	Block2	Block3	Block4
Mt+1	420	887	499	322
Best model	M_h	M_0	M_b	M_b
Capture probability (p)	p (1) =0.01 (±0.002) p (2) = 0.1 (±0.01)	0.02 (±0.001)	0.03 (±0.004)	0.02 (±0.006)
Recapture probability (c)			0.008 (±0.001)	0.01 (±0.001)
Population size (N-hat)	1195.20 (±244.38)	1825.55 (±81.80)	703.91 (± 49.55)	618.78 (±114.17)
95% CI (N)	844.03 – 1837.21	1678.42 – 2000.03	627.42 – 825.97	465.28 – 936.72
Density (D)	37.35 (±7.62)	60.85 (±2.73)	25.13 (±1.78)	44.19 (±8.15)
95% CI (D)	22.40 –52.25	55.49 –66.20	21.63 –28.62	28.20 –60.17
Average density (blocks combined)	41.88 (±5.07)			
95% CI (Avg. density)	31.93 –51.82			

CI = Confidence interval

Table 4.9: REM parameter estimates for four blocks with standard errors mentioned in brackets.

Parameters	Block 1	Block 2	Block 3	Block 3
EDR (meters)	5.37 (± 0.13)	6 (± 0.14)	7.35 (± 0.24)	4.04 (±1)
EDA (radians) (borrowed)	0.81 (± 0.01)			
Activity level (p) (all blocks combined)	0.36 (± 0.01)			
Speed (meters/second) (borrowed)	0.36 (±0.01)			

EDR = Effective detection distance; EDA = Effective detection angle

Table 4.10: Table showing REM based block wise as well as combined (four blocks) estimates of chital encounter rate and density with associated standard errors and percentage co-efficient of variation. 95% confidence intervals of the estimates are also presented.

	Effort (trap days)	Encounter rate	Density/km^2	%CV	95% CI
Block 1	668	3.63 (±2.88)	31.38 (±22.73)	72.43	13.17 –173.35
Block 2	372	3.87 (±1.71)	61.4 (±24.17)	39.3	14.08 –138.55
Block 3	608	1.25 (±0.47)	14.14 (±5.4)	38.18	3.55 –89.0
Block 4	309	0.25 (±0.08)	5.47 (±36.56)	36.56	1.55 –77.13
Combined	1957	2.66 (±1.05)	30.18 (±10.26)	34.0	10.07 –50.28

Table 4.11: Line transect distance sampling based block wise as well as average (combined) density of chital with associated standard error and percentage co-efficient of variation is reported. Modelling parameters with standard errors are also reported. 95% confidence interval of the density estimates are reported.

	Effort (km)	n	ESW (m)	p	E(S)	Density /km^2	%CV	95%CI
Block 1	29.51	17	35.27 (±6.23)	0.36 (±0.06)	5.11 (±1.09)	41.78 (±16.32)	39.06	19 –92
Block 2	34.43	34	25.57 (±3.61)	0.26 (±0.04)	4.64 (±0.64)	89.71 (±44.65)	49.78	29.51 – 272.68
Block 3	27.37	11	32.38 (±11.41)	0.33 (±0.11)	4.27 (±0.78)	26.51 (±12.08)	45.58	11 -66
Block 4	21.95	17	57.68 (±8.76)	0.60 (±0.10)	5.64 (±1.03)	37.90 (±16.68)	44.02	14.3 -100
Combined						51.91 (±14.87)	28.66	22.76 –81

n = number of chital observations; ESW = Effective Strip Width; p = detection probability; E(S) = Mean group size; CV = Co-efficient of variation; CI = Confidence interval

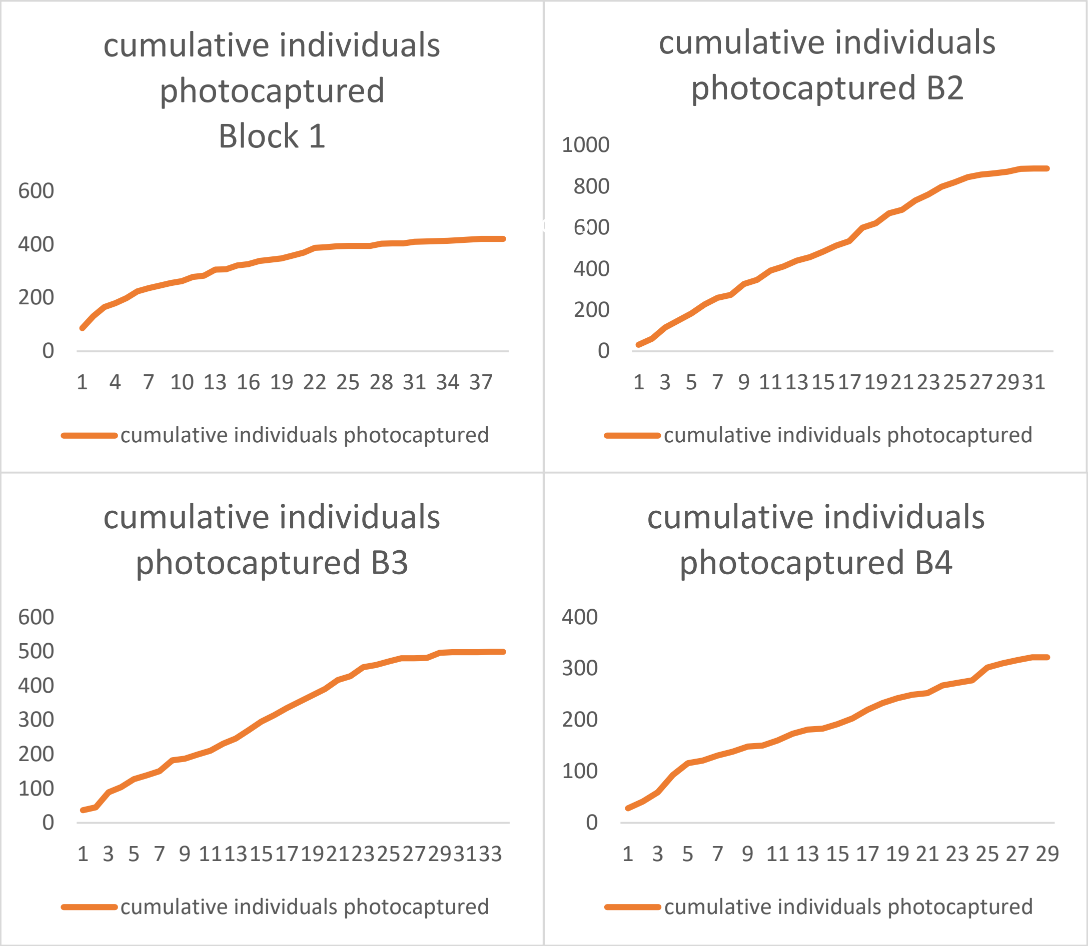


Figure 4.13: Plots showing block wise photo capture of cumulative number of individuals against occasions. Cumulative

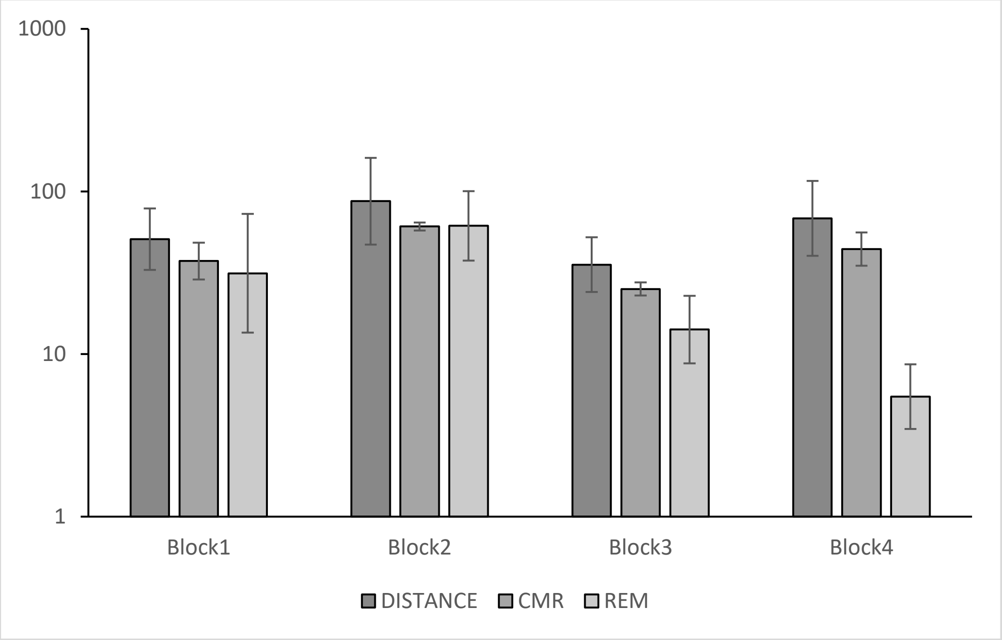


Figure 4.14: Comparison of block wise density estimates of chital using line transect based distance sampling (Distance), capture-mark-recapture (CMR) and random encounter model (REM). Figures are provided as individuals per km^2 with 95% confidence intervals.

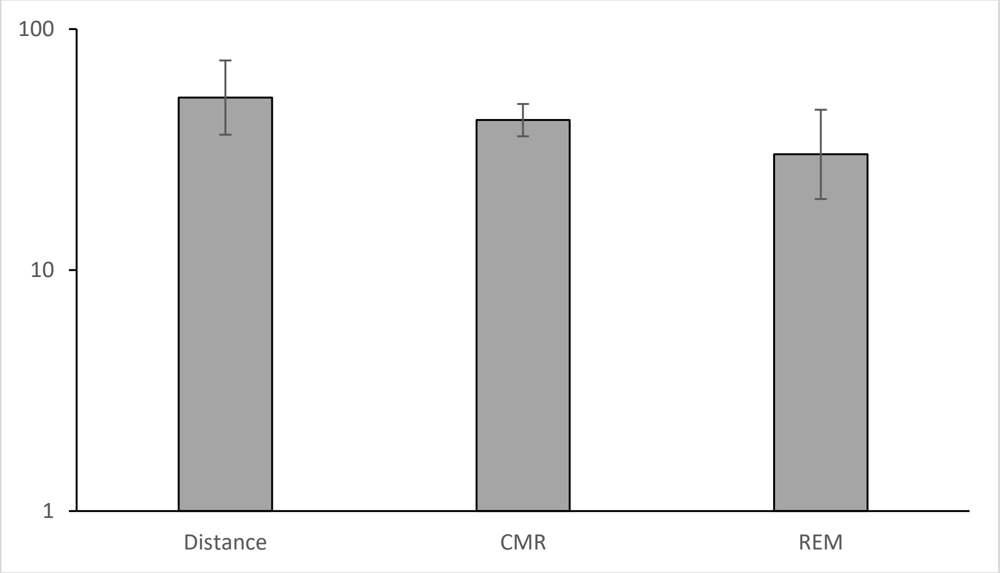


Figure 4.15**:** Comparison of average density estimates (average of four blocks) of chital using line transect based distance sampling (Distance), capture-mark-recapture (CMR) and random encounter model (REM). Figures are provided as individuals per km^2 with 95% confidence intervals.

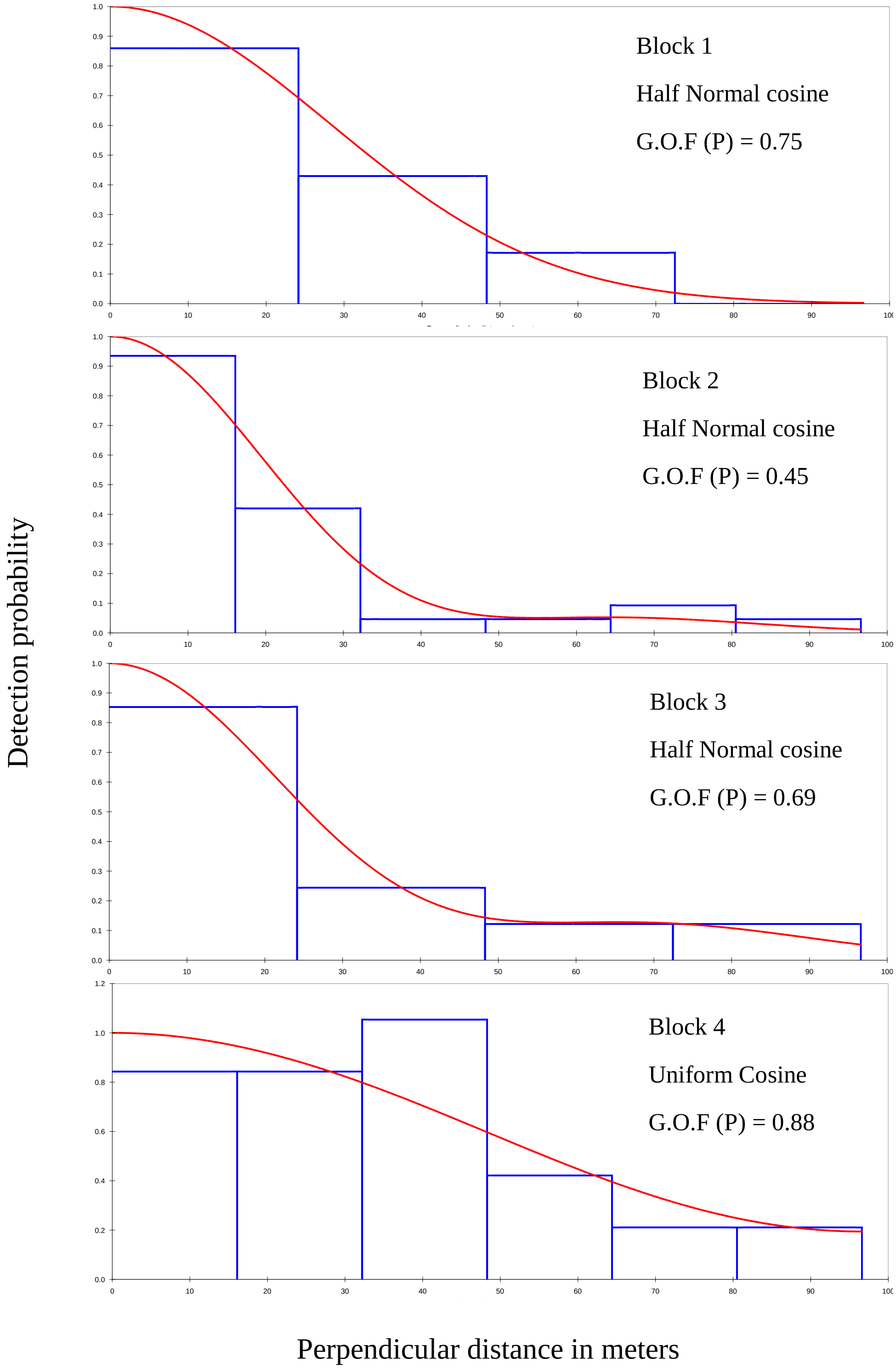


Fig 4.16: Detection function plots of best selected models on perpendicular distances of chital observations. The best model and the goodness of fit (G.O.F.) score for each fit is shown.

4.4 DISCUSSION

Acceptance of a technique for wildlife population monitoring and management is primarily reliant on its ability to deliver accurate and precise estimates of species abundance in a cost effective manner (Witmer, 2005). Although my study of comparing ungulate density estimates between REM and distance sampling could not evaluate the accuracy of the techniques, owing to the absence of an independent measure of known population size, I however had the advantage of using distance sampling as the more established method to test the reliability of REM estimates based solely on camera trap data.

The first study has demonstrated that REM can be used as a technique for estimating density of multiple species simultaneously, in a dense forested habitat with complex topography (Rovero and Marshall, 2009; Soofi et al., 2017). The study was also among the very few where REM has been successfully used in estimating density of group living species, the chital and the wild pig (see also Zero et al., 2013 on Grevy's zebra). Sampling effort using 45 camera traps, each operating for a minimum of 20 days, was adequate for successful application of REM as suggested by Rowcliffe et al., 2008. Furthermore, by placing cameras in a systematic grid design, with minimal deviation from the predetermined points, I believe that I was able to satisfy the key REM assumption that animal movement is random with respect to the camera locations (Rowcliffe et al., 2013).

REM also depends critically on precise and unbiased estimation of species-specific effective detection area, defined by effective detection distance (EDD) and effective detection angle (EDA), from initial encounters of animals with the camera.

The overall camera trap sampling effort in the preceding study returned adequate independent initial encounters of all the four species (Table 4.1), much more than the minimum sample required (Rowcliffe et al., 2008), for modelling the species specific EDD and EDA with sufficient precision (Table 4.1). Factors such as vegetation density, temperature, humidity and animal body size can influence EDD across sites and species. Rowcliffe et al., 2011 and Hofmeester et al., 2017 highlighted the strong positive relationship between EDD and animal body size. However, I did not observe any such trends, possibly due to limited body mass range, or possibly due to differences in grouping behaviour of some of the species (Table 4.1).

I could not conclude whether the species-specific speed estimates were unbiased, due to a lack of comparable movement estimates for these species under similar habitat and terrain conditions, which can affect the movement speed or day range of a species (Vásquez et al., 2002). Most of the studies applying REM have used species movement information available either from radio telemetry data (Zero et al., 2013; Caravaggi et al., 2016) or by observing focal individuals (Rowcliffe et al., 2008). I have calculated speed by digitizing animal positions from camera trap images for the first time, which, although it provides a finer resolution of measurement, can be inaccurately estimated if animal positions on images are incorrectly marked, especially those which are far from the camera. Hence, it becomes important to compare speed estimates collected in this way with either fine resolution telemetry data or with movement distances in camera trap images manually measured in the field (Rowcliffe et al., 2016). However, I believe I have reduced the possibility of such error through accurate calibration and subsequent meticulous digitization of animal positions using the software.

Variability in trapping rate of the four ungulate species by terrain attributes partly reflects the known habitat preference of the species. The much higher trap rate of chital from cameras in relatively flat areas is consistent with the generally observed preference for flat terrain by the species (Schaller, 1984). A similar pattern was observed for wild pig although, unlike chital, the species is not known to prefer any particular type of terrain or habitat (IUCN 2019). Sambar on the other hand, which is known to prefer hilly tracts (Kumar, 2000; Johnsingh et al., 2004), did not exhibit any such variability in trapping rate. Although barking deer is known to inhabit a wide range of terrain (IUCN 2016), I found a higher trap rate of the species in hilly areas in my study, however this pattern was driven by relatively higher captures in just two of the camera traps.

Line transect based distance sampling has traditionally been the preferred method for estimating ungulate density across many habitats and regions, primarily due to its practicality and affordability, and the ability to obtain density estimates of multiple species simultaneously (Burnham et al., 1980; Focardi et al., 2005, Jhala et al., 2020). Long-term monitoring of ungulate population in CNP has accordingly been done by line transect sampling annually. However, I could not use the 2015 line transect data from the study area alone to compare with REM derived densities, because I had fewer than the minimum number of observations required to robustly model the detection probability of the four ungulate species in that year within the REM sampling site (Buckland et al., 2001). I therefore pooled distance observations of four different sampling years from the study area to model the species-specific detection functions, and used the species average densities to compare with REM derived densities. Line transect sampling effort within the study area was highly variable across these sampling years, with as little as 24 km (4 transects) in 2010 to a higher effort of 60 km (14 transects) and 75 km (15 transects) in 2012 and 2018 respectively. Even with the higher line transect sampling effort of 2012 and 2018, number of observations of chital, the most abundant of the four ungulates, were still fewer than the recommended 40 observations (Buckland et al., 2001) in each of these years. Despite pooling data over the four years, line transects failed to yield the recommended number of observations for wild pig to reliably estimate its density and hence comparisons for this species density with REM density was not possible.

A key limitation of line transects which did not affect the REM study was that a substantial region remained unsampled by line transects because of the steep, densely forested terrain where it was exceedingly difficult to maintain random straight lines. In contrast, navigating to a pre-selected random point to deploy a camera trap was much easier and less labour intensive. Camera trap sampling, using passive infrared cameras with no white flash, was also significantly less invasive than laying and walking a line transect through such dense habitat. Ungulates can readily detect the observer on line transect first and can tend to move away to avoid being detected. Moreover, such sudden movement of animals can violate the critical assumption of recording distances of the point where the animal was initially detected. Although, every attempt was made to accurately measure distances and angles of animals from the observer on line transects, I must acknowledge that accurate measurement can often be difficult in dense forested habitat like that in my study area. In contrast, there were very few instances where animal showed wariness of the cameras, alleviating the potential for bias arising due to non-detection or evasive movement. Apart from these, there was a heightened risk of elephant and tiger attack associated with the amount of time spent in laying transects (2 days for one transect) and walking them multiple times (minimum of 1.5 hours to walk a 2km transect in such terrain and dense habitat) compared to the amount of time needed for one-time deployment of a camera and its calibration (minimum 1.5 hours, excluding the walking time to reach as it varied considerably between locations). Furthermore, REM potentially samples a much larger area, by running the cameras 24 hours for the entire duration, compared to line transects.

Applying REM and distance sampling to the three ungulate species, I observed that both the techniques produced comparable density estimates of chital and barking deer, while for sambar, REM produced a significantly lower density estimate than distance sampling. The reason for disparity between methods in the case of sambar is unclear to us and requires further investigation. In case of wild pig, although my camera trap sampling generated adequate samples to model all the required REM parameters and successfully enumerate density of the species, line transect however failed to estimate its density due to very low overall encounters of the species on transects (n=18). Therefore, it appears that for elusive species like wild pig (in the current study) or for species with similar traits found elsewhere, such as mouse deer and four-horned antelope, line transect sampling is not a suitable density estimation technique. Camera trap-based sampling seems to be a superior method to obtain density estimates of such species (Jhala et al., 2020 reports that in areas where these species were present, line transect failed to sample these species while camera trap sampling generated an abundance measure).

Comparing the financial cost associated with both the techniques, the initial cost of implementing REM was higher than line transect, primarily due to the expenditure of purchasing camera traps and accessories. However, this initial investment for camera traps can be a sustainable and profitable choice, as camera traps will mostly last for several surveys (accounted in the cost computation) and will also sample a much larger effective area (Table 4.4). Camera traps, although can cost-efficiently sample a much larger effective area compared to line transects, but they remain fixed at a particular location and sample the same area essentially over time. On the other hand, line transect being linear samplers can potentially better cover the heterogeneity of an area more than a camera trap. Ideally there should be sufficient number of cameras to cover the area so as to sample all representative habitat type adequately. However, increased cameras translate into increased costs. A trade-off between cost and effective sampling can be addressed by moving the camera traps between random stratified sampling locations within the area of interest so as to cover all habitat strata (Rowcliffe et al., 2011).

Even though line transects are more economical in terms of equipment, it is more labour-intensive than REM with respect to field work. Under similar field condition as in the current study, it would require a much larger effort in terms of laying transects and physically sampling them multiple times (Table 4.4) to generate an adequate amount of data in order to achieve a robust sample during a single survey. However, REM requires a considerably larger effort in data processing and analysis following the procedure applied in the current study. To this end, judging by the cost-effectiveness as observed from my study findings, line transect seemingly appears to be a favourable technique to adopt, for both short and long term surveys, primarily for its low initial cost and less time required in post processing of data. Line transect surveys may be particularly effective in open areas where species density is high and observer access is good. Under these same circumstances, REM analyses can be particularly time consuming due to the number of individuals captured in an image. However, on the other hand, in hilly and heavily vegetated terrain, line transect surveys are prone to violation of crucial assumptions and such habitat conditions were present in large areas of the current study. With appropriate selection of robust yet affordable camera trap models, REM, will become an increasingly effective long term population monitoring tool. Moreover, building computer applications to improve processing time of REM data (currently under development) will reduce the processing time requirements, further enhancing its applicability as a monitoring tool.

Chital as one of the most abundant and important prey species of large to medium carnivores in Indian forests requires considerable conservation attention, for the long term survival of predators. It is therefore important to monitor its population using methods which yield precise estimate of population size/density, is easy to implement, and, additionally is non-invasive. I believe, my study on capture-mark-recapture sampling of chital population has highlighted such possibilities through use of remote camera traps as samplers, augmented by comparing it with the well-established and extensively used line transect method and camera trap based random encounter model. This attempt of CMR based estimation of chital density was a novel aspect of my research. The only study I am aware of using capture-recapture to estimate chital density was by Pariwakam, 2006 (unpublished) in Bandipur Tiger Reserve, which however had used hand-held photo capturing of chital. I took similar attempts of manually photo capturing chital from vehicle, however observed that except in very few open areas it was exceedingly difficult to photo capture the species as individuals exhibited extreme wariness of my presence and would often escape into thick vegetation. On the other hand, passive infrared Reconyx camera traps enabled me to obtain a large number of multiple photo captures and recaptures of individuals by continuous photo-recording. This particular camera type was almost non-invasive as it did not use white flash while delivering good quality images (till a limited distance) even at night. I acknowledge, care should be taken in spacing of the camera traps, which in my case I believe was large (to maximize sampling area with limited camera traps) thereby leading to proportional less recaptures of individuals, or, moving the cameras inside the trapping area can possibly be another way to deal with the issue. Very low recaptures of individuals in more than two camera traps rendered the possibility of applying spatial capture-recapture, which should be attempted to obtain an accurate density estimate, in contrary to non-spatial capture recapture. Trapping occasion of 30-35 days should be enough to fulfil the closure assumptions for CMR as evident from the plots of cumulative photo captured individuals. Judging by the field methodological requirements, camera trap based CMR definitely is the most beneficial technique to use among the three methods. Line transect based distance sampling which requires physical presence can prove to be an invasive method in areas like CNP. Placement and calibration of random cameras in difficult terrain like CNP also entails a much higher physical labour than CMR sampling. However, CMR sampling would require a larger data processing effort than distance sampling but lower than REM sampling. Given the analytical advantage of estimating least number of modelling parameters, CMR gains an edge over the two other sampling techniques, albeit with the only disadvantage of few restrictive assumptions, especially in compare to REM. I acknowledge a lack of comparable sampling effort, particularly in case of line transect, which probably have led to the imprecise chital density estimates. For REM, however, effort should be given in accurate estimation of the modelling parameters such as speed and detection distance on which the method is critically dependent. Comparing the computer algorithm based estimate of these parameters with manually measured estimates collected on ground will help in establishing the accuracy of the parameters. Thereby, judging the three techniques by both methodological and analytical aspects, as well as effective estimation of density, CMR appears to be a much more beneficial technique to use for monitoring individually identifiable species. (Zero et al., 2013) has drawn similar inferences by using these three techniques on the endangered Grevy

CHAPTER V DEMOGRAPHY OF CHITAL USING CAMERA TRAP

5.1 INTRODUCTION

Population dynamics is a process, not only defined by population abundance over space and time, but also, largely by other population characteristics such as age-sex ratio, natality, age and sex specific survival and mortality, fecundity etc. Studying these parameters to understand how they are affected by factors such as, environmental variation, density-dependence, individual heterogeneity, resource, predation and disease, to mention a few, is what essentially known as demographics (Lebreton and Gaillard, 2016). Demographics is of paramount importance in wildlife biology and management, as it enables us to understand the vitality, status and behaviour of populations (Skalski et al., 2005). While population vitality is the change in population size over time, population status is indicated by the current state of the population abundance, age and sex structure and by nutritional and physiological health (Skalski et al., 2005), of which, we will be focusing particularly on age-sex structure and health in this chapter.

Wildlife management, solely based on monitoring change in population abundance can often be unreliable as information about different environmental factors driving such change in the population size is often ignored (Lebreton and Gaillard, 2016). However, monitoring a population by its age-sex structure rather than only abundance allows us to obtain a more reliable assessment of population dynamics of long-lived species as well as to assess population extinction risk (Lebreton and Gaillard, 2016). In this context, it is imperative to discuss why and how different age-and-sex classes, particularly young-adult female ratio, as well as individual health condition can play a vital role in population dynamics. This component of my research was focused only on the spotted deer or chital among other herbivore species found in CTR, owing to the population characteristics described under the literature review of the species.

Age and sex structure

Large herbivore population are characterized by a strong age-and-sex structure with at least four discernible population age classes, viz. fawn, juvenile, sub-adult and prime adult (Gaillard et al., 2000). Each of these demographic classes is subject to variable survival and reproduction under consequence of temporal variation in habitat, different environmental factors (Gaillard et al., 2000), population density (Vincent et al., 1995) and predation (Barber-Meyer & Mech, 2008; Skogland, 1991). It has been observed that effect of change in population density is reflected initially in juvenile survival, followed by age at first reproduction, adult fecundity and eventually adult survival (Bonenfant et al., 2009). Besides, selective predation (due to choice or predator density) on any of the age classes can also affect the overall prey population structure (Gese & Knowlton, 2001; Skogland, 1991) and hence is an important parameter for prey population management. Among the age classes, young to adult female ratio has often been used as a proxy of birth rate (Eberhardt et al., 1996; Fryxell, 1987; Laurian et al., 2000) and similarly, temporal decline in female to young ratio and the ratio between yearling: female ratio in year t+1 and calf: female ratio in year t have been generally used to obtain juvenile survival rates (Sarno et al., 1999; Byrom, 2002; Crampe et al., 2002). However, such count ratio based information without accounting for temporal changes or variability in detection of different age and sex classes can be misleading (Nichols, 1992). Information on age structure can thereby act as ecological indicator of a population's response to ion and population size, through the variable response of age and sex specific survival and reproduction (Coulson et at., 2001). Apart from age structure, population sex-ratio is also vital, as it indicates, the reproductive potential of a population (De and Spillet, 1966), as well as, differential effect of various factors acting upon a population (Skalski et al., 2005). For instance, selective predation of adult males of spotted deer by large predators, due to their body mass and certain male spacing behaviours, can lead to a skewed female ratio (Karanth and Sunquist, 1995; Ramesh et al., 2012), thereby shifting from the otherwise equal male to female ratio in populations, free of selective shooting or predation (De and Spillet, 1966). Among the other factors reported to effect age structure and sex ratio of herbivore populations are predation (Messier, 1994, Laundre et al., 2001, Gervasi et al., 2012), harvest (Langvatn and Loison, 1999) and poaching or illegal harvesting (Corlatti et al., 2019).

Body condition

Body condition or nutritional condition among individuals of a population is a sensitive and easily measured response of an animal to environmental variation (Sinclair and Duncan, 1972). Body condition of an animal is an assimilation of nutritional intake and demand and has a direct influence on survival and reproduction (Parker et al., 2009). Body condition being a density dependent response factor (Gaidet and Gaillard, 2008), is a crucial measure for describing the complex mechanisms that support demography of ungulates, and eventually reflects and influences the nutritive carrying capacity of an area (Stephenson et al., 2020). Population vital rates, such as pregnancy, age of first reproduction, juvenile and adult survival, which drive population dynamics (Gaillard et al., 2000) are all linked to nutrition at varying degrees. For example, body fat was strongly associated with pregnancy in caribou and moose (Gerhart et al., 1996; Testa and Adams, 1998, Stephenson et al., 2020), with age of first reproduction in bighorn sheep and mule deer (Jorgenson et al., 1993; Monteith et al., 2014) and maternal body fat influencing survival and recruitment of young mule deer (Monteith et al., 2014). Individual body condition carries information on population performance, indicative of presence of inter or intraspecific competition (Couturier et al., 2008; Stephenson et al., 2020), disease prevalence (Leader-Williams., 1982) and the potential of the population to increase (Clutton-Brock et al., 1997). Population demography of ungulates driven by nutritional limitations of an area can also get confounded under the effect of predation due to large carnivores (Chowns and Gates, 2004). In order to minimize threat, animals tend to strategize maximizing their seasonal nutritional demand often at a cost of giving up higher nutritional intake (Festa-Bianchet et al., 1998), which can get manifested in animals physiological condition. Furthermore, vulnerability of individual animals can to some extent be driven by the nutritional status. Juvenile or maternal body condition under certain level of resource limitation has been observed to significantly influence predation rates (Linnell et al., 1995). For examples, poor nutrition of white-tailed deer juveniles can be a dominant cause of higher rate of predation by wolves (Mech, 2007).

Why chital?

Age-sex structure

Chital is a gregarious species with prominent sexual dimorphism and distinct population age classes (see review). The species, although exhibits a fission-fusion system of fluid group formation and dissolution (Schaller, 1967; Fuchs, 1977; Barrette, 1991), a herd is generally comprised of two or more basic social units which usually consists of an adult female, her offspring from the preceding year, and a fawn (Ables, 1974). Chital exhibits open membership social structure and their group size and constitution has been observed to change temporally in relation to factors such as habitat, animal density, rainfall and breeding seasonality (Dave, 2008; Raman, 1997). Change in these factors might affect different age and sex classes of chital differently. Hence, with easily distinguishable age classes of chital, unlike in other cervids of Indian subcontinent, the species can be a preferred subject to understand the underlying mechanism of ungulate population dynamics, and, has been studied across different landscapes of the country (Dave, 2008; Johnsingh, 1983; Khan & Vohra, 1992; Sankar & Acharya, 2004). Studies which have accounted for population sex ratio of chital, found it to be female biased (Karanth and Sunquist, 1992, Khan et al., 1994; Ramesh et al.,2012). However, the reasons behind such skewed sex ratio has not been addressed.

Body condition

Being the most abundant ungulate species in the tropical forests of India, occupying almost all the habitat regimes, chital serves as the most crucial prey for large to medium sized predators, such as tiger, leopard and wild dog. Such relatively high abundance of chital, in compare to other ungulates, can have a greater impact on the nutritional availability (or conversely nutritional carrying capacity) of an area.

Imbalance in the equilibrium, exacerbated by presence of large predators limiting access to resources or through direct predation, can seemingly at best be observed in physiological conditions of different life-history stages of the species (discussed above). Additionally, higher observability, prominent sexual dimorphism, discernible age classes and, individual identification are some of the favourable traits for studying body condition of the species.

Studying age-sex structure, to obtain knowledge about population dynamics is conventionally done through data collected by direct observation of individuals for a significantly long duration, sampling representative populations to understand both temporal and spatial effect. Appropriate indexing of body condition on the other hand although is best done by capturing animals, ocular estimation methods, either through direct observation or photographic record, however have proven to be an effective non-invasive alternative and has been increasingly used (Riney, 1960; Smiley et al., 2020). In this chapter, I however report both age-sex structure and body condition of chital in a snapshot sampling of populations in Corbett National Park (CNP) using remote camera traps. Age-sex structure data was combined from three different blocks which were already sampled with camera traps (Chapter IV). I compared, adult male to female ratio, and, fawn to adult female ratio between two of these block which varied by tiger density. I assumed, fawn-adult female ratio of chital will decrease with higher predation risk. Similar block-wise comparison of chital body condition scores was done assuming that body condition of chital will be poor in area with higher tiger density. Although I acknowledge that my study lacks controlling for habitat, important to understand whether the effect was solely due to higher predation risk, however broadly, since the sampling areas were well representative of all the habitat types of

CNP and sampling was done almost at the same duration, I think predation driven effect can be a reasonable factor in this case.

5.2 STUDY AREA

The sampling in CNP was done in three different blocks of varying sizes and varying tiger density (Block 1 was high density area while Block 2 and 3 were of medium tiger density) which were already delineated for earlier works (Figure 5.1 and Figure 4.12 of chapter IV). The sampling blocks were representative of all the major habitat types of CNP.

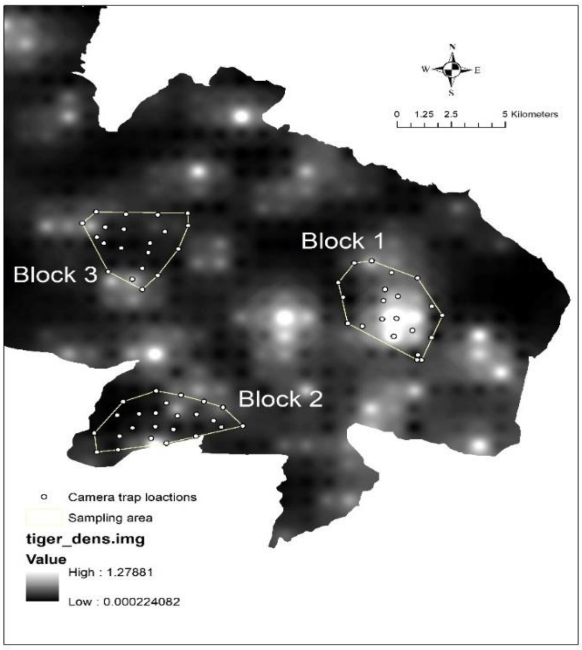


Figure 5.1: Map showing the position of three sampling blocks (Block1, 2 and 3) and the different tiger density of the respective blocks in CNP. White circles show the camera trap locations.

5.3 METHODS

20-25 IR-based single sided Reconyx camera traps were deployed in each of the three blocks which were programmed to take 10 photographs at a rate of 1 frame per second to capture continuous movement of an entire herd or a single individual without any omission. Cameras were placed at a distance of 800 -1000 m from each other. Cameras were operated for 24 hours for a duration of 20-25 days, which delivered sufficient images to sample age-sex structure and body condition of the chital populations. Images of both day and night were used for aging, sexing and body condition scoring. Sampling was done between 15th January to 28th April of 2019.

Age –sex structure

Camera trap photographs were analysed to classify chital into easily distinguishable four age and the two sex classes (Schaller, 1967). Age and sex classes were, 1) fawn (< 6 months), characterized by height lower than belly size of the accompanying mother almost always (Figure 5.5, (b)), 2) juvenile male/female (< 1 year but > 6 months), characterized by body height ranging between the adult belly size and shoulder and initial appearance of the pedicle bone for male, while absence of the same for female (Figure 5.5, (e) and (f)), 3) sub adult male/female (< 2 years but > 1 year), characterized by almost similar body size to that of adult, and, formation of spike or simple branched antler with 4/5 points and not so prominent antler base (Figure 5.5, (c) and (d)), 4) adult male/female (> 2 years), characterized by large body size with round belly and no antler for female, while adult males were characterized by stout sternum and flank portion and a thick neck and were with prominent pedicel base either with smaller velvet antlers (at the beginning of sampling) or large velvet or hard antlers (from mid to later stage of sampling) (Figure 5.5, (a) and (b)).

Age-sex classified data of CNP were from 61 camera traps from the three sampling blocks together. Photographs were analysed to estimate adult male to female ratio and fawn to adult female ratio to understand the population structure. Percentage contribution of each age-sex classes to the total population was also calculated to evaluate population composition in each block as well as all the blocks combined as representation of overall CNP. For estimating ratio and variance of adult female to male, as well as fawn to adult female I used single sampling with replacement approach (Skalski et al., 2005), as camera traps possibly captured the same animal multiple times. Ratio estimation followed the equation,

Ὑ$_{F/M}$ = ὩΤά (ratio of number of females to number of males) (equation 3.12)

where,

f = number of females in the sample size of n

m = number of males in the sample size of n

Variance was estimated following the delta method as;

Var (Ὑ$_{F/M}$) = nf / m^3 (equation 3.14)

where,

n = number of animals examined for gender

Body condition

For body condition scoring I used 25-35 samples of each age-sex categories (adult male, adult female, sub adult male, sub adult female, juvenile male and juvenile female). As representation of CNP as well as comparison, I used data of block 1 and block 2 only, as tiger density in both block 2 and block 3 was almost similar (Figure 1). Chital individuals of block 1 and 2 were already identified for mark recapture sampling (chapter IV) hence scores were unique to each individual. Scoring was based on indexing five different regions of the body, viz. pectoral girdle, pelvic girdle, rump, ribs and tail on a score of 1 to 5, where 1 signified poor and 5 indicated very good condition (Riney, 1960). Pectoral girdle indexing was based on inconspicuous to conspicuous scapula. Pelvic girdle was based on shape, from round to straight (round meaning good and straight meaning poor) (Figure 5.6). Evaluation of rump was based on appearance of being round to angular. Ribs were considered very good when fully covered and poor when visible. Appearance of tail from being round to angular was indexed as very good and poor respectively (Figure 5.6).

Scores of the five different body parts were likely to be correlated. Therefore, I used principal component analysis (PCA) on the scores to reduce the dimensionality and loss of information (McGarigal et al., 2000). Principal component score was then used to statistically compare chital body condition between two blocks of CNP (block 1 and block 2). The analysis was done using SPSS Statistics 28.0.1.

5.4 RESULTS

Age-sex structure

Number of females per male was higher in block 1 than block 2 (Table 5.2). Number of fawn per female was however higher in block 2 than block 1. Overall number of females per male for CNP was 1.66 (± 0.06) and number of fawns per female for CNP was 0.25 (0.01) (Table 5.2). Percentage contribution by fawns in the population was much higher in block 2 (14.1%, SE = 4.13) than in block 1 (5.72%, SE = 1.65) (Table 5.1).

Body condition

Running PCA for block 1 and block 2 of CNP on the five factors i.e. scores of the five body parts, generated a principal component that explained 58.63 % of observed variation. Condition scores of five factors contributed differently to this principal component (Table 5.3), however with a factor loading of over 0.7 (Table 5.3).

Comparing block 1 and block 2 based on PCA factor-1 I observed that body condition of chital was significantly poorer in block 1 than in block 2 (Figure 5.4) (One-way ANOVA, F = 3.93, p = 0.05).

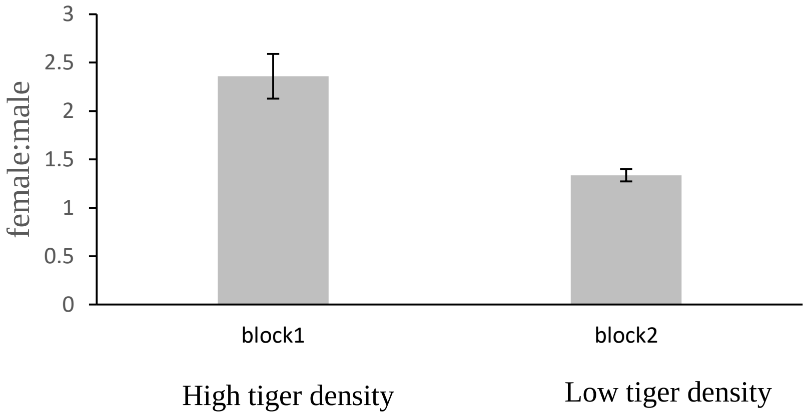


Figure 5.2: Plot showing adult female to male ratio in two sampling blocks with varying tiger density. Error bars are standard error.

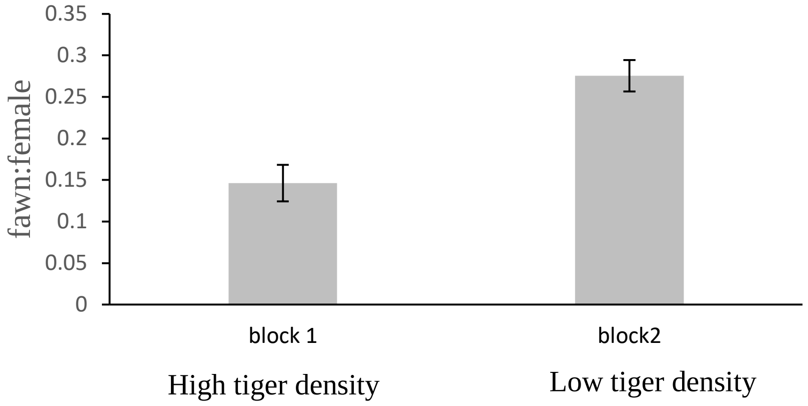


Figure 5.3: Plot showing fawn to adult female ratio in the two sampling blocks with varying tiger density. Error bars are standard error.

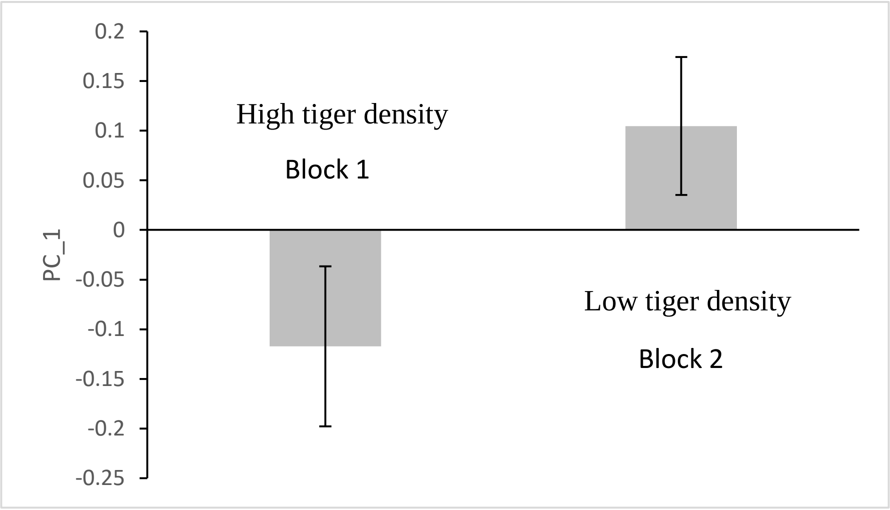


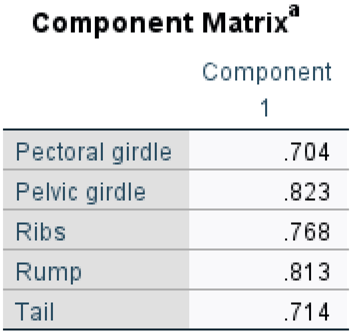
Figure 5.4: Body condition of chital compared between block 1 and block 2 based on scores of the first principal component. Error bars are standard errors.

Table 5.1: Percentage composition, with associated standard error, of different age-sex classes of chital in two blocks of CNP separately for comparison, as well as three blocks combined (CNP-overall).

Area	Adult		Sub adult		Juvenile		Fawn% (SE)
	Male% (SE)	Female% (SE)	Male% (SE)	Female% (SE)	Male% (SE)	Female% (SE)	
CNP-block1 (n=1095) (high tiger)	15.32 (2.63)	30.48 (2.48)	6.70 (1.54)	26.34 (2.21)	4.51 (1.11)	10.92 (2.26)	5.72 (1.65)
CNP-block2 (n=2631) (low tiger)	22.82 (3.76)	40.93 (3.94)	5.74 (1.28)	10.96 (1.44)	0.67 (0.27)	4.80 (1.06)	14.1 (4.13)
CNP-overall (n=4883)	18.26 (1.93)	36.08 (1.93)	5.70 (0.79)	18.70 (1.46)	2.65 (0.47)	7.27 (0.97)	11.40 (1.93)

Table 5.2: Adult female to male and fawn to female ratio of two comparative blocks (block 1 and block 2) as well as three blocks combined (CNP-overall)

Area	Number of females/male	Number of fawns/female
CNP-block1 (n=1095) (high tiger density)	2.35 (0.23)	0.15 (0.02)
CNP-block2 (n=2631) (low tiger density)	1.33 (0.06)	0.27 (0.02)
CNP-overall (n=4883)	1.66 (0.06)	0.25(0.01)



Component Matrix[a]

	Component 1
Pectoral girdle	.704
Pelvic girdle	.823
Ribs	.768
Rump	.813
Tail	.714

Table 5.3: Principal component loading by different body condition indices on PC-1 (Component Matrix Extraction Method: Principal Component Analysis).

a) Adult male b) Fawn with the mother (adult female)

c) Sub adult male d) Sub adult female

e) Juvenile male f) Juvenile female

Figure 5.5: Camera trap photos showing different age-sex classes of chital

Very good body condition (adult male and adult female)

Very poor body condition (adult male and adult female)

Figure 5.6: Camera trap images showing different body regions used for evaluating nutritional condition of chital individuals.

Top-left –showing a healthy pectoral girdle

Top-right - showing a healthy pelvic girdle region

Bottom-left –showing poor condition angular rump and almost invisible tail

Bottom-right –showing visible poor condition visible ribs

5.5 DISCUSSION

Obtaining information on demography of ungulates in a prey-predator ecosystem is crucial from both ecological and management perspective, and requires long-term monitoring of populations to understand population trajectories under the influence of various factors such as habitat, season, predation etc. However, limitation of resources, in respect of time and logistics, can often hinder such long-term monitoring of important population vital rates such as fecundity, juvenile survival, fawn recruitment etc. This study demonstrates, the potential of camera trap as an effective population monitoring tool in generating important baseline information on population age-sex structure and demographic ratio, measures that are considered useful indices indicating current status and dynamics of a population, within a short span of time. Moreover, in the current study area, characterized by dense forest with thick undergrowth, remote camera traps appeared to be a comparatively better non-invasive medium of observing chital individuals, than direct observation. Several studies have used camera trapping to generate similar population level data for different ungulate species (Brommer et al., 2021; Ikeda et al., 2013; Jacobson et al., 1997; Macaulay et al., 2020; Peres et al., 2017).

Camera trap based estimates of percentage composition and ratio of different age-sex classes of chital in CNP corroborated well with the general observed pattern as demonstrated by other direct observation based studies on chital in different areas (Dave, 2008; Khan & Vohra, 1992; Ramesh et al., 2012). Chital individuals of the sampling blocks were already identified from their unique spot pattern except for the fawns. Therefore, I derived the ratio estimates (both adult female: adult male and fawn:

adult female) from image count and not using the identified individuals. However, I evaluated the image count based ratio estimate of adult female to adult male (2.35) with that of identified individual count based ratio of adult male to adult female (2.02) of block 1 to rule out any large possibility of duplication of counts. Female to male ratio was highly skewed towards female in block 1, which can probably be attributed to higher selective predation of males by tiger. The much lower number of fawns per female in block 1 than in block 2 can either be due to predation by both tigers as well as other meso-carnivore in the area like jackal or due to low detectability of fawns in the camera traps during the sampling duration, an important aspect which is lacking in the study and needs careful consideration for future studies. However, contrary to the generally reported trend of higher predation of juveniles which might result in their lower number, block 2 which is low-medium dense tiger area had a much lower percentage of juvenile in the population (Table 5.1). In this context, I also acknowledge a low possibility of misclassification between the juvenile and sub-adult age categories particularly for animals captured somewhat far from the camera traps.

In addition to demographic data, the same camera trap images could be easily utilized to generate sufficient samples for indexing body condition in a cost effective and non-invasive manner, thereby highlighting the manifold potentiality of camera traps as an efficient tool once again. The poorer body condition of chital in block 2 can be attributed to higher predation related physiological stress and unavailability of areas with higher forage quality due to presence of tigers. Important to note here, is the significance of controlling for habitat which is lacking, although given the sampling duration (January to March) when forage should be fairly abundant in the area, effect of habitat on the physiological condition in this case can be of a lower possibility.

CHAPTER VI SYNTHESIS AND CONCLUSIONS

Corbett National Park holds immense importance as an ecosystem in the larger Terai-Arc Landscape, owing to its heterogeneous habitats and hydrological features and a very healthy and diverse ungulate prey base which helps in sustaining the single largest tiger population in the world, sourcing tigers almost in the entire landscape. Despite such value, little was known about the functioning of such a high density tiger population, until the extensive work by Bisht, 2019, which generated some very valuable information on the population dynamics and biology of tigers in the area. However, it is imperative that conservation and management of tigers in such an area will automatically necessitates gaining insights into the prey population as well, beyond just density, which was also lacking. On the face of such requirement, my study is an attempt to somewhat fill that information gap. Although my study lacks addressing a fine resolution, over encompassing aspect of prey population in the area, however I strongly feel that the information generated from the study will most definitely act as valuable baseline knowledge for future studies on ungulates in the area and for management decisions.

Modelling detection-probability based absolute densities of the ungulates both year-wise and habitat-wise helped in understanding the population status over time as well as the apparent preference/avoidance of habitats by the species respectively. Moreover, the detection corrected spatial modelling of the ungulate abundance and generating density surface maps of the species augments the understanding of relationship of the ungulates with habitat and other important environmental correlates. Such information holds both ecological and management importance. I acknowledge that, although my data has tried to account for the spatial heterogeneity as much as possible, by way of random representative sampling of the area, however it lacks the important aspect of temporal sampling (season wise), and, equivalent effort allocation for each stratum (although proportional with the occurrence), which should be given careful consideration. I suggest, generating the required sample size before sampling by simulation using this data will help in obtaining sampling adequacy and make the comparisons more robust.

The key highlight of my thesis is testing the efficacy and cost effectiveness of two different density estimation techniques on the four ungulates which differ significantly by their biology. Such a comparison brings out the underlying nuances of the sampling methods and possibility of assumption violation, which will critically help the management to choose a method by judging the trade-off between precision and cost, based on their respective available logistics. Comparing direct observation based line transect distance sampling vs camera trap based Random Encounter Model (REM) definitely establishes the easiness of camera trap sampling in areas like CNP where terrain is complex and accessibility is limited. Testing REM in estimating density of the important ungulate assemblage in CNP, to my knowledge is the second such attempt in the country, and I believe will largely aid in its acceptance among the conservation practitioners and the managers. The ability of REM in estimating density of a range of non-individually identifiable species in a non-invasive manner is what makes it a potential wildlife monitoring technique. Although the comparison of distance sampling and REM comes from a considerably large sized area of 100 sq.km encompassing the major habitats of CNP, however I believe future studies should target sampling all the available habitats equally, to obtain more robust estimates of density. Camera trap mark-recapture based density estimation of chital once again highlights the efficiency of camera trap based sampling. Such application of camera trap on chital is the first such study in India to my knowledge. An important future consideration I would like to highlight, is appropriate spacing of the cameras for species like chital which will allow spatial capture recapture modelling of density.

Using camera trap my study successfully yielded the generally observed demographic structure of chital, thereby highlighting the effectiveness of camera trap in this case as well. The gradient of tiger density in the two sampling blocks provided an excellent opportunity to investigate how differential predation or predator presence can affect the demography and body condition of the prey, in this case the chital, and I believe my study has conformed to the general findings reported in similar studies.

To summarise, I would reiterate, that more studies should focus using camera trap as a sampling tool (however not for addressing questions which essentially require direct observation by physical presence), which is capable of delivering important ecological data in a non-invasive long-term yet sustainable fashion, especially in areas where direct observation is relatively difficult due to reasons such as vegetation density, complex terrain, evasiveness of animals and risk of encountering dangerous carnivores. Additionally, in compare to direct observation, camera trap can generate valuable observational data on elusive/cryptic species (for example wild pig in my study). However, sufficient care should be given in appropriate sampling design using available knowledge of species biology, without which estimates can be biased.

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Senior Editors: **Jos Barlow, Nathalie Pettorelli, Phil Stephens, Martin Nuñez, Romina Rader and Tade**

Impact Factor: 6.53

2020 Journal Citation Reports (Clarivate Analytics):
4/60 (Biodiversity Conservation)
14/178 (Ecology)

Online ISSN: 1365-2664

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RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Demography of a high-density tiger population and its implications for tiger recovery

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Funding information
Uttarakhand Forest Department; National Tiger Conservation Authority

Handling Editor: Matt Hayward

Abstract

1. Prioritizing conservation of source populations within landscapes is proposed as a strategy for recovering tigers globally. We studied population dynamics of tigers in Corbett National Park (CNP) in Indian *Terai*, which harbours the largest and highest density tiger population in any protected area of the world. Through population viability models, we demonstrate the importance of CNP in tiger recovery within western *Terai*.
2. We camera trapped 521 km^2 of CNP using open population capture–mark–recapture framework between 2010 and 2015 to estimate annual abundance, spatially explicit density, survival, recruitment, temporary movements, sex ratio and proportion of females breeding. We model metapopulation persistence with and without Corbett as a source within western *Terai* landscape at different levels of poaching and habitat connectivity.
3. In 6 years, we recorded 6,202 photo-captures of 307 individual tigers. Annual tiger abundance and density were stable at 120 (*SE* 19) and 14 (*SE* 3) per 100 km^2 respectively. Detection probability of tigers was 0.18 (*SE* 0.03) and detection-corrected male:female sex ratio was female biased (0.80 *SE* 0.13). Apparent annual survival probability was 0.79 (*SE* 0.05) for females and 0.60 (*SE* 0.04) for males. Survival of tigers in CNP (0.68 *SE* 0.12) was lower than that reported for other populations. CNP tigers showed high reproduction with 54.8 (*SE* 5.1)% females breeding and with addition of 35 (*SE* 8)% as new recruits to the population each year. Small tiger populations in western *Terai* with moderate poaching could only persist through dispersal from CNP.
4. *Synthesis and applications*. Corbett tiger population was characterized by a stable high density, high reproductive rate and low survival, resulting in high turnover rates (32%–48%) between successive years. Such source populations could sustain low-level poaching and with habitat connectivity, recover tiger populations across the landscape. This study establishes potential thresholds that can likely be achieved by tiger populations under optimal natural conditions and highlights the importance of prioritizing conservation of source populations within tiger landscapes. This information can be used to plan and implement realistic tiger recovery programmes globally.

KEYWORDS

breeding tigresses, Corbett National Park, population dynamics, PVA, recruitment, source population, survival, *Terai* Arc

1 | INTRODUCTION

Tigers (*Panthera tigris*), the flagship species of Asian forested ecosystems, have lost over 40% of their range in the last two decades primarily due to demand-driven poaching, loss of habitat and its prey (Dinerstein et al., 2007). In densely populated Asia, space allocation for tiger conservation is one of the most limiting factors. The situation becomes even more challenging since protected areas (PA) by themselves are often too small to sustain viable tiger population in the long term (Wikramanayake et al., 1998). The average size of a PA in India, which is home to about 70% of the world's wild tigers (Jhala, Qureshi, & Gopal, 2015), is 393 km^2 (http://www.wiienvis.nic.in/Database/ProtectedArea854.aspx). However, due to high prey densities, some of these PAs have the potential to support high tiger density and if they lie embedded in a contiguous forested landscape, they can help maintain viable tiger population in that landscape. Therefore, tiger conservation strategy in India aims to preserve such small areas within larger connected landscapes as metapopulations (Qureshi et al., 2014). High-density tiger population in core areas of tiger reserves is achieved by making them free of human settlement and their impacts through incentivized voluntary relocation (Wildlife Protection Act, 1972; amendment 2005 http://www.indiaenvironmentportal.org.in/files/THE-20WILD-20LIFE.pdf) and habitat management for enhancing prey density. These activities require high investments, and the National Tiger Conservation Authority spent 7–20 million USD annually on incentivized voluntary human resettlement from within core areas of Tiger Reserves between 2010 and 2015 (https://projecttiger.nic.in/content/144_6_VillageRelocation11thPlan.aspx and https://projecttiger.nic.in/content/148_6_VillageRelocation12thPlan.aspx). This strategy is in consonance with Walston et al. (2010) who recommended protecting source tiger populations as a priority since these areas encompass only 6% of the current tiger distribution but harbour nearly 70% of wild tigers. This tenet has been debated widely with opponents proposing that landscape scale conservation should be the priority for a wide-ranging carnivore like the tiger (Wikramanayake et al., 2011). Metapopulation models parameterized with realistic tiger demographic data that evaluate tiger population persistence at landscape scales along with real-life data on tiger recovery would help resolve this debate.

Information on tiger vital rates is sparse and pioneering work of Sunquist (1981) and Smith (1993) that used radiotelemetry on tigers in Nepal *Terai* still remains the best source of information on the subject. Subsequently, Kenny, Smith, Starfield, and McDougal (1995), Kerley et al. (2003), Karanth, Nichols, Kumar, and Hines (2006), Duangchantrasiri et al. (2016), Majumder, Qureshi, Sankar, and Kumar (2017) and Sadhu et al. (2017) used camera trap-based capture–mark–recapture (CMR) and known fate models to estimate survival and movement parameters of tigers. Studying wildlife demography through telemetry provides information on survival, dispersal and helps tease apart temporary movement from permanent ones. However, such studies are constrained by the number of animals that can be radio-tagged due to the limitation of resources and permission for capture. Alternatively, camera trap-based CMR has proved to be a useful approach to study vital rates of large carnivore populations (Duangchantrasiri et al., 2016; Harmsen et al., 2017; Karanth et al., 2006; Majumder et al., 2017; Sharma et al., 2014). Although camera trap-based CMR approach addresses the limited sample size of telemetry studies, the vital rates obtained by CMR cannot distinguish between mortality and permanent emigration (Pollock, 1982). However, information generated by well-designed camera trap study is useful in understanding many aspects of demography that include vital rates such as apparent survival, recruitment, movement, time-specific detection-corrected sex ratio and percentage of breeding females in the population. Recent approach using spatially explicit open capture (SECR) CMR models has attempted to distinguish between emigration and mortality (Ergon & Gardner, 2014; Gardner, Sollmann, Kumar, Jathanna, & Karanth, 2018). However, these approaches are still under development (Efford, 2019) and require a very large-scale camera trapping to capture dispersal events of large carnivores, making them impractical for application (Ergon & Gardner, 2014).

The *Terai* landscape is renowned for its productivity, high concentration of ungulates and therefore, ability to sustain some of the highest density of tigers in the world (Dinerstein, 1980; Sunquist, 1981; Smith, 1993). Long-term work on tigers in the Nepal *Terai* has provided information on tiger demography through telemetry (Smith, 1987, 1993; Sunquist, 1981) and camera trapping (Barlow et al., 2009). Most of our knowledge on population dynamics and vital rates of tigers in India is from central India (Majumder et al., 2017; Panwar, 1979; Sadhu et al., 2017; Schaller, 1967) and from the Western Ghats (Karanth et al., 2006). While Corbett on the Indian side of *Terai* harbours the single largest tiger population in a single protected area in the world, estimated at 169–261 tigers, with a density of 16 ± 1.60 tigers per 100 km^2 (Bisht et al., 2015; Contractor, 2007), this population remains data deficient in our understanding of tiger demography and ecology. Corbett provides a unique opportunity to study a system that has been able to sustain one of the highest tiger densities in the world. The mechanisms behind this are of importance in current times of limited space and vanishing large mammals. The demographic parameter estimates from a high-density tiger population at/or approaching carrying capacity can be used for model-based predictions (Karanth & Stith, 1999) so as to gain an understanding of long-term population dynamics as well as form a basis for management interventions. This information will also help set realistic targets for achievable tiger numbers, enabling work towards reaching the set objective of 'TX2 commitment' by Tiger range countries (https://www.wwf.de/fileadmin/fm-wwf/Publikationen-PDF/Global-Tiger-Recovery-Program-Nov-4.pdf, Global Tiger Initiative, Global tiger recovery program 2010–2022).

We sampled Corbett National Park (CNP) from 2010 to 2015 using camera trap-based open CMR framework. Apart from abundance, we estimate sex-specific survival rates, sex ratio, reproductive and turnover rates in this high-density tiger population. We subsequently use these parameters to model the metapopulation of tigers in western *Terai* and evaluate the importance of the source value of Corbett tiger population in sustaining long-term tiger persistence within the landscape. We compare our model results with observed recovery of tigers in the western *Terai* Landscape (Jhala, Qureshi, & Gopal, 2008; Jhala, Qureshi, Gopal, & Sinha, 2011; Jhala et al., 2015).

Most tiger populations are plagued with low density, low reproductive rates and high mortality rates. Tigers of Corbett are a contradiction of sorts, as they occur at high density with a reasonably large population and have high reproductive rates. Our study provides insights in the demographic processes that operate in high-density populations like Corbett. It spells hope for tiger conservation efforts and shows that establishing source tiger populations similar to that of Corbett within each tiger landscape is the first step towards global tiger recovery.

2 | MATERIALS AND METHODS

2.1 | Study area

Terai Arc Landscape in India can be divided into two parts, Western *Terai* between the Yamuna and Sharda rivers and Eastern *Terai*, the area east of the Sharda river (Harihar & Pandav, 2012). The study was conducted in 521 km^2 of CNP situated in the Western *Terai* (Figure 1), comprising the foothills of the Himalayas, the Shivalik range and the *doon* valley. Corbett Tiger Reserve forms the major source population of tigers in Western *Terai*, while Chitwan National Park in Nepal is the major source in Eastern *Terai*. Most striking feature of this landscape is the perennial water streams called *sots* that act as water sources for wildlife throughout the year. The rich alluvial system and perennial water source support a thriving ungulate population (64 [*SE* 8.6] Chital [*Axis axis*] per km^2 and 9 [*SE* 1.1] Sambar

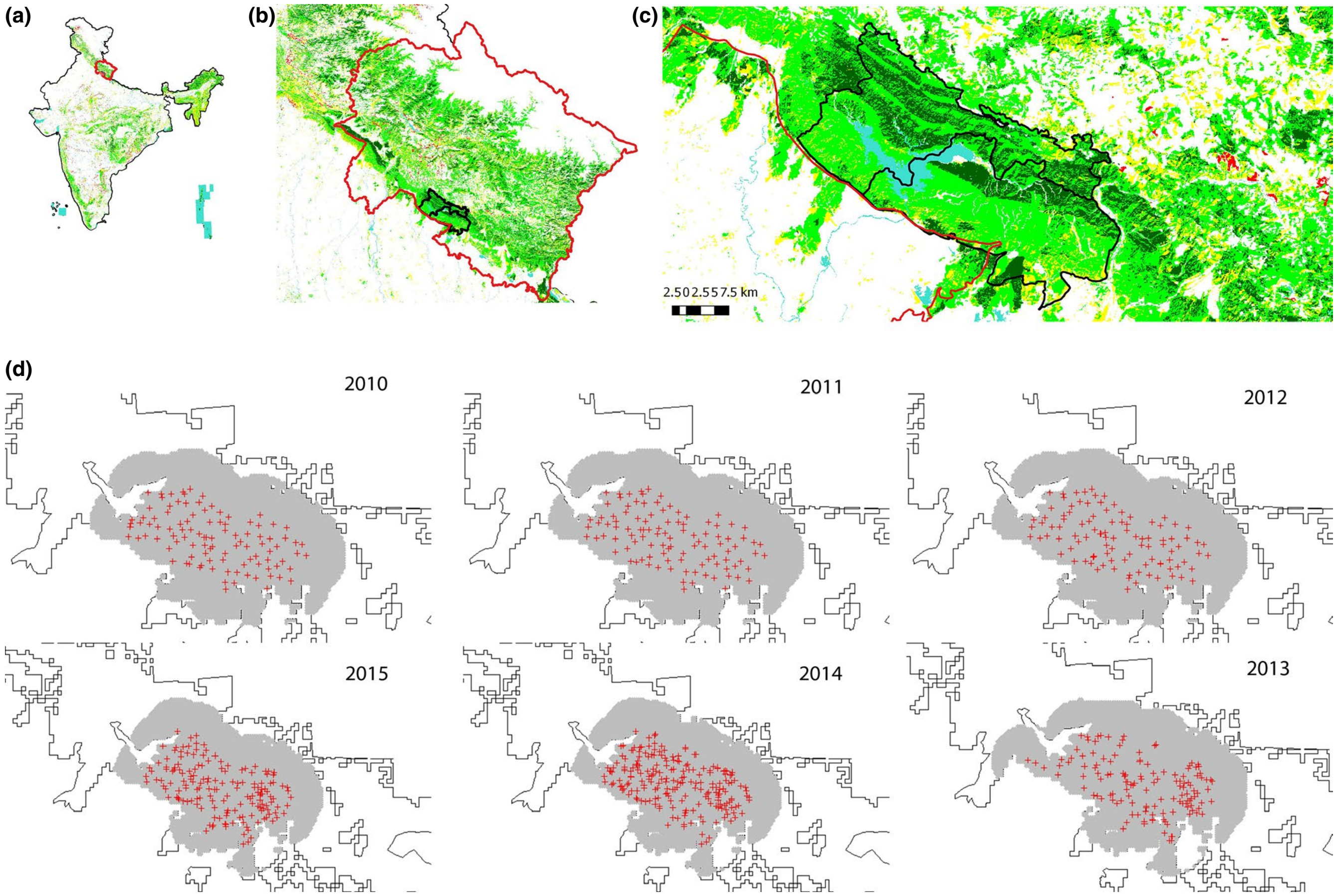

FIGURE 1 Map showing position of study area (Corbett National Park) overlaid on forest cover (green colour) map in (a) India and (b) state of Uttarakhand, (c) Corbett Tiger Reserve and (d) Camera trap locations (+) with a buffer of 8 km overlaid on tiger habitat mask for years 2010–2015 (clockwise)

TABLE 1 Tiger density (per 100 km^2) and major prey density (per km^2) from some important tiger conservation sites in India

Sites	Tiger	*SE*	Chital	*SE*	Sambar	*SE*	Source
Kanha	6.1	0.7	30.1	4.34	15.34	3.34	Awasthi et al. (2016), Kumar et al. (2015)
Ranthambhore	6.4	1	33.8	6.52	25.67	4.56	Sadhu et al. (2015)
Sunderbans	5.8	1.2	5.24	1.23	NA	NA	Roy et al. (2016)
Pench (Maharashtra)	3	0.6	15.69	7.14	6.6	2.9	Bhagat, Reddy, Joshi, Pariwakam, and Bansod (2015)
Rajaji	2.9	0.9	16.2	5.79	12.06	3.75	Pandav et al. (2015)
Nagarhole	11	0.9	29.85	4.36	3.56	0.57	Karanth, Kumar, Parameshwaran, Srivastha, and Sharma (2015)
Corbett	14	3	64	8.6	9	1.1	Bisht et al. (2015)

[*Rusa unicolor*] per km^2, Jhala et al., 2015) in the park as compared to some of the other Tiger Reserves in the country (Table 1).

Champion and Seth (1968) classified forests of CNP into three major types, namely Northern moist deciduous (3C), Northern tropical dry deciduous (5B) and Himalayan subtropical pine forest (9). Other than the Tiger, the park supports felids like Leopard *Panthera pardus*, Leopard cat *Prionailurus bengalensis* and Jungle cat *Felis chaus*. Other carnivores include Golden jackal *Canis aureus*, Sloth bear *Melursus ursinus*, Himalayan black bear *Ursus thibetanus*, Yellow-throated Marten *Martes flavigula*, Indian grey mongoose *Herpestes edwardsii*, Palm civet *Paradoxurus hermaphroditus*, Large Indian civet *Viverra zibetha*, Small Indian civet *Viverricula indica* and Smooth-coated otter *Lutrogale perspicillata*. Herbivores include Elephants *Elephas maximus*, Sambar, Chital, Barking deer *Muntiacus vaginalis*, Wild pig *Sus scrofa*, Hog deer *Axis porcinus*, Nilgai *Boselaphus tragocamelus*, Serow *Capricornis thar* and Goral *Naemorhedus goral*. The avifauna of CNP is also very rich with 554 species of resident and migratory birds of which 21 species are globally threatened (https://avibase.bsc-eoc.org).

2.2 | Data collection

We used CMR in a robust design framework (Pollock, 1982) by camera trapping 521 km^2 area of CNP consistently between 2010 and 2015. We deployed camera trap units that function on activity and passive infrared triggering mechanism to photograph tigers. Camera traps were deployed in pairs at each station, on either side of trails, so as to photo-capture both flanks simultaneously of each passing animal (Karanth & Nichols, 1998). Distance between camera trap stations was maintained between 1 and 1.5 km so as to ensure no 'holes' in the sampled area. This high camera density (Figure 1) ensured that all tigers in the study area had a good chance of photo-capture with no tiger having zero probability of photo-capture (Pollock, Nichols, Brownie, & Hines, 1990). Camera trap stations were selected based on reconnaissance sign surveys as well as expert knowledge of local field assistants. Potential camera trap point locations were recorded on the ground using a handheld GPS (Etrex 30 and Garmin 72); these locations were then plotted on Google Earth to select points for camera deployment to adhere to above-mentioned camera distance and correct for any sampling holes.

Due to logistic constraints (limited number of camera traps and field biologists) during the initial years (2010–2012), we sampled the study area in two blocks of ~250 km^2 area each. These two blocks were sampled 120–150 days apart. With increased availability of camera traps and trained field staff, we camera trapped the entire study area (521 km^2) simultaneously in 2013–2015 (see Table S1).

2.3 | Data analysis

Photographic captures and subsequent identification of tiger individuals through program EXTRACTCOMPARE (Hiby et al., 2009) yielded capture histories of individuals in the standard X-matrix format (Otis, Burnham, White, & Anderson, 1978). All CMR analyses excluded cubs (<1 year old) because of their low photo-capture probability and high mortality (Karanth et al., 2006). We grouped remaining >1-year-old tigers into a single age class because of difficulty in differentiating between adults and subadults from camera trap photos alone (Sadhu et al., 2017). Owing to a large sample size (n = 307) and ability to sex most individuals, we were able to obtain gender-specific parameter estimates.

2.4 | Population dynamics

We analysed capture data under the Robust design initially proposed by Pollock (1982) and subsequently modified by Kendall, Pollock, and Brownie (1995), Kendall, Nichols, and Hines (1997). Pollock's (1982) robust design was a two-stage analysis where abundance was estimated using closed population models for each primary period, while transition parameters were estimated between primary periods. All analyses were done in program MARK 8.x version 2017 (White & Burnham, 1999). Our study consisted of 6 years (2010–2015) of data with each year as a 'primary period' (Kendall et al., 1995, 1997; Pollock, 1982; Williams, Nichols, & Conroy, 2002). The tiger population was expected to be open to gains and losses between these primary periods while closed within the duration of sampling (42 days secondary periods) within each year. Kendall et al. (1995, 1997) developed a full likelihood approach that combined

Pollock's (1982) two step analysis into a single analysis. The full likelihood approach allows an animal to be unavailable for capture at any given time (or a temporary emigrant). The probability of availability is modelled to be (a) completely random or depends on whether the animal was (b) available for capture in the previous primary period or (c) actually captured in the previous primary period (Kendall et al., 1997). We first modelled capture probability (*detection models*) and subsequently, conditioning on the best selected detection model, we modelled state and transition parameters of interest (i.e. abundance, survival and movement) that were in consonance with tiger ecology.

Each of our primary period consisted of 42 camera trap nights (secondary periods). Between 2010 and 2012, sampling was carried out in two blocks (see Table S1). Between 2012 and 2013, due to the shift from two block sampling to a single block, tigers from the second block were exposed to an interval of 6 months between primary periods instead of 12 months. We explicitly account for this single shorter primary period by estimating separate survival rate for this 6-month period in MARK (Cooch & White, 2011) and subsequently converting it to annual survival for estimating average survival across years. By merging the blocks for analysis, we could likely violate the population closure assumption required for abundance estimation. Tigers are long-lived in comparison to our sampling interval (Mazak, 1981). We therefore tested if model selection and abundance estimates differed when (a) the two blocks were analysed separately (see Table S2a,b) and (b) data from the two blocks were merged for a single analysis (see Table S2c–f). Total population abundance for each year for this block analysis was estimated using a more parsimonious model (see Table S2c) in MARK that did not account for sex-based heterogeneity in detection and considered transition parameters to be constant. This approach was preferred for estimating total population size as a simpler model provided better precision on total abundance estimates. Since results from separate analyses of the two blocks and the combined analysis yielded abundance estimates that were not different from each other (see Table S2f,g), we subsequently report results from the combined dataset analyses as this increased sample size allowed us to estimate gender-specific parameters.

2.5 | Detection models

Here, we model individual detection probability based on the frequency of recaptures within a primary period, using maximum likelihood approach. We modelled individual detection probability (capture probability (p) and recapture (c)) by addressing the following sources of variability:

1. We hypothesized that the detection of tigers was likely to differ between sexes since territory size and movement rates differ between male and female tigers (Smith, 1993; Sunquist, 1981) and as also observed in jaguars (Sollmann et al., 2011). We modelled this potential source of variability in capture probabilities by incorporating sex as a covariate in the detection model.
2. Camera trap density was relatively low at 1 per 5 km^2 for the years 2010–2012 compared to a relatively high camera trap density of 2 per 5 km^2 for 2013–2015. We expect that detection probability of tigers would be higher during years (2013–2015) with higher camera trap density. We, therefore, modelled detection with two time period effects; period (a) 2010–2012 with low camera trap density and period (b) 2013–2015 with high camera trap density.

The full detection model (P) was ($P \sim p_{(m(ct),\, f(ct),\, u(ct));}\ c_{(m(ct),\, f(ct),\, u(ct))}$) where capture (p) and recapture (c) were different for male (m), female (f) and unsexed tigers (u) for the two time periods (ct) that differed in camera density.

By accounting for heterogeneity caused by gender, effect of camera trap density along with traditional behaviour response ($p \neq c$) (Otis et al., 1978; Williams et al., 2002), we address the specific conditions in our study that could potentially account for variation in detection probability of tigers. Even though we had a 'large' sample (n = 307) of photo-captured tigers, this sample size was too small for more complex detection models like heterogeneity within gender groups, as these models did not converge.

2.6 | State and transition models

We modelled transition parameters such as survival and temporary movement rates using maximum likelihood approach on detection/non-detection of individuals across primary periods after accounting for detection probability within a primary period. Hence, using the best detection model(s), we subsequently model the state and transition. For these parameters, we evaluate the following hypotheses:

2.7 | Survival

There was no reason to suggest that habitat, prey or poaching differed in CTR between study years that could affect survival rates. Hence, we did not expect survival rates to differ between years. However, males and females have differential life-history traits (Smith, 1993) and should have different survival probabilities. We expected males to have lower survival compared to females as observed in most mammalian species (Krebs, 1972). We therefore modelled survival as constant (null model $S_{(.)}$) or differing between sexes ($S_{(g)}$).

2.8 | Movement

We did not expect movement parameters to change between years for the same reason as mentioned above. Males are the dispersing sex in tigers while females are more philopatric (Smith, 1993; Sunquist, 1981); we therefore expected movement in and out of the study area to differ between sexes. Corbett has one of the highest tiger densities in the world (Bisht et al., 2015; Contractor, 2007) and therefore competition for resources (food and mates) would also likely be high. If we found movement estimates to be very small (e.g. <0.1%) for either gender, we considered them to be negligible, and in our subsequent models, we fixed them at zero for parsimony and ease of computation.

Two movement parameters (Kendall et al., 1997), that is, temporary emigration (G″) and temporary immigration (1-G′) as defined below, were modelled.

1. Temporary emigration (G″) is the probability of going out of study area in a primary period if the animal was present in the previous primary period but remaining within the super population, and
2. Probability of staying away (G′) from the study area in a primary period given that the animal was part of the super-population in the previous primary period.

We fitted 16 models for the entire robust design analysis. We used sample size-corrected Akiake's information criteria (AIC_c) (Akaike, 2011) to select models which best explained our data from candidate competing models. To account for uncertainty associated with model selection, we used model averaging by AIC_c weights to average model parameters (Akaike, 2011).

2.9 | Abundance and spatially explicit density

The open CMR models (mentioned above) provide estimates of annual abundance ($\hat{N}$) as derived parameters in program MARK 8.x (White & Burnham, 1999). Density ($\hat{D}$) was estimated through likelihood-based spatially explicit capture recapture of tigers (Borchers & Efford, 2008; Efford, 2004) using package *secr ver.* 3.0.1 (Efford, 2017) in program R *ver* 3.4.1 (R Core Team, 2013). In SECR, we tested models where spatial scale of detection (σ) and capture probability of activity centres (g_0) were gender specific or similar between sexes.

2.10 | Sex ratio and reproductive rate

We estimated detection-corrected number of males and females from our best model to arrive at sex ratio. We examined each photo-capture event of females and termed them as 'breeding' if they were pregnant or lactating (Sadhu et al., 2017). Full udders and prominent nipples in a breeding female are visible about 7–10 days before parturition and till the cubs are weaned by 165 days (Gittleman, 1986; Smith & McDougal, 1991). From our long-term ad libitum observations in the study area, we found that one of the female's lactation period lasted for 155 days, which was similar to the lactation period mentioned in Gittleman (1986) and Smith and McDougal (1991). We sampled the study area for 42 days in a year; therefore, all females that delivered cubs ≤5 months before our sampling period would comprise the pool of breeding females available for sampling each year.

We estimated the actual number of breeding females (B_f) during the primary sampling by correcting the number of breeding females photo-captured by the detection probability of breeding females. $B_f = n_L/p_{bf}$, where n_L = number of breeding females detected in each primary sampling period, p_{bf} = probability of detecting a breeding female.

Since birth seasonality is not profound in tigers (Sunquist, 1981), we consider tigers to breed throughout the year for our computation. Breeding females (B_{fy}) in a year would be:

$$B_{fy} = B_f \times (\text{Days in a year} \div \text{Sampling Days}) \times (\text{Days Detected as Breeding} \div \text{Sampling Days})$$

$$B_{fy} = B_f \times (365 \div 42) \times (165 \div 42)$$

Since we could potentially have 8.69 intervals of 42-day sampling in a year and pregnancy/lactation was detectable for 165 days, a single breeding female could potentially be detected in 3.93 sampling intervals in 1 year.

2.11 | Recruitment and population trend

Recruitment is the number of new individuals added to the population in time *t* per individual at time *t* − 1. Recruitment in case of a camera trap study is the product of fecundity and survival from cub to >1-year-old tigers as well as immigrants from neighbouring areas. We estimated number of recruits (B_t) in time *t* as;

$$B_t = \hat{N}_{t+1} - \hat{N}_t \times S$$

where $\hat{N}_{t+1}$ = abundance estimate at time *t* + 1, $\hat{N}_t$ = abundance estimate at time *t*, *S* = *s*urvival probability (Skalski, Kristin, & Millspaugh, 2010).

Another important parameter for population dynamics is the population trend. We regressed natural log of tiger density against years (2010–2015). The slope of the regression provides an estimate of the instantaneous growth rate (*r*) (Caughley, 1977; Skalski et al., 2010). A significant positive slope implies an increasing population and a negative slope implies population decline, while a slope of zero implies a stationary population (Caughley, 1977). For a population near its carrying capacity, we expect the growth rate not to be significantly different from zero. With high potential for reproduction in tigers (Mazak, 1981), we hypothesize that, at carrying capacity, the recruits from CNP would disperse into the larger landscape so as to maintain a stationary population (growth rate near zero).

2.12 | Metapopulation viability analysis

In early 2006, the western *Terai* tiger population consisted of separate populations constituted by (a) Rajaji NP, (b) Corbett tiger reserve, (c) Ramnagar forest division and (d) Nandhore forest division. These populations though distinct, probably exchanged individuals occasionally through forested corridors constituted by the Shivalik hill forests and some remnant forests in valley habitats. Distances between these populations ranged between 1 and 146 km with varying magnitude of resistance to tiger movement in the intervening corridor habitats. Corbett NP harboured the largest tiger population numbering close to 108 ± 4.5 (Contractor, 2007). We evaluate the importance and role of Corbett tigers in sustaining and promoting tiger occupancy and abundance within the Western *Terai* landscape by modelling a Population Viability Analysis in Vortex ver. 9.9 (Lacy, 1993) using published tiger demography and parameters estimated by us in Corbett (Kenny et al., 1995; Sadhu et al., 2017; Smith, 1987, 1993; Smith & McDougal, 1991). We varied cub survival in our models to be between 0.65 and 0.55 to capture observed empirical estimates (Smith & McDougal, 1991) as well as reduced survival rates of juveniles and subadults to capture the lower limits of population persistence. We modelled realistic scenarios (see Table S3) wherein we evaluate persistence of single isolated populations of varied sizes (20, 50 and 100 tigers) exposed to various levels of poaching and catastrophic events. Subsequently, we model a metapopulation depicting the western *Terai* scenario with four populations and their initial tiger numbers as estimated in 2006 (initiation of the country-wide tiger estimation, Jhala et al., 2008). We model the metapopulation with Corbett population being small ~20 tigers and with its observed population size (≥200) to understand its role in sustaining long-term tiger persistence within the landscape. We also model a scenario wherein the landscape was depleted of tiger populations with only the source (Corbett) remaining. These scenarios address the specific case of prioritizing source population at the cost of smaller populations, answering whether such a strategy would permit long-term tiger persistence in the landscape. Movement rates between the four populations were based on our field observations from camera trap data (Jhala et al., 2008, 2011, 2015) and reducing these to half, so as to depict a higher resistance to movement in the landscape (loss of corridors). With the above models we test, Walston et al.'s 6% solution hypothesis wherein the authors propose to prioritize conserving source population within landscapes. We elucidate our model results by comparing them with observed increase in tiger occupancy and abundance within western *Terai* landscape.

3 | RESULTS

A total sampling effort of 35,784 camera trap-nights yielded 6,202 photographic captures of 307 individual tigers during our 6-year study (2010–2015) (Table 2). Of the 307 individuals, 130 were females, 118 males and 59 individuals whose gender could not be ascertained. Individuals in the unidentified gender group had 1–2 captures in a given primary period and were not photo-captured in succeeding years. Across all years, males on an average were photo-captured 11 (*SE* 1.2 range 1–72; median 6) times, while females had average photo-captures of 11.6 (*SE* 1.1 range 1–62; median 7).

3.1 | Open-CMR-robust design-based vital rates of tigers

3.1.1 | Detection probability

Tiger detection probability was best explained by the model that accounted for (a) gender-based differences (b) behavioural response of tigers and (c) the camera density. The closest competing model differed by a Delta AIC_c of 2.64 (Table 3). Detection probability for all years was high at 0.86 (*SE* 0.04) for all tigers with no difference between males (0.86, *SE* 0.01) and females (0.87, *SE* 0.01). The overall capture probability was 0.8 (*SE* 0.04) during years with low camera trap density and 0.92 (*SE* 0.05) for high-density camera trap years.

Using the best detection model, the state and transition model that had the lowest AIC_c (Table 3) accounted for gender differences in survival had no temporary movement for males and unidentified gender class while accounting for random temporary movements in females. Model estimates of survival and movement parameters differed between males (0.6 *SE* 0.04) and females (0.79 *SE* 0.05) with females having higher survival and temporary movements (Table 4).

3.1.2 | Abundance, density and recruitment

Tiger numbers ranged from 109 to 139 over the 6 years of study (Table 5). Estimates of detection probability (g_0) at the activity centre for males (0.08 *SE* 0.02) and females (0.12 *SE* 0.05) were similar. While the spatial scale of detection, σ, which is a measure of activity range radius for males (2.11 *SE* 0.24 km), was almost

TABLE 2 Details of sampling effort, detections and number of individual tigers photo-captured within 521 km^2 of consistently camera trapped area of Corbett National Park, 2010–2015

Primary period	CT density	Trap-nights	No. photo-captures	M_{t+1}	Cumulative no. of tigers	#M	#F	No. breeding females
2010	Low	4,326	466	89	89	36	43	11
2011		4,410	461	98	129	34	37	10
2012		4,410	925	93	162	30	33	8
2013	High	6,300	1,183	109	201	31	39	8
2014		9,324	1,135	118	251	34	62	7
2015		7,014	2,032	115	307	50	62	16

Abbreviations: CT density, Camera trap density; Low, one per 5 km^2; High, two per 5 km^2; M_{t+1}, unique individuals photo-captured; #M, Number of male tigers; #F, Number of female tigers.

TABLE 3 Model selection statistics for detection and transition models using the robust design analysis on tiger photo-capture data from Corbett National Park, 2010–2015

S. no	Model	AIC_c	Delta AIC_c	AIC_c weights	Model Likelihood	Num. par	Deviance
Detection models							
1	$S_{(.)}G'_{(.)}G''_{(.)}\ p_{(M(ct),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,408.82	0.00	0.82	1.00	14	17,217.96
2	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g,ct)}c_{(g,ct)}$	17,412.53	3.71	0.13	0.16	16	17,217.63
3	$S_{(.)}G'_{(.)}G''_{(.)}p_{(g)}c_{(g)}$	17,521.81	112.98	0.00	0.00	9	17,341.03
4	$S_{(.)}G'_{(.)}G''_{(.)}p_{(ct)}c_{(ct)}$	17,743.04	334.22	0.00	0.00	7	17,566.29
5	$S_{(.)}G'_{(.)}G''_{(.)}p_{(.)}c_{(.)}$	17,898.81	489.99	0.00	0.00	5	17,726.07
6	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(g)}$	17,917.80	508.98	0.00	0.00	6	17,743.06
7	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(t)}$	18,148.45	739.63	0.00	0.00	5	17,975.72
8	$S_{(.)}G'_{(.)}G''_{(.)}p{=}c_{(.)}$	18,306.76	897.94	0.00	0.00	4	18,136.03
Transition models							
1	$S_{(g)}G'_{(F,M=U=0)}G''_{(F,M=U=0)}p_{(M(ct),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,404.70	0.00	0.60	1.00	17	17,207.77
2	$S_{(g)}G'_{(.)}G''_{(.)}\ p_{(M(ct),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,407.34	2.64	0.16	0.27	17	17,210.41
3	$S_{(g)}G'_{=}G''_{(.)}\ p_{(M(t),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,408.41	3.71	0.09	0.16	16	17,213.50
4	$S_{(.)}G'_{(.)}G''_{(.)}\ p_{(M(ct),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,408.82	4.13	0.08	0.13	14	17,217.96
5	$S_{(.)}G'_{=}G''_{(.)}\ p_{(M(ct),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,410.14	5.44	0.04	0.07	13	17,221.30
6	$S_{(.)}G'_{=}G''_{(g)}\ p_{(M(ct),\ F(ct),\ U(.))}c_{(M(ct),\ F(ct),\ U(.))}$	17,411.06	6.37	0.02	0.04	14	17,220.20
7	$S_{(g)}G'_{(g)}G''_{(g)}p_{(g,ct)}c_{(g,ct)}$	17,414.18	9.48	0.01	0.01	22	17,207.11

Abbreviations: S, survival; G'', temporary emigration; G', probability of staying away; p, capture probability; c, recapture probability; g, gender; M, males; F, females; U, unidentified gender; ct, are the two time periods differing in camera trap density; (.), parameter kept constant.

TABLE 4 Model averaged estimates of capture (p),recapture (c) probability, survival (S) and temporary movement (G''& G') for female and male tigers in Corbett National Park, 2010–2015

Gender	Camera trap density	Detection parameters	Estimate (*SE*)	Survival (*SE*)	Gamma' (*SE*)	Gamma'' (*SE*)
Female (*n* = 130)	Low	p	0.05 (0.007)	0.79 (0.05)	0.58 (0.24)	0.22 (0.06)
		c	0.12 (0.005)			
	High	p	0.07 (0.007)			
		c	0.18 (0.005)			
Male (*n* = 118)	Low	p	0.06 (0.007)	0.60 (0.04)	0	0
		c	0.14 (0.006)			
	High	p	0.06 (0.007)			
		c	0.20 (0.007)			

Abbreviations: G'', temporary emigration; G', probability of staying away.

double than that of females (1.1 *SE* 0.75 km). Overall tiger density was stable at 14 (*SE* 3) per 100 km^2 from 2010 to 2015 (Table 5). Detection-corrected sex ratio (male:female) was 0.80 (*SE* 0.13, Table 5).

3.1.3 | Reproductive rate

During each sampling period, 32%–39% of photo-captured females were found to be breeding (Table 2) and the proportion of females actually breeding was estimated to be 54.8 (*SE* 5.1)%, amounting to an average of 28 (*SE* 3.2) females breeding each year within the study area.

3.1.4 | Population trend

The slope (*r*) of the regression of ln (D) versus years was not different from zero ($r = 0.003 \pm 0.03$, $p = 0.93$, $R^2 = 0.002$) suggestive of a stationary tiger population (Figure 2).

3.1.5 | Metapopulation viability

Small tiger populations <20 were liable to go extinct by themselves in the next 100 years (Table 7); such populations were extremely sensitive to poaching with extinction probability increasing to almost 100% even with one tiger being poached annually (Table 7). Medium

TABLE 5 Abundance, spatially explicit density, sex ratio, movement parameter (σ) and detection probability (g_o) at activity centres of tigers in Corbett National Park, 2010–2015

Abundance estimates from MARK					Density estimates from SECR					
Yr	$\hat{N}_F$ (*SE*)	$\hat{N}_M$ (*SE*)	$\hat{N}$ (*SE*)	M:F	ESA (km^2)	$\hat{D}$ (*SE*)	σ F (*SE*) (km)	σ M (*SE*) (km)	g_0 F (*SE*)	g_0 M (*SE*)
2010	50 (4.10)	43 (3.39)	124 (8.92)	0.84	586	16 (1.6)	1.43 (0.06)	2.12 (0.09)	0.03 (0)	0.03 (0.003)
2011	43 (3.67)	40 (3.37)	117 (8.57)	0.92	601	14 (1.6)	1.06 (0.03)	2.01 (0.08)	0.12 (0.01)	0.05 (0.004)
2012	39 (3.38)	36 (3.01)	109 (8.15)	0.91	635	14 (1.6)	0.8 (0.02)	2 (0.05)	0.05 (0)	0.2 (0.002)
2013	46 (3.81)	37 (3.08)	109 (8.15)	0.79	590	12 (1.2)	1.3 (0.05)	2.56 (0.1)	0.01 (0)	0.08 (0.009)
2014	68 (3.22)	37 (2.36)	124 (6.25)	0.55	735	17 (1.5)	1.04 (0.7)	1.8 (0.6)	0.3 (0.02)	0.09 (0.006)
2015	68 (3.22)	56 (3.03)	139 (6.74)	0.81	790	15 (1.4)	1 (0.07)	2.18 (0.02)	0.2 (0)	0.04 (0.003)

Abbreviations: $\hat{N}_F$, population estimate of females; $\hat{N}_M$, population estimate of males; $\hat{N}$, overall population estimate (including unsexed tigers); M:F, detection corrected male to female ratio; $\hat{D}$, spatially explicit density; σ, sigma, the movement parameter; g_0, detection probability; ESA, effective sampling area; Yr, year.

(>50) to large populations (>100) had high persistence probability and large populations could also buffer low levels of poaching-related mortality (2M and 1F annually). The simulated landscape of western *Terai* had very high persistence for the next 100 years in the absence of poaching and could also accommodate moderate tiger offtake/poaching from each of the four populations before the survival of the metapopulation was at risk (Table 7). However, in the absence of Corbett as a source population thereby reducing immigration, individual populations showed extinctions (Table 7, Scenario 16 &17).

In the scenarios when all tiger populations (except Corbett) were extirpated, dispersal from Corbett re-established these populations in the landscape. Reducing permeability of corridors connecting these populations by half impacted recolonization and increased extinction risks (Table 7, Scenario 13).

4 | DISCUSSION

Tiger density (12–17 per 100 km^2) within CNP is one of the highest recorded in the world and leads to a quiver of questions about how large carnivore populations might behave when crowded to this extent. In the first ever long-term monitoring of tigers in the Indian *Terai*, we attempt to characterize this population and provide useful and novel insights into this important source population. This study constitutes one of the largest camera trap dataset obtained for any large carnivore in the world, enabling us to model complex combinations of parameters (Gerber, Ivan, & Burnham, 2014) and for the first time estimate gender-specific survival and other vital parameters for tigers.

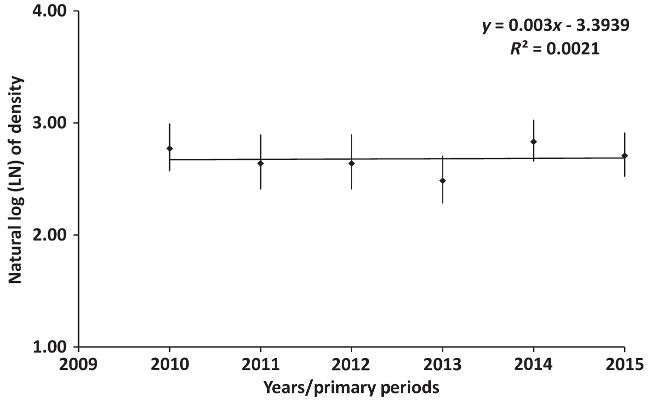

FIGURE 2 Natural log of tiger density (with 95% confidence intervals) plotted against years for 2010–2015 in Corbett National Park

For the robust design, population closure is a prerequisite for abundance estimation within secondary periods, while the population is open between primary periods for estimates of survival and movement parameters. Therefore, our block approach in sampling (2010–2012) could adversely affect population estimates due to violation of population closure assumption within the primary periods but would not have any influence on other parameter estimates like survival which were addressed with appropriate analysis. However, independent and pooled estimates of abundance of the blocks did not differ (see Table S2g). Since both adjacent blocks had high tiger density, movement between them was restricted, and we found only 4–5 individual tigers common between the two adjacent blocks (amounting to 4% of the population). Therefore, combining the data of the two blocks for the first 3 years did not alter our inferences on annual population abundances.

4.1 | Detection probability

Larger movement of males, that is, larger home range leads to a greater σ in SECR compared to females. Tigers in our study had high capture probabilities. Increase in camera trap density resulted in increased capture probability by 12%, mainly due to better detection of the proportion of the population that inherently had low detectability (unsexed tigers). While for sexed individuals (males and females), the capture probability increased by about 4%.

4.2 | Survival

Survival estimated in CMR studies is apparent survival which includes death and permanent emigration. Survival probability

TABLE 6 Comparative review of camera trap-based open capture–mark–recapture studies carried out on tigers from across their range

Parameters	Nagarhole[a]	Huai Kha Khaeng[b]	Pench[c]	Corbett[d]
Survival	0.77 (*SE* 0.05)	0.80–0.96	0.66 (*SE* 0.04)	0.68 (*SE* 0.02)
Temporary emigration	0.10 (*SE* 0.07)	Not reported	Not reported	0.2 (*SE* 0.08)[e]
Mean maximum distance moved (km)	3.74 (*SE* 0.56)	4.37 (*SE* 1.05)	5.33 (*SE* 0.91)	4.6 (*SE* 0.96)M 2.8 (*SE* 0.77)F
Density/100 km^2	9.7 (*SE* 1.8)	1.68 (*SE* 0.69)	3.70 (*SE* 0.8)	14 (*SE* 3.0)
Growth rate (%)	3 (*SE* 0.2)	5 (*SE* 0.3)	15 (*SE* 0.11)	0.3 (*SE* 3.0)

Note: Mean Maximum Distance Moved-For all individual tigers with recaptures the maximum distance between camera traps with captures was recorded and averaged. For Corbett, we have separate estimates for males (M) and females (F).

[a] Karanth and Sunquist (1995), Karanth et al. (2006), Karanth and Sunquist (2000).

[b] Duangchantrasiri et al. (2016).

[c] Majumder et al. (2017).

[d] Current study.

[e] Temporary emigration estimate for the females, males in the study did not show temporary movements.

varied between genders, where apparent annual survival probability of males (0.60) was much lower than that of females (0.79). Of 130 females photo-captured during the study period (2010–2015), we identified 61 (~50%) to be residents since they were photo-captured in two or more primary periods compared to 38% males who were residents. Females are philopatric and this is reflected in their survival rates, while low survival rate of males is characteristic of large carnivores, which are exposed to higher risks and are the dispersing gender in tigers (Smith, 1993). None of the published studies on population dynamics of tigers from open CMR have estimated gender-specific survival because of relatively small datasets (Karanth et al., 2006, *n* = 78; Majumder et al., 2017, *n* = 66 and Duangchantrasiri et al., 2016, *n* = 90) (Table 6). Hence, lack of gender-specific estimates from India and across the tiger's range limits our comparison of estimates. The overall estimate of annual apparent survival of adult tigers (0.68) in Corbett was lower than that reported for tigers in South India (0.77, Karanth et al., 2006) and in Thailand (0.82, Duangchantrasiri et al., 2016). High density likely leads to intense competition which is reflected as depressed apparent survival rates. A telemetry study on Corbett tigers and/or large-scale (>2,000 km^2) long-term camera trapping (Ergon & Gardner, 2014) is required to further tease apart emigration from mortality as well as provide insights into dispersal and territoriality.

4.3 | Recruitment and source population

Corbett tiger population is a paradox of sorts as it maintains a stable high-density population yet has low apparent survival rates. With over 54.8 (*SE* 5.1)% females found breeding each year with a high level of recruitment (35 [*SE* 8]%), this likely results in high emigration and turnover rates in the population. The number of breeding females within CNP exceeds the number recommended for long-term viable tiger source populations (20–25, Chapron et al., 2008; Gopal, Sinha, Mathur, Jhala, & Qureshi, 2007 and PVA results Table 7). Tiger population in Nagarhole and Russian Far East were observed to increase at 3%–6% (Karanth, Nichols, Kumar, Link, & Hines, 2004 and Miquelle, Smirnov, Zaumyslova, Soutyrina, & Johnson, 2015). CNP tiger population remained stable across years. The population fluctuated between 109 and 139 tigers within the study area of ~500 km^2 and was likely to be at carrying capacity where recruitment replaces deaths and emigration. Considering the mortality rate of Corbett tigers to be similar to tigers in Ranthambhore (10%–16%, Sadhu et al., 2017) which was also at high density, the apparent mortality of 32% can then be partitioned into actual mortality (10%–16%) and 16%–22% to emigration. This suggests that 19–26 tigers disperse annually out of CNP, highlighting the importance of CNP as good source population (Pulliam, 1988) for the landscape.

4.4 | Movement

Competition renders temporary movements inefficient as individuals are unlikely to regain territories once lost. We found different temporary movement rates between females and males in Corbett. Males showed little to no temporary movement. This suggests that males either moved permanently out of the study area or died. This is in consonance with tiger ecology (Smith, 1993) where males are the dispersing sex and permanently disperse out of the natal area to minimize inbreeding (Pusey, 1987).

Industrial development, mining, palm plantations, highways and other linear structures are fragmenting prime wildlife habitat across Asia. Large carnivore conservation is limited by shrinking space as forested areas are converted into smaller islands. This problem is amplified in India which is a hub for development. Tiger occupancy within India's tiger landscapes is maintained by protecting at least one significant source population within each landscape. Our simulation results show the importance of a large source in a landscape, as also proposed by Walston et al. (2010). In the absence of such a source connected to other populations, tiger persistence within smaller populations in a landscape was prone to extinction events and could not tolerate even moderate offtake by poachers. Small isolated tiger populations were extremely vulnerable to extinction especially in the face of poaching as also shown by Chapron et al. (2008). Due to the current illegal demand for tiger body parts, it would practically be impossible to stop poaching entirely. Although efforts to minimize

TABLE 7 Single and metapopulation viability analysis results for the western Terai landscape from 17 scenarios (Table S3a–c) in Vortex 9.9. All the results are from models run with parameters reported in Table S3b and the models with reduced parameters are reported in Table S5

Scenario	PopName	N_0	K	Dispersal	Harvest	S-r (*SD*)	PE	*N*-ext (*SD*)	*N*-all (*SD*)	Me.TE
1	SmallPop	15	20	NA		0.04 (0.17)	0.24	16.4 (3.84)	12.48 (7.71)	54
2	MedPop	30	50	NA		0.05 (0.11)	0	45.22 (5.12)	45.09 (5.68)	65
3	MedPop	30	50	NA	1M+1F	−0.01 (0.15)	0.71	37.03 (11.18)	10.94 (17.95)	39
4	LargePop	75	100	NA		0.05 (0.09)	0	92.47 (7.91)	92.47 (7.91)	0
5	LargePop	75	100	NA	2M+1F	0.03 (0.09)	0	88.88 (8.69)	88.79 (9.13)	61
6	LargePop	75	100	NA	2M+2F	0.03 (0.11)	0.1	89.16 (9.91)	79.92 (28.71)	44
7	Rajaji	15	50	Normal		0.06 (0.13)	0	42.24 (7.45)	42.24 (7.45)	0
	Corbett	120	200			0.02 (0.08)	0	175.68 (15.89)	175.68 (15.89)	0
	Ramnagar	35	50			0.06 (0.13)	0	42.02 (7.72)	42.02 (7.72)	0
	Nandhore	10	30			0.08 (0.15)	0	25.24 (4.98)	25.19 (5.08)	43
	Metapop	180	330			0.04 (0.06)	0	285.12 (22.18)	285.12 (22.18)	0
8	Rajaji	15	50	Normal	1M	0.06 (0.15)	0.04	41.38 (9.13)	39.94 (11.47)	19
	Corbett	120	200		2M+1F	0.02 (0.08)	0.01	169.3 (18.12)	168.29 (22.31)	51
	Ramnagar	35	50		1M	0.06 (0.14)	0	41.89 (7.54)	41.82 (7.71)	68
	Nandhore	10	30		1M	0.06 (0.19)	0.11	22.53 (7.29)	20.61 (8.82)	23
	Metapop	180	330		5M+1F	0.03 (0.06)	0	270.66 (29.83)	270.66 (29.83)	0
9	Rajaji	15	50	Half		0.06 (0.13)	0	41.21 (7.69)	41.17 (7.79)	33
	Corbett	120	200			0.04 (0.07)	0	182.34 (14.26)	182.34 (14.26)	0
	Ramnagar	35	50			0.05 (0.13)	0	41.48 (7.71)	41.48 (7.71)	68
	Nandhore	10	30			0.06 (0.16)	0	24.26 (5.1)	24.21 (5.2)	46
	Metapop	180	330			0.04 (0.06)	0	289.19 (20.75)	289.19 (20.75)	0
10	Rajaji	15	50	Half	1M	0.05 (0.15)	0.22	39.57 (10.79)	31.17 (18.32)	17
	Corbett	120	200		2M+1F	0.03 (0.08)	0	178.34 (15.49)	178.34 (15.49)	0
	Ramnagar	35	50		1M	0.05 (0.14)	0	41.06 (8.4)	40.95 (8.64)	50
	Nandhore	10	30		1M	0.03 (0.22)	0.67	13.51 (10.2)	6.16 (8)	18
	Metapop	180	330		5M+1F	0.04 (0.06)	0	256.61 (27.5)	256.61 (27.5)	0
11	Rajaji	0	50	Normal		0.08 (0.15)	0	42.04 (7.79)	42.04 (7.79)	0
	Corbett	120	200			0.02 (0.08)	0	175.58 (16.13)	175.58 (16.13)	0
	Ramnagar	0	50			0.08 (0.15)	0	41.87 (7.54)	41.87 (7.54)	0
	Nandhore	0	30			0.09 (0.17)	0	25.56 (5.01)	25.56 (5.01)	0
	Metapop	120	330			0.04 (0.06)	0	285.05 (21.89)	285.05 (21.89)	0

(Continues)

TABLE 7 (Continued)

Scenario	PopName	N_0	K	Dispersal	Harvest	S-r (*SD*)	PE	*N*-ext (*SD*)	*N*-all (*SD*)	Me.TE
12	Rajaji	0	50	Normal	1M	0.049 (0.23)	0.32	27.9 (18.01)	20.17 (18.64)	0
	Corbett	120	200		2M+1F	0.02 (0.08)	0	169.66 (17.87)	168.98 (20.81)	43
	Ramnagar	0	50		1M	0.17 (0)	0.006	42.01 (7.89)	41.77 (8.44)	0
	Nandhore	0	30		1M	0.22 (0.22)	0.17	21.09 (8.46)	18.29 (9.95)	0
	Metapop	120	330		5M+1F	0.07 (0.004)	0.004	250.21 (30.43)	249.21 (34.23)	43
13	Rajaji	0	50	Half		0.07 (0.16)	0	41.39 (7.71)	41.39 (7.71)	0
	Corbett	120	200			0.04 (0.07)	0	181.81 (15.04)	181.81 (15.04)	0
	Ramnagar	0	50			0.07 (0.15)	0	41.19 (8.01)	41.19 (8.01)	0
	Nandhore	0	30			0.07 (0.18)	0	24.45 (5.32)	24.45 (5.32)	0
	Metapop	120	330			0.05 (0.06)	0	288.84 (21.41)	288.84 (21.41)	0
14	Rajaji	0	20	Half		0.05 (0.24)	0.84	9.71 (6.11)	1.87 (4.26)	0
	Corbett	20	30			0.03 (0.15)	0.1	24.27 (5.41)	21.85 (8.86)	60
	Ramnagar	0	20			0.05 (0.24)	0.57	10.2 (5.24)	4.7 (5.89)	0
	Nandhore	0	20			0.05 (0.23)	0.78	11 (6.41)	2.74 (5.36)	0
	Metapop	20	90			0.03 (0.13)	0.08	33.77 (11.35)	31.16 (14.14)	60
15	Rajaji	0	20	Reduced		0.06 (0.22)	0.95	24.69 (17.72)	1.51 (6.89)	0
	Corbett	20	30			0.04 (0.14)	0.06	25.06 (4.95)	23.6 (7.55)	59
	Ramnagar	0	20			0.06 (0.21)	0.78	25.68 (17.88)	5.85 (13.32)	0
	Nandhore	0	20			0.06 (0.23)	0.94	13.88 (10.29)	1.14 (4.28)	0
	Metapop	20	90			0.04 (0.14)	0.05	33.81 (17.17)	32.1 (18.3)	58
16	Rajaji	0	50	Half		0.13 (0.2)	0.51	41 (15.58)	20.25 (23.01)	0
	Corbett	20	30			0.10 (0.1)	0	28.47 (3.32)	28.47 (3.32)	0
	Ramnagar	0	50			0.12 (0.2)	0.12	43 (12.24)	38.02 (17.82)	0
	Nandhore	0	30			0.13 (0.2)	0.18	24.72 (7.91)	20.48 (11.62)	0
	Metapop	20	160			0.11 (0.13)	0	107.22 (34.22)	107.22 (34.22)	0
17	Rajaji	0	50	Reduced		0.04 (0.18)	0.24	16.09 (3.71)	12.23 (7.53)	49
	Corbett	20	30			0.04 (0.14)	0.03	25.48 (4.8)	24.77 (6.28)	62
	Ramnagar	0	50			0.03 (0.18)	0.18	14.57 (4.8)	12.09 (6.86)	56
	Nandhore	0	30			0.04 (0.18)	0.17	16.28 (3.98)	13.56 (7)	43
	Metapop	20	160			0.04 (0.09)	0	62.65 (15)	62.65 (15)	0

Abbreviations: S-r, Stochastic growth rate; PE, Probability of extinction; *N*, ext-Population size at year 100 for populations that did not go extinct; *N*-all, average population size for all the populations; M.TE, Median time for extinction; Me.TE, Mean time for extinction; M, adult male; F, adult female; PopName, Population name; LargePop, Large population (*n* = 75, K = 100); MedPop, Medium population (*n* = 30, K = 50); SmallPop, Small population (*n* = 15, K = 20); MetaPop, Metapopulation; N_0, Initial Population; K, Carrying capacity.

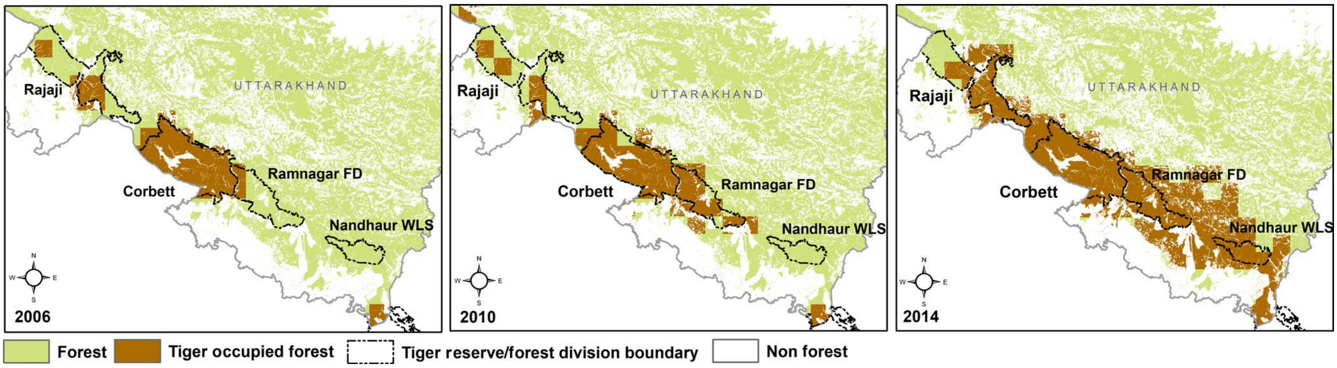

FIGURE 3 The *Terai* landscape was sampled for tiger signs by a 15 km search within each 15 km^2 forested patch as part of the occupancy survey for national tiger status evaluation (Jhala et al., 2008, 2011, 2015). Forest patches where tiger sign was detected are marked in brown. Expansion in tiger occupancy from Corbett Tiger Reserve across western *Terai* landscape is clearly seen from 2006 to 2014

poaching through patrolling and law enforcement are required, simultaneously, a strategy to increase recruitment by having a good source population (>100) in the landscape that buffers the offtake of poachers would ensure tiger persistence. The PVA results corroborate the prioritization of resource allocation to important source populations within landscapes (Walston et al., 2010) as without securing them first, tiger recovery within large landscapes is difficult. However, Walston et al. (2010) do not advocate conservation of only source populations but propose to prioritize them for allocating limited resources. Our results acknowledge the relevance of landscape scale conservation as tiger occupancy of the landscape can only be possible with functional dispersal corridors. Prior to 2006, tiger populations were estimated by unreliable means (Karanth et al., 2003) and the official tiger estimate for India was 3,642 tigers (Narain, Panwar, Gadgil, Thapar, & Singh, 2005). Subsequent to the local extinctions of Sariska and Panna tigers caused due to poaching in 2005 and 2009 (Check, 2006; Gopal, Qureshi, Bhardwaj, Singh, & Jhala, 2010), the first tiger status estimation based on modern scientific approach was implemented and put the population at a precariously low number of 1,411 (1,165–1,657; Jhala et al., 2008). At that time, camera trap study in CNP (2006–2007) estimated the population to be at 108 (*SE* 4.5) within the same area of 500 km^2 (Contractor, 2007) as the current study. This was identified as one of the few sources of tigers remaining within the country and was prioritized for conservation investment (Jhala et al., 2008). After 2006, investment in stringent protection and resettlement of human habitation were undertaken and over 300 families were rehabilitated from within the core area of Corbett TR under the new incentivized voluntary rehabilitation package (Narain et al., 2005; Wildlife Protection Act, 1972, 2006 amendment). By 2012, the entire Corbett Tiger Reserve (1,288 km^2) had a tiger density comparable to that of the CNP, with Corbett Tiger Reserve being home to about 143–198 tigers (Bisht et al., 2012). This strategy of high investment in a source population has paid dividends and resulted in an increase in tiger occupancy and numbers in the larger landscape of western *Terai* between 2006 and 2014 (Figure 3), where tigers have increased from 178 (*SE* 17) individuals occupying 1,901 km^2 to 340 (*SE* 41) individuals occupying 6,576 km^2 (Jhala et al., 2008, 2011, 2015).

The high-density source population of CNP was characterized by a stable population with high proportion of females breeding, high recruitment, low apparent survival and high turnover of individuals. These characteristics permitted tigers to be produced at rapid rates to disperse and populate most available habitat within the landscape within a period of 8 years. The optimal *Terai* and foothill habitats were almost all occupied by tigers by 2014, and tigers are now dispersing to high altitude habitats as well (Bhattacharya & Habib, 2016). Our study documents potential thresholds that can be achieved by tiger populations under optimal conditions. This information and the strategy of focusing conservation efforts on source populations within each landscape can be used to plan and implement realistic tiger recovery programmes globally.

ACKNOWLEDGEMENTS

The study was funded by a grant from the National Tiger Conservation Authority and small grants by the Uttarakhand Forest Department. We thank Rajesh Gopal, Rajiv Barthari, P. R. Sinha, V. B. Mathur, R. Mishra, C. K. Kavidayal, G. S. Karki for facilitating the study. We thank the Director, Dean and Research Co-ordinator of the Wildlife Institute of India for support. The Chief Wildlife Wardens, Uttarakhand and the park directors of Corbett Tiger Reserve are thanked for granting permissions for doing this research. S. Saini is acknowledged for assisting with the figures and S. Dutta for assistance with the analysis and review of the draft manuscript. We thank the researchers of 2010 and 2014 National Tiger Status Assessment team for assisting with data collection. We thank the two anonymous reviewers for their constructive comments and helping us improve the manuscript. We thank U. Kumar for translating the abstract to our native language.

AUTHORS' CONTRIBUTIONS

Y.J. and Q.Q. conceived, designed and secured the resources for the study; Shikha and Sudip conducted the field work; Shikha and Y.J. analysed the data; Shikha and Y.J. wrote the manuscript. All authors contributed critically to the drafts and revisions and gave final approval for publication.

DATA ACCESSIBILITY

Data for the Robust design CMR is available via the Dryad Digital Repository https://doi.org/10.5061/dryad.vc3143h (Bisht, Banerjee, Qureshi, & Jhala, 2019). Details of PHVA parameterization are available in the Supporting Information. Tigers are susceptible to poaching; therefore, Spatial Data on tiger captures have not been archived.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Bisht S, Banerjee S, Qureshi Q, Jhala Y. Demography of a high-density tiger population and its implications for tiger recovery. *J Appl Ecol*. 2019;00:1–16. https://doi.org/10.1111/1365-2664.13410

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5. FIRST RECORD OF ALBINO SAMBAR *RUSA UNICOLOR* (KERR) FROM CORBETT NATIONAL PARK, INDIA

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A rare sighting of an albino Sambar *Rusa unicolor* (Kerr 1792) was made on June 19, 2010, in the core area of the Corbett Tiger Reserve. The forest department informed us about the occurrence of a white-coloured Sambar in the Jamunagawd beat of Jhirna range. As a part of the tiger monitoring team, we visited the area to get photographic evidence.

At 29° 30' 0.8" N and 78° 55' 30.3" E, we observed a white Sambar fawn (Fig. 1) accompanied by its normal coloured mother. The fawn was pure white with reddish snout and red eyes. The inside of the ears was pinkish. The fawn was feeding on grass and did not exhibit any abnormal activity.

Earlier Champion (1938) sighted an albino Sambar hind in the mixed Sal and Chir pine forest near Chaukhamb in the hills of Kohtri valley. Pillay (1953) also reported seeing an albino Sambar hind and an albino Sambar stag from Talamalai range of north Coimabatore. Another record of a museum specimen of albino Sambar from the Archaeological Museum of Udaipur was given by Tehsin (2006). Sangai Express (March 30, 2010) published the birth of a white coloured fawn on March 23, 2010, at Manipur Zoological Garden, Iroishemba.

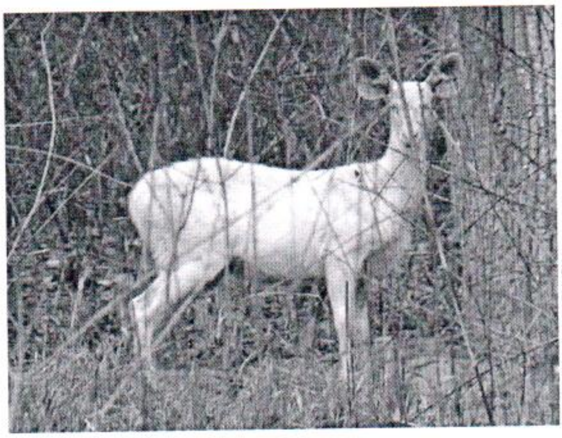
DEBMALYA ROYCHOWDHURY

Fig. 1: Albino Sambar *Rusa unicolor* sighted at Corbett Tiger Reserve

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6. CONSERVATION STATUS OF RAJAJI-CORBETT CORRIDOR FOR TIGER AND ELEPHANT MOVEMENT

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Rajaji-Corbett corridor, composed of two stretches of forests, connects two tiger-elephant national parks in northern India. The southern stretch (*c.* 300 sq. km), including the forests of Haridwar forest division and Bijnor plantation division, is highly fragmented and heavily disturbed. Although used by elephants (*Elephas maximus*), due to high levels of

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This is to certify that Mr. Sudip Banerjee has presented a talk on "Long-term ungulate population trend in Corbett Tiger Reserve" in the Annual Research Seminar of the Wildlife Institute of India in the year 2016.

Jhala.

Dr. Y.V. Jhala
Dean, FWS and Scientist – G
Wildlife Institute of India

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