Distribution and Demography of Carnivores in Some Parts of Semi-Arid Landscape of Western India

A THESIS
Submitted by

AYAN SADHU

for the award of the Degree of

DOCTOR OF PHILOSOPHY
in
WILDLIFE SCIENCE

Under the guidance of

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DECLARATION

I declare that the thesis entitled **Distribution and Demography of Carnivores in Some Parts of Semi-Arid Landscape of Western India** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2014 to 2020** under the guidance of **Dr. Yadvendradev V. Jhala and Prof. Qamar Qureshi**, Faculty at the Wildlife Institute of India. The thesis has been submitted to the Saurashtra University for the award of the degree of **Doctor of Philosophy in Wildlife Science**, and has not formed the basis for the award of any other degree, diploma, associateship, fellowship, titles in this or any other university or institution. 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.

Place: Dehradun
Date: 10th October 2020

(AYAN SADHU)
Doctoral candidate

Acknowledgements

Back in 2014, when I enrolled for the PhD, it was merely an academic target driven by the passion for wildlife and conservation. In all these years, I did not understand how it becomes an integral part of my life, beyond academic achievements. In this endeavour, I would like to thank each one of them who have contributed towards its successful and timely completion.

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The breathtaking cliffs adorned by leafless trees, scenic plateau tops covered in golden grass, silent ruins of the bygone era... how can I forget the magical landscapes of Ranthambhore and its magnificent beasts! Those dusty roads, pebbly river beds, the cacophony of grey francolin, and the changing colours (with season) of the '*dhonk*' forest, still take me away from this mundane city life. I fall short of words when thinking of describing the influence of Ranthambhore in my life.

CONTENT

DECLARATION

I declare that the thesis entitled **Distribution and Demography of Carnivores in Some Parts of Semi-Arid Landscape of Western India** submitted by me for the degree of Doctor of Philosophy is the record of research work carried out by me during the period from **2014 to 2020** under the guidance of **Dr. Yadvendradev V. Jhala and Prof. Qamar Qureshi**, Faculty at the Wildlife Institute of India. The thesis has been submitted to the Saurashtra University for the award of the degree of **Doctor of Philosophy in Wildlife Science**, and has not formed the basis for the award of any other degree, diploma, associateship, fellowship, titles in this or any other university or institution. 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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EXECUTIVE SUMMARY

Tiger populations have declined globally due to poaching, prey depletion, and habitat loss. The westernmost tiger population of Ranthambhore in India is typified by bottlenecks, small size, and isolation; problems that plague many large carnivore populations worldwide. Such populations are likely to have depressed demographic parameters and are vulnerable to extinction due to demographic and environmental stochasticity. A combination of techniques that included radio telemetry, camera traps, direct observations, and photo documentation was used to obtain 3492 observations on 97 individually known tigers in Ranthambhore between 2006-2014 to estimate demographic parameters. Tiger density was estimated from systematic camera trap sampling using spatially explicit capture-recapture (SECR) framework and subsequently compared model inferred density with near actual density (since all tigers in RTR were individually known). SECR tiger density was same as actual density and recovered from 4.6 (SE 1.19) to 7.5 (SE 1.25) tigers/100km^2 over the years. Male: female ratio was 0.76 (SE 0.07), and cub: adult tigress ratio at 0.48 (SE 0.12). Average litter size was estimated at 2.24 (SE 0.14). Male recruitment from cub to sub-adult stage (77.8%, SE 2.2) was higher than that of females (62.5%, SE 2.4). However, male recruitment rate as breeding adults from the sub-adult stage (72.6%, SE 2.0) was lower than females (86.7%, SE 1.3). Annual survival rates, estimated by known-fate models, of cubs (85.4%, CI95% 80.3-90.5%) were lower than that of juvenile (97.0%, CI95% 95.4-98.7%) and sub-adult (96.4%, CI95% 94.0-98.9%) tigers. Adult male (84.8%, CI95% 80.6-89.2%) and female (88.7%, CI95% 85.3-92.2%) annual survival rates were similar. Human-caused mortality was 47% in cubs and 38% in adults. Mean dispersal age was 33.9 months (SE 0.8), males dispersed further (61 km, SE 2) than females (12 km, SE 1.3). Higher age of first

reproduction (54.5 months, SE 3.7) with longer inter-birth intervals (29.6 months, SE 3.15) was likely to be an effect of high tiger density. Demographic parameters of Ranthambhore tigers were similar to other tiger populations. With no signs of inbreeding depression, there seems to be no imminent need for genetic rescue. The best long-term conservation strategy would be to establish and manage a metapopulation in the Ranthambhore landscape.

Maintaining a viable metapopulation structure requires securing the connecting links or corridors between the source and the sink populations. Industrial development and expansion of human land use have caused major fragmentation and degradation of wildlife habitats. Certain human land uses possess as barriers for large carnivore dispersal. The semi-arid tiger populations persist as small islands in a sea of human land use. Dispersal events of 29 tiger individuals from their natal area to established territory were monitored over nine years. Females (n = 13) settled down near to their natal area (<10 km in 75% cases), occupying their mother territories or areas adjacent to that. Males (n = 16) mostly established territories far (>10 km) from their natal areas. Six (five males and one female) long-distance dispersal events from Ranthambhore to the greater landscape were recorded during the study period. The tiger presence points (n = 139 from six individuals) were used to model habitat permeability (species distribution modelling with MaxEnt) for tiger dispersal in the landscape. This surface was further used in CIRCUITSCAPE to delineate potential habitat linkages. The MaxEnt modelling depicted the importance of scrubland-open forest areas, drainage, and rugged areas in terms of preserving connectivity. The ravines of Chambal and its tributaries, often treated as wastelands, act as the key conduit for tiger dispersal in this human-dominated landscape. However, the non-PA status of these habitats is the major challenge for conserving them

from the growing human disturbances and developmental projects. The identified corridors in the landscape need to be given legal sanctity, and restoration of the connectivity bottlenecks are crucial in order to secure dispersal in the landscape.

Tiger, being the top predator, shapes the population of other sympatric carnivores through interference competition and intra-guild predation. Theory suggests that subordinate predator like leopard should shift their activity centres (spatial) and activity peaks (temporal) in response to tiger space and time usage. I used camera trap data to estimate the spatially explicit density, space use, and time-activity pattern of leopards. Two-species occupancy was used to estimate the spatial co-occurrence of tiger and leopard in Ranthambhore. Ranthambhore had high stable leopard density (9.4±2.3 to 10.4±1.5 per 100 km^2). Occupancy analysis did not show any spatial avoidance between tiger and leopard inside the reserve. However, the spatially-explicit photo-capture rates showed leopard avoided areas frequented by tigers. Leopard's site use intensity was higher on the edges of the reserve with moderate human disturbances. Both tiger and leopards were nocturnal, while activity peaks of the two differed by 4-8 hrs. On average, the time interval between a tiger and leopard photo capture at a site was 4-5 hours. Thus, though leopards coexisted with tigers at high densities, they try to avoid lethal encounters with tigers by microscale selection of time for activity and space use.

Besides Ranthambhore, I camera trapped other wildlife habitat patches in the larger landscape with varying degree of protection. I used camera trap detection/non-detection data in occupancy framework with covariates to understand factors that may govern carnivore distributions in these areas. Furthermore, the species presence points were used to model the suitable habitats and to find out factors governing carnivore distribution in the landscape. Site occupancy of striped hyena was estimated at 0.59 (±0.005) of about

4000 km^2. Hyena occupancy probability increased with decrease in tiger usage, proximity to water sources, less human disturbances, and near to roads. Leopard occupancy was estimated at 0.66 (±0.004) of about 4000 km^2 and increased with woodland cover, proximity to water sources and lower tiger usage. Out of ~ 4000 km^2, site occupancy of sloth bear was estimated at 0.49 (±0.002). Sloth bear's occupancy probability decreased presence of scrubland-open forest areas in the grid, and positively correlated with proximity to water sources and increasing distance from human settlements. Estimated site occupancy of honey badger was 0.39 (±0.003) out of ~4000 km^2. The site occupancy probability was decreased with increasing distance to water sources and protection, while increased with increasing distance from human settlements. Large tract of suitable habitats outside of the protected area network was found suitable for large carnivores (MaxEnt outcomes). All the large carnivores showed avoidance towards areas very close to human settlements. Presence of scrubland-open forest habitats was the primary determinant for wolf distribution in the landscape.

The present study showcased one of the very few long-term research on tigers, elaborating their vital rates, survival parameters, and dispersal. The vital rates of Ranthambhore tigers did not depict any evidence of inbreeding depression despite the recent bottlenecks and isolation. As a long-term conservation strategy, this semi-arid tiger population needs to be conserved in a metapopulation framework. Thus, the dispersal linkages modelled using the actual dispersal points of Ranthambhore tigers needs legal sanctity to safeguard the connectivity in the landscape. The species distribution modelling showed the importance of the PAs and also highlighted areas to direct conservation investments outside the protected areas. Many of these areas hold great conservation significance in terms of tiger

dispersal as well as large carnivore conservation in the landscape. Therefore, conserving these habitats is the need of the hour.

Caracal (Caracal caracal), the name came from 'kara-kulak' (Turkish), explicitly pointed out the distinct ears of the cat. Large-scale habitat destruction & conversion to human habitat-use caused severe range loss and population decline in the Indian subcontinent. Ranthambhore is the last known stronghold of caracal in the entire country. During the period of this study, a decrease in the caracal photo-capture rate was observed.

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CHAPTER 1

General Introduction

Following the footsteps: *Tigers use mud roads & animal trails for patrolling their territory.*

GENERAL INTRODUCTION

Carnivores are one of the most charismatic taxa that play a crucial role in shaping the structure and functioning of ecosystems through trophic interactions (Ripple and Beschta 2006). Apart from their ecological benefits, carnivores are also important in terms of economy as they generate revenue through tourism. In spite of their unparalleled contribution, carnivores have experienced severe decline in their population as they compete with human interests, thus persecuted (Ripple et al. 2014). Tiger, the largest felid, serves as an umbrella and flagship to the forested ecosystems in Asia, lost more than 90% of their historical range (Dinerstein et al. 2007). To conserve tiger, large habitat patches with ample large bodied prey and no human-disturbances are needed (Fig. 1.1); however, many of the tiger populations are restricted in small, isolated habitats (Jhala et al. 2020).

The westernmost tiger population of Ranthambhore (India, Fig. 1.2) is typified by bottlenecks, small size, and isolation (Sadhu et al. 2017); problems that plague many large carnivore populations worldwide. Such populations are likely to have depressed demographic parameters as a result of severe inbreeding and are vulnerable to extinction due to demographic and environmental stochasticity (Keller and Waller 2002). Therefore, studying demography of such populations are important to assess the population vigour and to formulate apt conservation strategies. My research presents demographic parameter estimates collated over nine years from 97 individually known tigers and annual density estimates of Ranthambhore tiger population from camera traps (Chapter 2). Ranthambhore tiger population is well protected and showed a steady increase over the years. This study aimed to estimate the demographic parameters of Ranthambhore tigers, and subsequently compare them with other tiger populations.

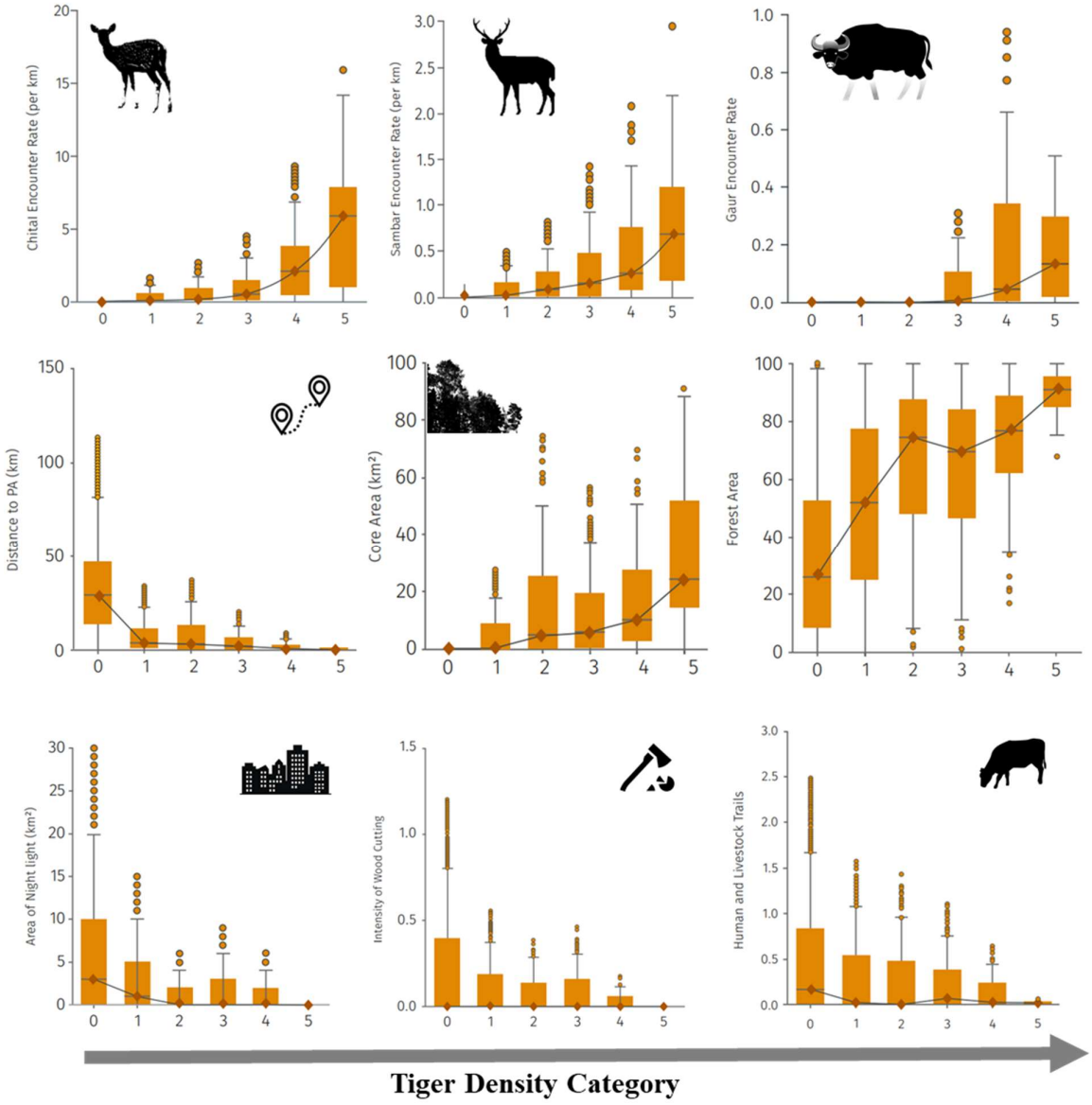


Figure. 1.1 *The relationship between tiger density classes (0 – No tigers to 5 - >10 tigers/100 Km^2) with prey, habitat, and human disturbance across India (source: Jhala et al. 2020). The study showed, conservation of tigers required availability of large prey species (top row), large contiguous forest patches with protection (middle row) and least human disturbances (bottom row). Different tiger density categories (0 to 5) depicted very low (<1tiger /100 Km^2) to very high (10 tigers/100 km^2) tiger density areas.*

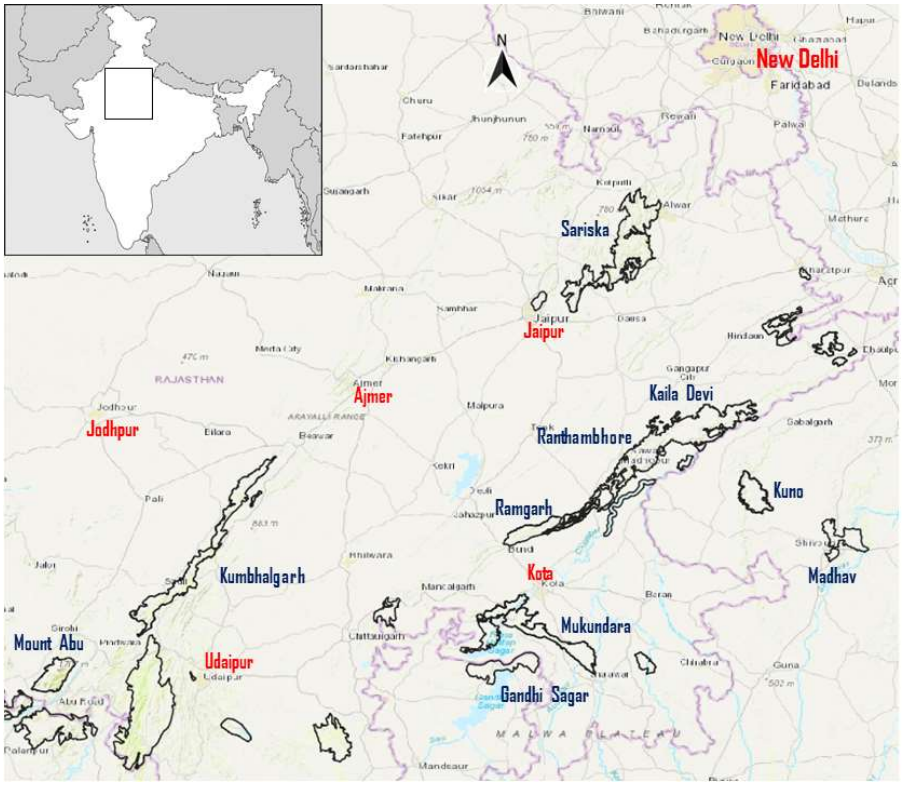


Figure 1.2 *Location of protected areas in the western Indian landscape with respect to country's capital (New Delhi) and major cities (names written in red).*

Figure 1.3 *Top (left): Illegal mining in the wolf habitat; Top (right): Road widening project inside Ranthambhore; Bottom: Snapshot captured a common activity where hundreds of trucks loaded with illegally mined river sand passing through dry river bed of Chambal. ©Dharmendra Khandal, & granthshala.com.*

Carnivores disperse from their natal area to avoid inbreeding (breeding with parents, offspring or sibs) (Packer and Pusey 1993). Large carnivores occur in low density and disperse long-distances to establish their territories (Santini et al. 2013). Habitat linkages in the landscapes reduce the adverse effects of isolation, inbreeding, and demographic stochasticity. The small isolated forest patches cannot sustain a viable large carnivore (here, tiger) population in long-run, thus need to be managed as in a metapopulation framework (Hanski 1991). Dispersal opportunities in the dry forests of western Indian landscape are limited; thus, dispersal events are less and sporadic. Moreover, mining and the recent surge of developmental activities, especially in the Chambal river basin, are causing large-scale destruction and fragmentation in the landscape (Fig. 1.3). Identification structural corridors need assessment permeability or cost of dispersal in the landscape, and using this cost surface, most potential areas or paths need to be identified. Habitat suitability models (using species presence/or absence points) are often used for the preparation of the cost surface. Radio telemetry studies on dispersing individuals provide the best data in this regard, but they are often constrained by sample size and logistics (Fagan & Calabrese, 2006). Therefore, species presence points obtained from the resident individuals (easy to collect) often used to model the cost surface (Zeller et al. 2012). The habitat used by resident individuals should be suitable for dispersal; however, dispersing individuals often negotiate and traverse through degraded/low-quality habitats which are not suitable for harbouring resident individuals (Elliot et al. 2014). Therefore, the cost surface prepared using presence information of the resident individuals will be a conservative assessment of permeability in the landscape. During the long-term monitoring of the Ranthambhore tiger population, tiger dispersal events from Ranthambhore to nearby patches were recorded (six tiger individuals) (Chater 3). These

dispersal points were situated outside the protected area network. I hypothesised, the actual dispersal points used for modelling the connectivity will provide a broader range of available connectivity in the landscape. The objectives of the present chapter were: a) to model the habitat connectivity for tigers in the semi-arid landscape, b) to compare the potential of presence points collected from the protected areas (using camera trapping, sign survey, and radio-telemetry) with actual dispersal points.

Mechanism facilitating carnivore sympatry has long been studied by researchers and considered as an essential aspect to make conservation decisions. Sympatric carnivores exhibit niche differentiation to avoid agnostic encounters and minimise the effect of interspecific competition. However, the mechanism of co-occurrence can vary from peaceful co-existence to avoidance to interspecific killing (Creel and Creel 1996). At large scale, species distribution is often shaped by spatial segregation. However, when habitats are small and isolated, spatial segregation becomes difficult and often competing species avoid each other by temporal separation (Sozio and Mortelliti 2016). Tiger and leopard co-occur in much of their distributional ranges (Nowell and Jackson 1996). Tiger, the larger and dominant species, exploits a wide range of resources that overlaps extensively with that of leopards (Karanth and Sunquist 1995), thereby tigers often dictate the abundance and behaviour of leopards (Schaller 1967). Along with tigers, Ranthambhore harbours a sizable population of leopards. Camera trapping data over the years were used to estimate leopard density and understand the mechanism of co-occurrence pattern exhibited by the large carnivores in Ranthambhore (Chapter 4). The hypotheses were - a) leopard will avoid areas frequented by tigers (spatial segregation), and b) in overlapping areas, leopards will avoid encounters with tigers by temporal separation. The specific aims of this chapter were: a) to estimate the density of leopards

in Ranthambhore, b) to understand the mechanism of co-occurrence between tiger and leopard: i) to estimate spatial avoidance, ii) to estimate temporal avoidance, iii) to assess spatio-temporal separation.

Carnivores that are large ranging and occur at low densities pose major challenges to conservation practitioners. These large-ranging carnivores are notably sensitive to habitat fragmentation, destruction, and exploitation by human (Woodroffe 2001). Change in carnivore population density may result in cascading effects throughout the ecosystems (Terborgh et al. 1999). Striped hyena (*Hyaena hyaena*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), Indian wolf (*Canis lupus*), and honey badger (*Mellivora capensis*) are found in the dry forests of western India (Fig. 1.4). Illegal mining (sandstone, limestone, marble, & river sand), developmental projects (road construction & widening) and expansion of human habitation in the semi-arid landscape of western India is the biggest threats to this fragile ecosystem and its unique assemblages of flora and fauna (Fig. 1.3). Protected areas in this landscape are few and isolated, also much of the potential habitats for these large carnivore species situated beyond the PA boundaries, thus vulnerable to the threats mentioned above. Therefore, conserving these carnivores in the human-dominated landscape requires an in-depth understanding of distribution and factors affecting their distribution. In the present study, the occupancy of large-ranging carnivores in four protected areas was assessed from the camera trap presence/absence data (Chapter 5). This data was further used to model the distribution of these species in the landscape and identifying landscape-level factors affecting species distribution.

The objectives were:

1. To estimate occupancy and factors influencing occupancy for large ranging carnivores inside the PAs in a semi-arid landscape.

2. To predict the landscape level distribution and identification of landscape-level drivers to aid future conservation planning.

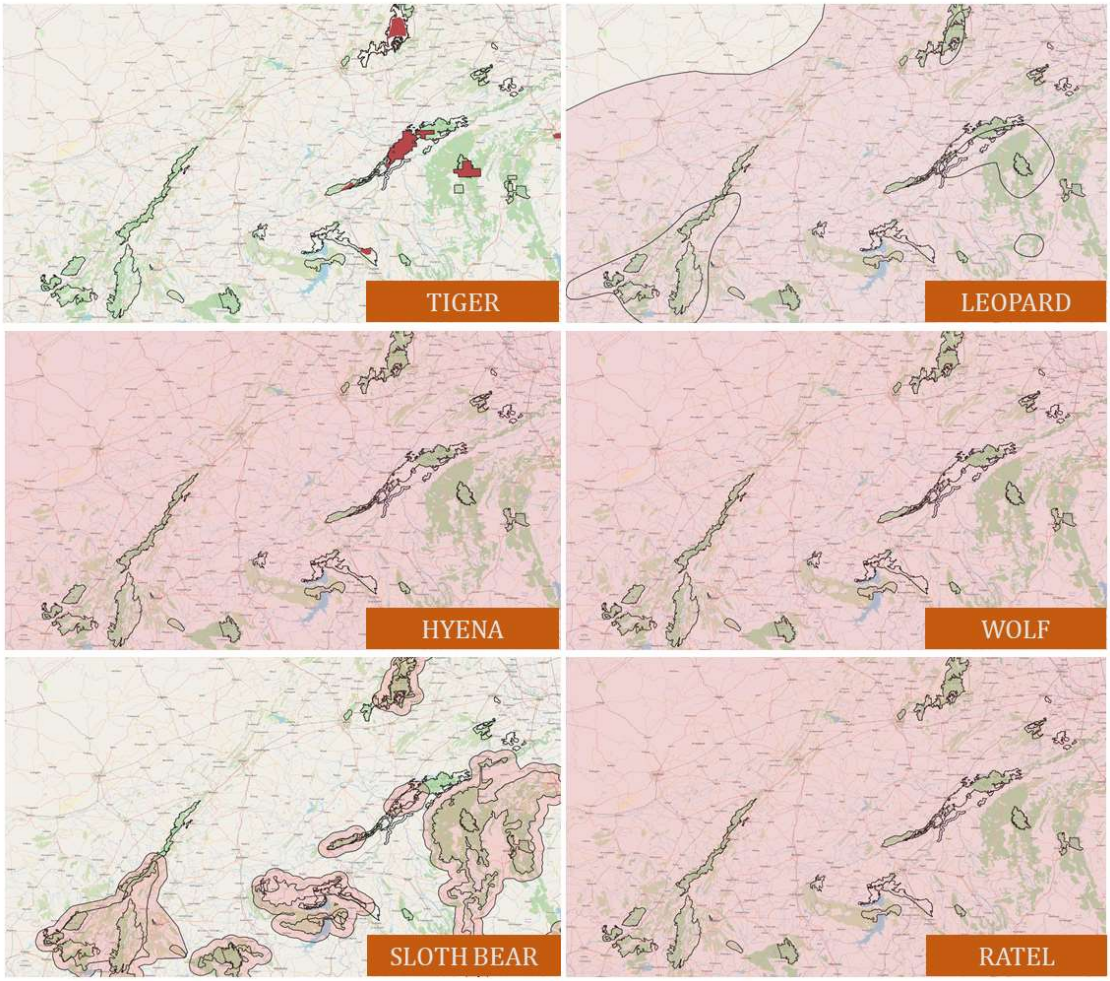


Figure 1.4 *Distribution of large ranging carnivores (the pink coloured region) in the semi-arid landscape of western India (Tiger- Jhala et al. 2020, rest of the species – IUCN Red list, www.iucnredlist.org)*

Demography of a small, isolated tiger population from semi-arid landscape of western India

The dry forests of Ranthambhore with very less ground vegetation gives an excellent opportunity to observe tiger from a safe distance.

1. Introduction

At the onset of the nineteenth century, India was home to nearly 40,000 tigers (*Panthera tigris tigris*, Linnaeus) (Gee 1964), while currently there are around 3000 left (Jhala et al 2020). The decline in tigers was primarily due to hunting, prey depletion, followed by habitat loss (Dinerstein et al. 2007). A timely and proactive conservation measure, in the form of Project Tiger initiated in 1973 by the Indian Government (Panwar 1987), initially halted the rapid decline caused by trophy hunting. But an increased demand for tiger body parts in China and Southeast Asia in the past 25 years has severely impacted wild tiger populations. Demand driven poaching resulted in the local extinction of tigers in Sariska and Panna Tiger Reserves in India (Check 2006, Gopal et al. 2010). Most tiger populations currently are small, isolated, and highly structured (Ranganathan et al. 2008, Yumnam et al. 2014). Such populations are vulnerable to extinction events caused by environmental and demographic stochasticity (Caughley 1994, Purvis et al. 2000). Ranthambhore was a famous hunting reserve for the *Maharajas* of Jaipur, and numerous *shikar* (hunting) camps were organized in pre and post-independence era [Singh 1999]. Subsequent to India's independence, intensity of hunting increased since tiger *shikar* was considered a social status symbol. This unregulated hunting combined with poaching caused a severe decline in Ranthambhore tiger population, and before the onset of Project Tiger (1973), there were only around 14 tigers left in Ranthambhore (IBWL 1972). After an initial recovery in 1980's, rampant poaching in 1992 and 2005, caused Ranthambhore tiger population to decline below 15 individuals from about 40 (Jackson 2010, Sharma and Wright 2005). Local extinctions in the last five decades suggest that tigers of the semi-

arid region of western India are most vulnerable (Chundawat et al. 2016). The tiger population of Ranthambhore is the only population that survives in western India. It typifies the problems many large carnivore populations face globally i.e. small founder population and lack of connectivity with other source populations. Small isolated populations like Ranthambhore are susceptible to loss of genetic variability caused by genetic drift and inbreeding depression (Allendorf and Leary 1986, Frankham et al. 2002). Such populations often lose their ability to adept in response to environmental changes and some manifest deleterious effects in the form of morphological abnormalities and depressed population vigour (Keller and Weller 2002, O'brien 2003). Hence, understanding demographic parameters of a potentially genetically compromised population to determine the need for genetic rescue is important for developing appropriate conservation strategies (Pimm et al. 2006). Quantifying demographic parameters needs long-term data over multiple generations and for long-lived carnivores such datasets are rare (Balme et al. 2012). Till date most population studies conducted on tigers aim at estimating abundance (Karanth et al. 2004, Harihar et al. 2009, Jhala et al. 2010, 2014, 2020), while studies on demographic parameters have been sparse (but see Smith and McDougal 1991 for *P. t. tigris* and Kerley et al. 2003, Goodrich et al. 2008 for *P. t. altaica*).

Herein, demographic parameters of free ranging tigers from Ranthambhore Tiger Reserve from a nine-year study were reported from 97 individually monitored tigers. The tiger density over the years were estimated by spatially explicit capture-recapture using camera traps. By 2012 due to intensive monitoring, almost all tigers of Ranthambhore were photo-

captured and had developed a catalogue for individually identifying them. This information was used to compare snapshot density estimated by model-based inference with near reality. Finally, the demographic parameters of Ranthambhore tigers were compared with those of other tiger populations. It showed though Ranthambhore tigers have undergone population bottlenecks with limited gene flow and small population size, their demographic parameters do not seem to be compromised.

2. Methods

2. 1 Study area

The study was conducted from 2006 to 2014 in Ranthambhore Tiger Reserve (hereafter RTR, latitudes $25^0$41' N to $26^0$22' N and longitudes $76^0$16' E to $77^0$14' E) which is situated at the junction of two ancient mountain ranges, the Aravalli and the Vindhya. RTR is part of the western Indian landscape that has Sariska Tiger Reserve in the north, Kuno Wildlife Sanctuary and Madhav National Park in the east, Ramgarh Visdhari Wildlife Sanctuary and Mukundara Hills Tiger Reserve in the south-western part (Fig. 2.1). The core area of RTR was composed of Ranthambhore National Park (392 km^2), Sawai Mansingh Sanctuary (290 km^2) while Kailadevi Wildlife Sanctuary (630 km^2) was designated as the buffer zone of RTR. Within this western Indian landscape, tigers were only present in Ranthambhore NP during the commencement of this study and subsequently colonised Sawai Mansingh Sanctuary in 2008-09. These together comprise the only source population of tigers in the landscape. During this study, tigers from this population were

reintroduced in Sariska (Sankar et al. 2010) and six tigers dispersed into northern as well as south-eastern and eastern part of the landscape (Fig. 2.1).

The sub-tropical dry climate of RTR experiences three distinct seasons: mostly dry winters (October-February, minimum average temperature 5˚C, relative humidity ~10%), hot summers (March-June, mean maximum temperature 45˚C, relative humidity 10-15%), and humid monsoons (July-September, average rainfall 700mm, relative humidity >60%). RTR primarily comprises of steep hills, gentle slopes, plateaus, and narrow valleys dotted with shallow man-made perennial lakes. The area is representative of dry deciduous *Anogeissus pendula* forests in association with *Acacia*, *Butea, Capparis*, *Zizyphus* and *Prosopis* species (5B/C_2 - Northern Tropical Dry Deciduous forests. 6B/DS1 - *Zizyphus scrub*, DS1 - Dry deciduous scrub and 5/DS4 - Dry Grasslands, of Champion & Seth 1968). A diverse assemblage of carnivore species (17 species from 7 different families) were recorded during the course of the study, which include tiger, leopard (*Panthera pardus*, Linnaeus), sloth bear (*Melursus ursinus*, Shaw), striped hyena (*Hyaena hyaena*, Linnaeus), caracal (*Caracal caracal*, Schreber), fishing cat (*Prionailurus viverrinus*, Bennett), jungle cat (*Felis chaus*, Schreber), desert cat (*Felis silvistris*, Schreber), rusty-spotted cat (*Prionailurus rubuginosa*, I. Geoffroy Saint-Hilaire), golden jackal (*Canis aureus*, Linnaeus), Indian fox (*Vulpes bengalensis*, Shaw), honey badger (*Mellivora capensis*, Schreber), common palm civet (*Paradoxurus hermaphorditus*, Pallas), small Indian civet *(Viverricula indica*, É. Geoffroy Saint-Hilaire*),* Indian gray mongoose (*Herpestes edwardsii*, É. Geoffroy Saint-Hilaire)*,* small Indian mongoose *(Herpestes auropunctatus*, Hodgson*),* and ruddy mongoose *(Herpestes smithi*, Gray*)*. Tiger prey

species present in the study area were chital (*Axis axis*, Erxleben), sambar (*Rusa unicolor*, Kerr), nilgai (*Boselaphus tragocamelus*, Pallas), chinkara (*Gazella bennetti*, Skyes), wild pig (*Sus scrofa*, Linnaeus), common langur (*Semnopithecus entellus*, Dufresne) and rhesus macaque (*Macaca mulata*, Zimmermann).

Ethics approval

Permissions for capture and collaring tigers were obtained under the Wildlife (Protection) Act 1972 from the MoEFCC, Govt. of India and the CWLW, Govt. of Rajasthan. The technical committee of the NTCA, which also considers the well-being of animals and ethics of research, approved the research project. Tigers were anesthetized using standard drugs under supervision by qualified veterinarians, observed till they fully recovered.

2. 2 Monitoring of tigers

We monitored 97 individual tigers during the study (2006 to 2014) through camera traps, radio-telemetry and routine patrolling (for direct sightings and photo-documentation) by researchers and forest staff. We developed criteria for classifying tigers into age groups by observing known-age individuals and use teeth eruption, ware, and body characteristics (see Supplement Appendix 1 for age estimation of tigers) similar to that of lions (Schaller 1972, Banerjee and Jhala 2012). We classified tigers into six age classes, namely, cubs (< 12 months), juveniles (12-24months), sub-adults (2-3 years), young adults (4-5 years), prime adults (6-10 years) and old adults (> 10 years). Of the 97 tigers,

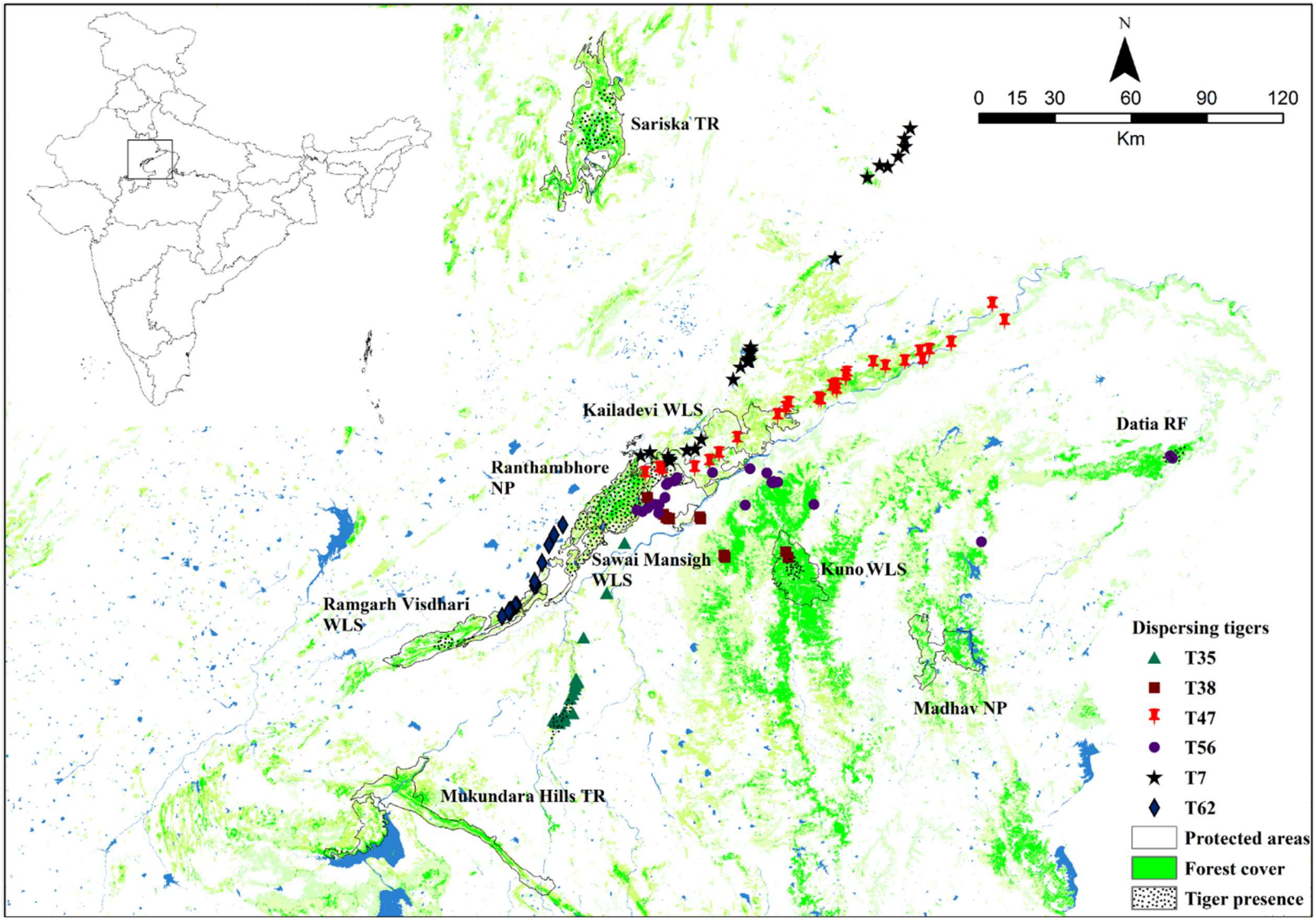


Figure 2.1 *Landscape of Ranthambhore showing the tiger reserve and other tiger occupied forest patches in western India. Locations of six individual tigers that dispersed out of the tiger reserve are shown. The map inset shows the location of Ranthambhore Tiger Reserve within India. TR - Tiger Reserve; NP - National Park; WLS- Wildlife Sanctuary; RF – Reserve Forest; Ranthambhore NP, Sawai Mansingh WLS and Kailadevi WLS together constitute the Ranthambhore Tiger Reserve.*

74 were known since cub stage, and their age was known to the exact month. Sex of the individuals was ascertained by the time cubs were six months old.

2. 2. 1. Camera trapping: Camera traps were used a) in a systematic grid-based design (4km^2 in 2006, 2009, 2012 and 2013, and 2km^2 in 2014) for a short duration to estimate tiger abundance, and b) to target specific areas so as to determine the presence and use of the area by particular individual tiger throughout the study period.

a) The entire tiger occupied part of RTR was sampled in a systematic manner during the study by placing a pair of camera traps at each selected location within a grid. After conducting a reconnaissance survey, camera traps were placed on dirt roads, animal trails, fire lines and dry river beds at locations that maximized the chances of photo-capturing a tiger. A pair of camera traps (TrailMaster® Lenexa KS USA, Cuddeback™ Green Bay USA, MOULTRIE® Alabama USA, or Stealth Cam® LLC Grand Prairie USA), facing each other, were placed at each location to get both flank photos of tigers at the same time. Each Camera was programmed with unique trap ID, time and date stamp on each photograph. Location of each camera trap was recorded by handheld GPS unit (Garmin 72™ and Garmin Etrex® 10, Kansas, USA) and plotted on a digitized map of RTR in GIS domain to ensure no sampling holes were present. Cameras were checked every 2-3 days to ensure proper functioning and recovery of data. Each photo captured tiger was identified to individuals by comparing their stripe patterns and given a unique id (e.g. T1, T2, and so on). The entire study area was sampled simultaneously within a period of 28 to 51 days so as to adhere to the assumption of population closure (Chao and Huggins 2010). The camera trapped area sampled each year as

estimated by joining the outer most camera traps ranged between 139 to 492 km^2 (Table 2. 1).

b) Besides systematic camera trapping conducted once in a year, cameras were also used in a need based manner to record photographs of specific tigers. Areas of tigers that were not seen for over 60 days were specifically targeted. These special efforts were carried out by placing multiple camera traps and conducting an intensive ground search in most probable locations of that tiger. The effort continued till the fate of that tiger was ascertained by locating it or confirming its death or dispersal. Since the landscape outside of the tiger reserve was human-dominated, the presence of dispersing tigers was quickly detected by reports of livestock kills and sighting of tigers or their signs by villagers. The research team along with forest department staff subsequently tried to locate each such tiger and ascertain its identity through sighting, camera traps or hand held photography.

2. 2. 2 Radio telemetry: Eight tigers (three adult males, one adult female, three sub-adult males and one sub-adult female) were radio-collared between April 2007 to May 2009. Tigers were anesthetized with ketamine hydrochloride in combination with medetomidine injected intramuscularly using a gas-powered projectile dart delivery system (Kreeger 1996). Tigers were collared with a Very High-Frequency transmitter (Telonics, Arizona, USA) and in most cases with a Global Positioning System with ground download facility (HABIT, British Columbia, Canada). Soon after the radio-collaring operation, Atipamezole was administered for reversing the effect of the tranquilizer (Kreeger 1996). Animals were left after natural reflexes and behaviour returned and subsequently monitored through telemetry. Radio-collared tigers were tracked and regularly monitored (>three times a week) from a

vehicle or on foot throughout the functional period of those collars. Tigers were tracked with the help of a hand-held directional 3- element Yagi antenna and Telonics and HABIT receivers. After the battery life of the radio-collars, the surviving collared tigers were monitored through camera traps and visual sightings.

2. 2. 3 Routine patrolling: Due to intensive camera trapping over the years and photo documentation by researchers and park officers, we were reasonably certain that almost all tigers of RTR were photo-captured by 2012 and were individually known. Our claim of knowing almost all RTR tigers was substantiated by the fact that in subsequent years no unknown adult tiger was recorded either by camera traps or by any other means. All additions to RTR population from 2012 onward till date were from known cubs. A photo album was developed and shared with the staff and officers of RTR in 2012 with additions and deletions done every six months. Since adult tiger numbers ranged between 20 to 40 individuals, it was possible to identify each tiger on most occasions it was sighted and often photographed with digital cameras by forest department staff and researchers. When in doubt these photographs were compared with the photo-album or on the computer to ascertain the tiger's identity. A daily record on all tiger observations was maintained in a register which was subsequently transferred to a database.

2. 3 Estimating demographic parameters of tigers

2. 3. 1 Tiger abundance: We used likelihood based spatially explicit capture-recapture (SECR, Efford 2011) in package ‘secr’ on R platform (Efford 2015, R Core Team 2017) to estimate tiger density from the systematically sampled camera trap data over the years (2006, 2009, 2012, 2013, and 2014; Table 2. 1). SECR consists of two sub-models. The distribution

sub-model depicts the spatial distribution of detectors and animal captures in the landscape. The detection sub-model (g(x)) declines with the increasing distance between the animal's activity centre, and this spatial scale of detection is parameterized by sigma (σ). A spatial capture history matrix, a trap layout matrix, and a habitat mask that excluded non-habitat areas from the SECR model space were prepared and used in secr. Home-range size (as indexed by σ, the movement parameter) is often correlated with density of the population (Efford et al. 2015). Since tiger population of RTR increased during the study period, therefore, σ and g0 (capture probability at the activity centre) was parameterized separately for each year. Male and female tigers were likely to differ in their ranging patterns. Hence we used gender as a covariate to model heterogeneity in movement parameter (σ). Half-normal detection function was used to model the scale parameter (σ). We used AIC_c (Akaike Information Criterion corrected for sample size) (Akaike 1974) to compare models with the null model (where g0 and σ were constant) and amongst themselves. Models with less than five delta AICc values were considered probable and the parameter estimates were obtained by AICc weighted model averages (Burnham and Anderson 2002). Cubs (<12 months) were excluded from density estimation since this cohort is underrepresented in camera traps and has relatively high mortality (Sharma et al. 2010). Since by 2012 we were reasonably certain that almost all the tigers in RTR were individually known to us, we used this information to compare estimates obtained by SECR with actual known density.

2. 3. 2 Sex Ratio and Female reproductive parameters: Since sex of all tigers was known, we have calculated sex ratio (adult males: adult females) in each year (sampling without

replacement) by counting the total number of males and females in the population, and an estimate of its versatility between years (Skalski et al. 2005).

Before giving birth, females restricted themselves in a small area of their territory (Sunquist 1981), and were often detected through frequent photo-captures and higher intensity of use at a particular site. Births were confirmed from photo-captures or direct sighting of lactating females (Supplement Appendix 1), while most cubs were recorded (photo-captured or sighted) with their mother only after they were about two months old. Since litter size at birth was rarely known, the reported litter size could be an underestimate as mortality before two months' age was not known. The ratio of cub: adult tigress was computed. Age at first reproduction was determined by recording first birth of tigresses that were monitored since they were cubs. Inter-birth intervals were recorded from intensively monitored tigresses that littered more than once during the study period. We recorded intervals between two successive litters when all cubs of the previous litter died before reaching dispersal age (more than two years) and compare these with intervals between two successive litters when cubs of the previous litter reached dispersal age.

2. 3. 3 Reproductive success and recruitment: We recorded reproductive success of tigresses as the number of cubs that survived to the age of independence (24 months). Individually identified tiger cubs that were monitored up to young adult stage allowed us to determine the age at which these tigers acquired territories either by displacing established tigers or in vacant habitats through dispersal. We calculated recruitment as the proportion of cubs that survived to the sub-adult stage (≥ 24 month). We also computed recruitment of sub-adults to successful breeders as the proportion of sub-adults that subsequently established

territories. Territoriality was inferred when a young-adult exclusively used an area that was earlier used by other adult tigers of the same gender or dispersed to a vacant habitat and lived there for several months.

2. 3. 4 Survivorship: We estimated stage specific (cub, juvenile, sub-adult, young adult, prime adult, and old adult) survival probabilities of tigers by using known-fate model (Williams et al. 2002) in program MARK (*ver.*7, Cooch and White 2017). Known-fate models use Kaplan-Meier estimator [Kaplan and Meier 1958) to estimate survival which requires that fate of the individual is known with certainty during the period a particular individual is monitored. All individuals do not enter the study simultaneously but are added in a staggered manner known as staggered entry design (Pollock et al. 1989). Radio-telemetered individuals provide the best data for such analyses (Williams et al. 2002). However, in the present study, besides the eight collared tigers that were located several times a week, each known individual tiger was observed (camera trap photo-captured, directly observed or photographed from hand-held cameras) at least once every month, and its fate recorded (see Supplement Appendix 2). In rare cases when an individual was not observed during an interval the known-fate model allows its observation to be 'censored' from the analysis (Williams et al. 2002). Data on survival/death of tigers was compiled on a monthly basis. We subsequently pooled this data for a three-month period to have a good number of observations on each tiger as well as to have an interval that was meaningful for survivorship analysis of tigers that are reasonably long-lived. Live-dead encounter history matrix for tigers was made by pooling encounter histories of three months into one interval where *10* represented survival of the individual throughout the interval, *11* represented mortality of the

individual during the interval, and *00* represented censoring the individual when that individual was not observed during the three-month interval. Only 59 observations on seven tigers out of 3492 observations from 97 tigers were censored during the study (see Supplement Appendix 2), forming a very small proportion (1.6%) of observation where fate could not be ascertained for that interval. All of these seven tigers were observed in subsequent periods, but by censoring them for intervals they were not recorded, we add to the uncertainty in the estimates (Williams et al. 2002). Seven tigers (two juveniles, one sub-adult male, one young adult male, and three old adult females) out of 97 that we monitored went 'missing' during the study period. We considered two extreme scenarios for these individuals in the survival analysis: a) a highly likely conservative scenario, that these tigers were poached, and b) a more optimistic but less likely scenario that these tigers dispersed and we were unable to trace them. In case of scenario 'a', we modelled these tigers as dead, and in case of scenario 'b', we censored them from the analysis. The resultant estimates of survival would encompass the true estimate. For the analysis, the matrix was right censored for all the surviving tigers at the end of December 2014. Tigers that survived and were monitored from cub to adulthood were included in subsequent age classes (stages) with the assumption that survival rates were independent for different age classes. As part of tiger reintroduction program, seven tigers were translocated from RTR to Sariska Tiger Reserve during the study period (Sankar et al. 2013). These individuals were censored in the survival analysis at the time of their translocation since these tigers would be exposed to a different set of environmental factors in Sariska that determine their survival probability. We formulated and run different candidate models which were ecologically plausible and

compare them using AICc values. Model averaged survival estimates were obtained for models with less than five delta AICc values (Burnham and Anderson 2002).

Mortality events were confirmed when carcasses were recovered, and causes of mortality were recorded on the basis of post-mortem report compiled by experienced veterinary personnel and/or by questioning eyewitnesses (if any). Cub mortalities were confirmed when found dead. However, not all cub carcasses could be recovered. A cub was considered dead if it was not detected (not photo-captured or sighted) with its mother for more than a month. There were no incidents where a cub that was not recorded for over a month (considered dead) was ever seen again. We considered seven tiger cubs (ranging from 2 to 10 months) that were provisioned by park managers after the death of their mother, as dead since they were unlikely to have survived in the wild on their own.

The small and isolated nature of RTR made it possible for us to follow and ascertain dispersal events of tigers. Tigers that left the National Park had to traverse human-dominated areas where their presence was detected readily by local communities who were always on a high vigil for large carnivores. The presence of tigers was detected from signs and examination of livestock kills (which were compensated by the Government). Our research team and park managers ascertained the identity of these tigers by targeted effort of camera trapping and visual sighting. Due to the high profile nature of RTR as well as the small tiger population that was vulnerable to poaching, the park management along with the research team made a concentrated effort to locate each tiger individually to ascertain its wellbeing. Mortality events were categorized into natural mortality (death of the mother, infanticide, old age,

disease, intra-specific strife), human-caused mortality (poaching, poisoning, accidents due to human causes), and unknown.

2. 3. 5 Dispersal age and distances: We considered tigers to have reached dispersal age once they became ≥ 24 month old (considering the lowest age of dispersal). At this age most tigers no longer moved with their mothers and were capable of hunting on their own. Dispersals from the natal area were confirmed through telemetry, camera trap photographs, direct observations and hand-held photography of tigers. Dispersal distances (Euclidean distance) of these tigers were measured from the centre of their natal area to the most extreme location of that tiger.

3. Results

3. 1 Tiger Abundance: On the average an effort of 3715 (±1324) camera trap nights were invested each year (Table 2. 1). In most years the model having g0(.) as constant and movement parameter (σ) having sex-specific responses was selected as the best-fit model. In one year (2009) the null model (g0(.), σ(.)) was selected as the best model (Table S1). Annual model averaged density estimates varied from 4.6 to 8.7 tigers per 100 km^2 (Table 2. 1). The movement parameter (σ) was consistently larger for males than females and was found to decline asymptotically with an increase in density for males (Fig. 2.2). The density estimate obtained from SECR did not differ from near actual density (Table 2. 1).

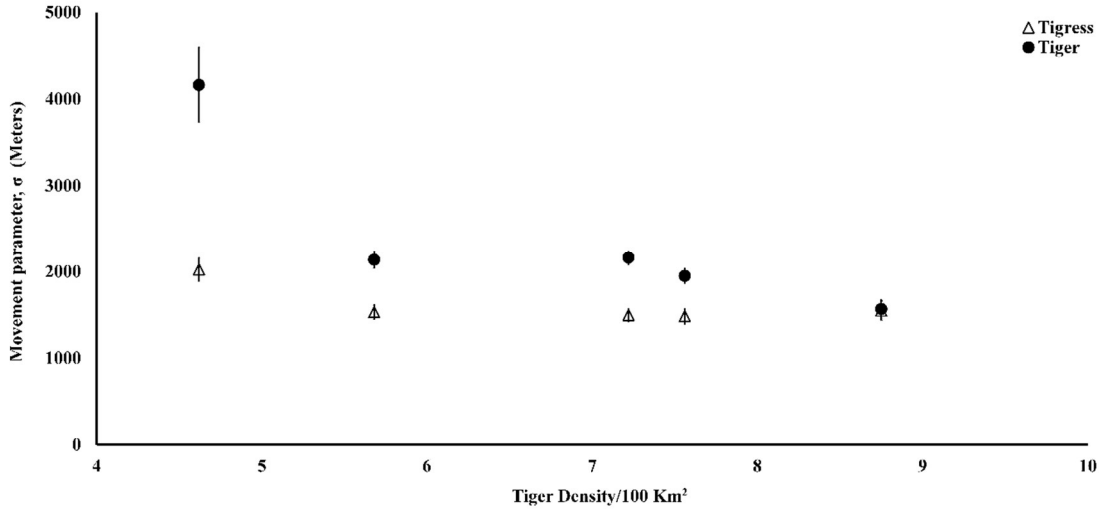


Figure 2.2 *The relationship between the movement parameter σ estimated using likelihood based spatially explicit capture recapture models and tiger density. Movement parameter σ for tigers declined asymptotically with increasing density while σ for tigresses remained relatively constant with increasing density.*

3. 2 Sex ratio and female reproductive parameters: Adult sex ratio (male: female) in the initial years (2006-07) was female biased (0.38± 0.04) and became marginally female biased (0.91± 0.04, 2008-14) in subsequent years. Overall male: female ratio was 0.76 (± 0.07) during the study period. The total number of breeding females in RTR ranged between 12 to 15 (see Fig. S1). We recorded litter size from 33 litters of 18 females, and the mean litter size was 2.24 (± 0.14; range= 1-4 cubs). Most of the litters were of two (50%) or three (31%) cubs (Fig. 2.3). Overall cub: adult female ratio (n= 9 years) was 0.48 (± 0.12). We could ascertain the age at first reproduction for 11 tigresses that were monitored since they were cubs as 54.5 months (± 3.7. range 33-68 months). Eight out of these 11 tigresses produced their first litter after four years of age, while only two tigresses gave birth before three years (see Fig. S2). The average interval between two successive litters (inter-birth interval) was

29.6 months (± 3.15; range= 7-51 months, n= 14 intervals from 8 tigresses). Intervals were shorter when all cubs of previous litter died before reaching independence (24 months, 15.0± 4.04 months, n= 3) than when cubs of previous litters survived till independence (33.64± 2.83 months, n= 11, see Fig. S3).

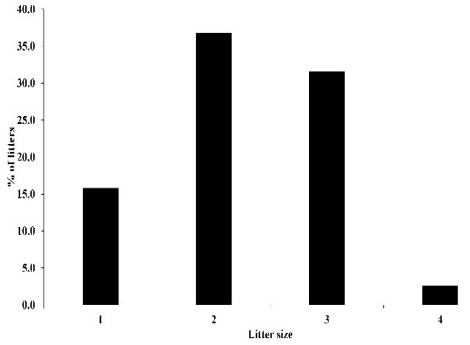


Figure 2.3 *Percent frequency of different sized litters (n= 33) of tigresses observed in Ranthambhore Tiger Reserve.*

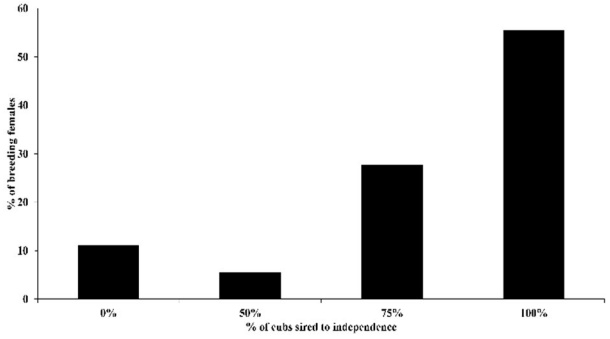


Figure 2.4 *Reproductive success of breeding females in Ranthambhore Tiger Reserve measured as a percentage of cubs that survived to recruitment age (24months) (n= 74 cubs from 33 litters of 18 females).*

3. 3 Reproductive success and recruitment: More than 50% of the intensively monitored breeding females (n= 18) successfully raised all their litters to independence, while around 10% of the females failed to raise any of their cubs during the study period (Fig. 2.4). Data on 51 individuals indicated that male recruitment rate from cub to the sub-adult stage was higher (77.8± 2.2%) than females (62.5± 2.4%). But male recruitment rate as breeding adults in the population from the sub-adult stage was lower (72.6± 2.0%) than females (86.7± 1.3%, Table 2.2).

3. 4 Survivorship: The average annual survival rate of cubs (85.4%) were comparatively lower than that of other age classes (Table 2.3). Annual survival rate increased after cub stage, remained constant till prime adult stage after which it declined (Table 2.3). Survival rates for males and females were similar for younger stages while females had marginally higher survival in older stages (Table 2.3). The survival estimates of the conservative approach of considering seven missing tigers as dead did not differ from survival estimates when these tigers were censored from the analysis (Table S2).

We recorded 25 mortality events (17cubs and juveniles, and 8 adults) during the study. Amongst all cub and juvenile mortality, 41% were natural (infanticide and death of mother due to natural causes), 47% were human caused (mother poached, accidents due to human causes and poisoning) and 12% of these could not be ascertained (Fig. 2.5). Amongst all adult mortality, 50% were natural (old age, disease, and intra-specific strife), and 38% were human-caused (poisoning and poaching, Fig. 2.5), the cause of 12% adult mortality could not be determined.

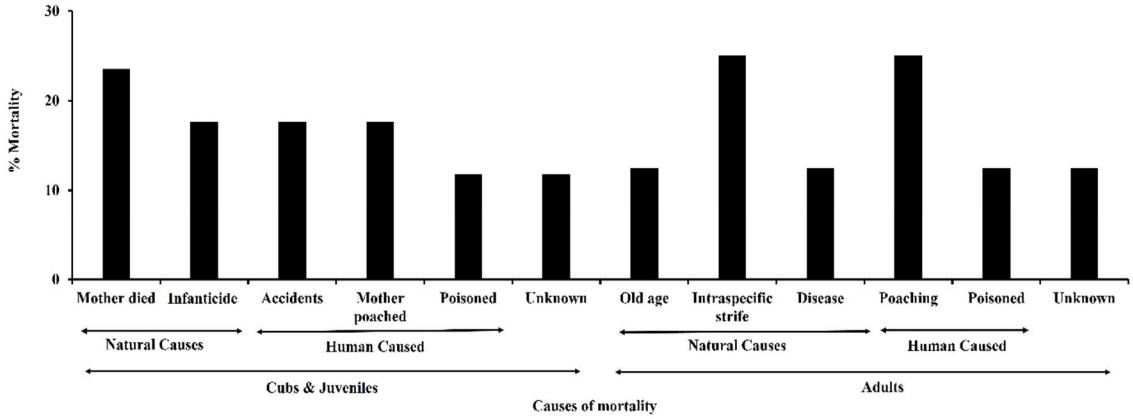


Figure 2.5 *Cause-specific mortalities of cubs and juveniles (n = 17) and adult tigers (n = 8) in Ranthambhore Tiger Reserve between 2006 to 2014.*

TABLE 2. 1 Sampling details and parameters estimates of tiger density from camera trap based spatial capture-recapture analysis in Ranthambhore Tiger Reserve.

Year	No. of camera locations	Camera trap Polygon (km^2)	Trap Nights	M_{t+1}*	$\widehat{N}$**(SE)	P‡	Known tiger population >1Year ♂	>1Year ♀	Cub	$\widehat{D}$ (SE) §§ /100km^2 ($CI_{95\%}$)	Known density§ /100km^2	g0 (SE)	σ (SE) Km
2006	40	139	48	16	16 (0.73)	1.0	5†	15†	15†	4.62 (1.19) (2.81 - 7.59)	-	♀: 0.06 (0.009) ♂: 0.03 (0.007)	2023.0 (131.6) 4162.6 (430.4)
2009	48	162	28	25	26 (1.52)	0.96	19†	17†	2†	8.75 (1.79) (5.88 - 13.02)	-	♀: 0.05 (0.009) ♂: 0.05 (0.009)	1547.0 (110.2) 1564.4 (104.3)
2012	60	223	45	22	30 (3.9)	0.73	12	16	6	5.68 (1.22) (3.74 - 8.64)	5.60	♀: 0.08 (0.008) ♂: 0.08 (0.007)	1529.0 (81.7) 2136.9 (97.2)
2013	76	464	51	37	40 (2.62)	0.92	18	20	14	7.56 (1.25) (5.47 - 10.44)	7.60	♀: 0.05 (0.005) ♂: 0.05 (0.005)	1480.7 (85.5) 1948.7 (83.3)
2014	182	492	48	39	39 (1.38)	1.0	21	21	12	7.22 (1.16) (5.27 - 9.88)	7.63	♀: 0.05 (0.006) ♂: 0.04 (0.003)	1496.5 (73.3) 2161.7 (78.4)

* M_{t+1}: Unique adult tigers photo-captured in camera traps

** $\widehat{N}$: Population estimates derived from spatially explicit capture recapture technique (regional population size using 'region.N');

§ Known density: Known tiger population/ tiger occupied area ♂: Male; ♀: Female

§§ $\widehat{D}$: Density estimates (model averaged); g0: detection probability at home range center; σ: movement parameter

‡ P: Proportion of the population detected by camera trap survey

† Since all tigers were not photo-captured, here we have reported the number of minimum known individuals

TABLE 2. 2 Recruitment of tigers with known fate (from ~2 months of age to age of independence >2 years and as territorial adults >3 years) in Ranthambhore Tiger Reserve.

Classes	No. of cubs	Recruitment to adult stage (%)	Recruitment as territorial adults (%)
Male	27	21 (77.8%, $CI_{95\%}$: 73.5-82.0%)	16 (76.2%, $CI_{95\%}$: 72.4-80.0%)
Female	24	15 (62.5%, $CI_{95\%}$: 57.8-67.1%)	13 (86.7%, $CI_{95\%}$: 84.1-89.2%)
All	51	36 (70.6%, $CI_{95\%}$: 64.2-76.9%)	25 (69.4%, $CI_{95\%}$: 64.0-74.8%)

TABLE 2. 3 Survival rates of tigers (n=97) in Ranthambhore between 2006 to 2014.

Age class	Gender	Sample size	Average annual survival rate* ($CI_{95\%}$)
Cubs (< 12 months)	Male	39	85.35 (80.3 – 90.4) %
	Female	35	85.40 (80.3 – 90.5) %
Juveniles (1-2 years)	Male	33	97.05 (95.4 – 98.7) %
	Female	26	97.06 (95.4 – 98.7) %
Sub adults (2-3 years)	Male	28	96.46 (94.0 – 98.9) %
	Female	19	96.49 (94.1 – 98.9) %
Young adults (3-5 years)	Male	20	93.87 (88.0 – 99.8) %
	Female	18	94.26 (89.0 – 99.6) %
Prime adults (5-10 years)	Male	15	82.53 (74.6 – 90.4) %
	Female	20	86.43 (80.7 – 92.1) %
Old adults (> 10 years)	Male	3	82.78 (76.9 – 88.7) %
	Female	12	84.52 (79.1 – 90.0) %
Adults (> 3 years)	Male	38	84.88 (80.6 – 89.2) %
	Female	50	88.74 (85.3 – 92.2) %
All adults (> 3 years)	Male and Female	88	86.99 (84.3 – 89.7) %

* Conservative estimates, where we have considered seven 'missing' tigers as dead in a more likely scenario.

TABLE 2. 4 Comparison of demographic parameters of tigers from Ranthambhore Tiger Reserve with published studies.

Sources	Area (sub-species)	Litter size	Female age at 1st reproduction (years)	Inter-birth intervals (months)	Cub survival probability	Adult survival	
						Male	Female
Sankhala 1978	Zoo, India (*Panthera tigris tigris*)	2.9 (n = 49)	3-6 years	24-36	NA	NA	
Smith & McDougal 1991	Wild, Nepal (*P. t. tigris*)	2.98 (n = 49)	3.4 years (n = 7)	21.6 (n = 7)	0.65	NA	
Chundawat et al. 2002	Wild, India (*P. t. tigris*)	2.3 (n = 12)	NA	21.6 (n = 14)	NA	NA	
Kerley et al. 2003, Goodrich et al. 2008	Wild, Russia (*P. t. altaica*)	2.4 (± 0.6) (n = 16)	4 (± 0.4) years (n = 4)	21.4 (± 4.4) (n = 7)	0.53 – 0.59	0.63 (±0.2)	0.81 (±0.1)
Singh et al. 2013 [32]	Wild, India (*P. t. tigris*)	2.9 (± 0.2) (n = 18)	NA	25.2 (± 1.8) (n = 9)	NA	NA	
Singh et al. 2013 [32]	Wild, India (*P. t. tigris*)	2.3 (±0.1) (n = 22)	NA	33.4 (± 3.7) (n = 7)	NA	NA	
Present study	Wild, India (*P. t. tigris*)	2.24 (±0.14) (n = 33)	4.54 (± 0.3) years (n = 11)	29.6 (± 3.1) (n = 14)	0.85 (±0.02)	0.84 (±0.02)	0.88 (±0.01)

NA- not available

3. 5 Dispersal age and distances: We recorded dispersal of 29 tigers, of these six were long distance dispersal out of RTR (Fig. 2.1). Mean dispersal age of tigers in RTR was 33.9 months (± 0.8, range= 24-42 months). Mean male dispersal distances (60.6± 2.1 Km) were larger than that of females (12.1± 1.3 Km, Fig. 2.6). Most of the females established their territory near their natal area while the majority of the males dispersed further from their natal areas. Five out of 16 males and one out of 13 females dispersed outside RTR and settled in forest patches within the larger landscape. These long distance dispersal movements ranged from 56 to 220 km Euclidean distance from their natal areas.

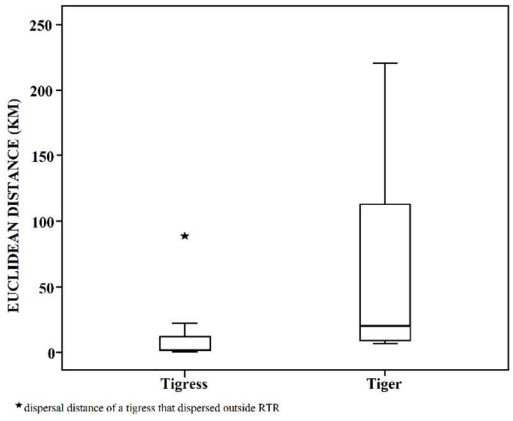


Figure 2.6 *Dispersal distances of tigresses (n =13) and tigers (n =16) from their natal area in Ranthambhore landscape.*

4. Discussion

Tigers are conservation dependent species and require substantial investments in terms of management and protection for their long-term persistence (Sanderson et al. 2010). Information on survival, recruitment, litter size, reproductive parameters, dispersal, sex ratio and density that we provide in this paper are the basis of estimating population viability and planning management interventions.

We mostly use standard methodology, but adept some and develop a few approaches required for procuring data from endangered carnivores. The subsequent analyses of these data do not violate any underlying assumptions of the analytical procedures. We believe that we were justified in using Known-Fate model for estimating survival due to the high frequency (every month) of observations of 97 individually known tigers for determining their fate (see Supplement Appendix 2). As explained in the methods, we 'censored' surviving individuals when the study was completed and for the few occasions in-between when we could not determine the fate of individuals (Williams et al. 2002). Open population capture-mark-recapture models cannot distinguish between emigration and mortality, and are confounded by the nuisance parameter of imperfect detection (Nichols 2010). Therefore, known-fate models though being data intensive, provide more precise and more informative parameter estimates.

During the initial phase of the study (i.e. 2006) tiger density in RTR was low (Table 2.1) as the population was recovering from a recent decline caused by poaching. In subsequent years, density increased with good protection and fluctuated between 5.6 to 8.7 tigers/ 100km^2 with a mean density of 7.5 (± 2.7) tigers/ 100km^2 (Table 2.1). This fluctuation in tiger density was likely due to synchrony in breeding by several females and recruitment of a large cohort of sub-adults that became available for camera trap sampling at an approximate interval of two years. As tiger density increases within a limited area, we would expect home-range to either decrease and/or show an increase in overlap. The movement parameter σ is an index of home-range radius over short time duration. Efford et al. (2015) show an asymptotic decline in σ with increase in tiger density from data across India. Herein, we demonstrate a similar relationship between σ and tiger density within a single population which we believe is

ecologically more meaningful (Fig. 2.2). The asymptotic nature of σ for males and a relatively constant σ for females suggests that male tigers' home range decline to some extent with increase in tiger density, while home range size in females, which is based primarily on food availability (Smith 1993), does not change with density. This could be interpreted to suggest that either tigresses do not invest energy in acquiring a home range larger than required to rear cubs or that Ranthambhore National Park was already near carrying capacity density with little scope of reduction in home-range sizes for tigresses. The increase in tiger numbers in RTR was accompanied with an increase in tiger occupancy while the number of breeding females remained relatively constant (12 to 15) during the study period (see Fig. S1). Camera trap data suggests that the entire core area of RTR (Ranthambhore National Park and Sawai Mansingh Sanctuary) was occupied by tigers by 2014. We also witnessed intense competition between mothers and daughters for breeding territories. This was another indication that tiger density was at or near carrying capacity within the core of RTR. For high density populations near carrying capacity regulatory mechanisms may include delayed age of first reproduction, increased inter-birth intervals, smaller litter sizes and depressed survival (Derocher and Stirling 1992). Delayed female age of first reproduction and longer intervals between two successive litters observed in RTR tigers were likely an effect of high tiger density at or nearing carrying capacity inside the core of RTR. Parameters that could potentially be depressed by inbreeding depression like litter size, cub survival, and disease caused mortality were either similar or better in comparison to other tiger populations (Table 2.4).

In highly inbred populations morphological abnormalities are often observed and resistance to disease is often compromised (Raikkonen et al. 2009). During the study we did not

encounter cubs with abnormalities or skeletal defects and mortality of tigers attributed to disease was only one. The morphometric measurement of RTR tigers captured for radio-collaring were among those of the largest recorded for tigers in India (YV Jhala, unpublished data). These observations along with comparable demographic parameters to other tiger populations suggest that there were no deleterious effects that had as yet manifested among RTR tigers due to population bottlenecks, small size and isolation (Keller and Waller 2002). This seems likely, since, till recent times the semiarid zone tiger population of central India was large and well connected (Chundawat et al. 2016) and the population bottlenecks that RTR tigers passed through did not remain very small for long periods of time (less than one generation time) (Reddy et al. 2002). However, we lack data on early infant mortality and foetal loss during pregnancy, which are some of the parameters that would be influenced by inbreeding depression. Reddy et al. (2012) conclude that RTR tigers had reasonable genetic diversity comparable to other central Indian tiger populations. Studies that link genetic variability with population size, connectivity, and ultimately with demography are required for conservation management of large carnivores.

Females that had lost cubs before their recruitment age gave birth within a smaller time interval as also reported in tigers (Karanth 2003) and in Asiatic lions (Banerjee and Jhala 2012). Due to a high level of protection, poaching was rare inside RTR during the study period. Therefore, long and stable tenures of territorial males were recorded (mean 5.6 years, range 4 to 11 years, n = 13). Only three cases of infanticide were observed during this study; this contrasts with studies on tigers in Chitwan National Park in Nepal and Asiatic lions in Gir (Smith and MacDougal 1991, Banerjee and Jhala 2012), where infanticide was a major

cause of cub mortality. Mean dispersal age of RTR tigers (~33 months) was higher than reported for Chitwan (~23 months) (Smith and MacDougal 1991), and Amur tigers (~19 months, Kerley et al. 2003). Young tigers were not compelled to leave their natal territories due to new male takeovers (Smith and MacDougal 1991). This stability in territorial male tenures allowed young tigers, especially males, to continue to live longer within their natal area enhancing their survival and achieving rapid growth to breeding body size. On four occasions we observed sub-adult male tigers occupy small ranges in peripheral areas of resident male territories. Once such tigers become sufficiently large so as to challenge resident males, they expand their range into that of the residential males' territory. By following this strategy relatively smaller and inexperienced sub-adult male avoid lethal encounters with larger and experienced males during their initial dispersal stage (Smith 1993).

Ten out of 13 sub-adult females established territories near their natal areas, two females established their territory inside RTR but ~20km away from their natal area, and one female dispersed outside the reserve (~90km). We observed that females either established their territory beside their mothers (n = 3) or occupied a part of their mother's territory and gradually pushed their mother off (n = 5). One female that initially occupied her mother's territory by displacing her mother produced her first litter in this territory, but subsequently shifted her territory with her 12-month-old cubs (of her second litter) ~10km away from her natal territory. This shift coincided with the takeover of her natal territory by a new male tiger. Her natal territory was subsequently occupied by her daughter from her first litter.

The dispersing sex in tigers is known to be males (Smith 1993). Amongst RTR tigers, males did disperse larger distances than females, but opportunities to disperse were restricted in this landscape. Large dispersal distances travelled by tigers (once out of RTR), and older age of dispersal reflects the difficulty a tiger faces in locating appropriate vacant habitat to settle. The small reserve size combined with very little and disjunct tiger habitat available outside the reserve system within a hostile human-dominated habitat matrix restricted dispersal. Males that managed to disperse and locate habitat patches tried to settle there, but due to lack of female tigers in these patches, were unable to breed. If areas of Kailadevi Wildlife Sanctuary (part of RTR buffer), Kuno Wildlife Sanctuary, Ramgarh Visdhari Wildlife Sanctuary and Mukundara Hills Tiger Reserve (Fig. 2.1) are made free of human settlements through incentivised voluntary relocation scheme (WPA 1972; 2006 amendment), these areas could harbour breeding population of tigers. Simultaneously dispersal corridors between these tiger habitats and with core of RTR need to be secured and restored to promote a metapopulation in this landscape. Initially, once these areas have been appropriately restored and have sufficient prey base, this tiger dispersal could be aided by translocating tigers. Establishing and managing the tiger population in the larger Ranthambhore landscape as a metapopulation (Hanski 1998) would be desirable for long-term conservation.

Park authorities often intervene by treating injured tigers *in situ* or supplementing food resources for orphan/sick cubs. These activities, although well intentioned, hinder the natural process of selection and the social dynamics of the species (Packer et al. 2011, Banerjee and Jhala 2012). Such interventions also reduce the genetic fitness of the population over time by ensuring the survival of unfit individuals especially if sick animals are treated, saved and

allowed to breed (Keller and Waller 2002). Interfering with the natural process may be necessary for highly endangered populations where every living individual counts. However, RTR is now a high tiger density area (Sadhu et al. 2015), and therefore, management interference of health care should be extremely selective, if any.

Our study did not find any evidence of detrimental effects resulting from a small population that could potentially be inbred and there seems to be no current need for genetic rescue (Pimm et al. 2006) of RTR tigers. Currently RTR has about 15 breeding units and adult female survival of about 88%, these are bare minimal requirements to ensure long-term persistence (Chapron et al. 2008). Managing the Ranthambhore landscape by restoring habitat patches and connectivity with RTR so as to promote a metapopulation of tigers would enhance the potential of long-term persistence of this last remaining semi-arid tiger population in western India.

Tiger tourism!

SUPPLEMENTARY MATERIALS

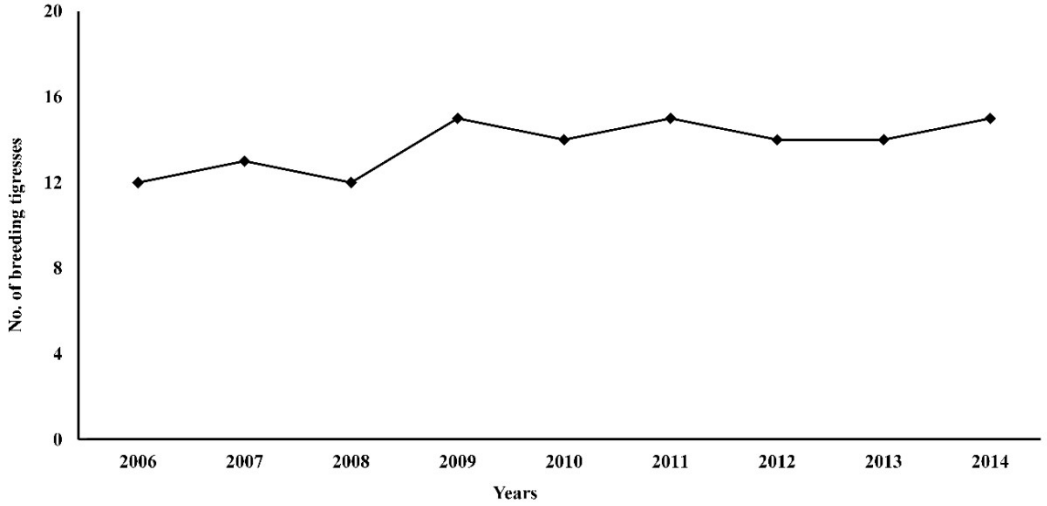


Figure. S1 *Number of breeding tigresses in each year observed in Ranthambhore Tiger Reserve during the study period.*

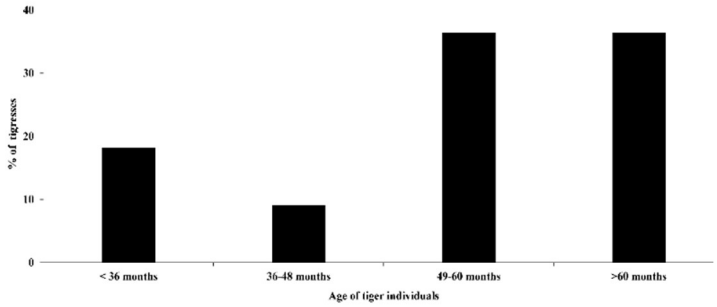


Figure. S2 *Age at first reproduction of tigresses (n=11) observed in Ranthambhore Tiger Reserve.*

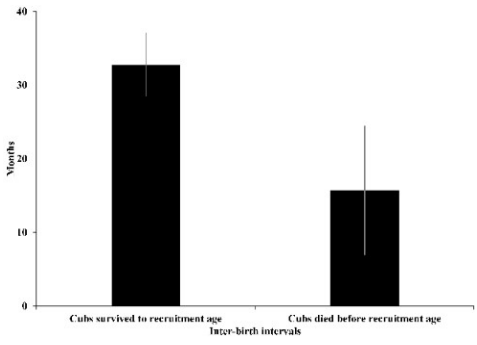


Figure. S3 *Inter-birth intervals of tigresses in Ranthambhore Tiger Reserve when all cubs of previous litter died before reaching independence (n=3 litters) and when cubs of previous litters survived till 24 months (n=11).*

Table S1 Sampling details and parameters estimates of annual tiger density from camera trap based spatial capture-recapture analysis in Ranthambhore Tiger Reserve.

Year	Model	No. of Parameters	AICc	*d*AICc	AICc weight	$\hat{D}$ (SE) /100 km^2	g0 (SE)		σ (SE) Km	
							Female	Male	Female	Male
2006	g0(sex) σ(sex)	6	758.748	0	0.8699	4.61 (1.19)	0.06 (0.008)	0.03 (0.008)	2005.2 (122.0)	4221.9 (414.7)
2006	g0(.) σ(sex)	5	762.549	3.801	0.1301	4.63 (1.16)	0.04 (0.005)		2145.8 (128.9)	3786.7 (322.3)
2006	g0(.) σ(.)	4	797.383	38.635	0	4.16 (1.06)	0.04 (0.004)		3005.6 (165.0)	
2006	g0(sex) σ(.)	5	801.337	42.589	0	4.18 (1.06)	0.04 (0.005)	0.04 (0.007)	2981.1 (165.8)	
2009	g0(.) σ(.)	4	481.486	0	0.635	8.75 (1.79)	0.05 (0.008)		1558.1 (99.0)	
2009	g0(sex) σ(.)	5	484.08	2.594	0.1736	8.77 (1.79)	0.05 (0.010)	0.06 (0.010)	1553.1 (98.7)	
2009	g0(.) σ(sex)	5	484.233	2.747	0.1608	8.77 (1.79)	0.05 (0.008)		1494.8 (132.0)	1594.0 (119.3)
2009	g0(sex) σ(sex)	6	487.545	6.059	0.0307	8.77 (1.79)	0.05 (0.012)	0.06 (0.011)	1526.3 (155.9)	1569.7 (128.1)
2012	g0(.) σ(sex)	5	917.948	0	0.7944	5.68 (1.22)	0.08 (0.006)		1518.9 (75.9)	2147.1 (94.1)
2012	g0(sex) σ(sex)	6	920.651	2.703	0.2056	5.7 (1.23)	0.07 (0.010)	0.08 (0.009)	1568.6 (91.8)	2097.9 (98.8)
2012	g0(sex) σ(.)	5	931.354	13.406	0	5.56 (1.2)	0.05 (0.006)	0.10 (0.009)	1914.1 (69.9)	
2012	g0(.) σ(.)	4	948.038	30.09	0	5.48 (1.18)	0.07 (0.006)		1945.6 (72.5)	
2013	g0(.) σ(sex)	5	1015.82	0	0.8057	7.55 (1.25)	0.05 (0.005)		1478.7 (82.6)	1950.4 (81.9)
2013	g0(sex) σ(sex)	6	1018.66	2.845	0.1943	7.58 (1.25)	0.05 (0.008)	0.05 (0.006)	1489.1 (96.2)	1941.7 (88.7)
2013	g0(sex) σ(.)	5	1026.66	10.845	0	7.43 (1.23)	0.04 (0.005)	0.06 (0.006)	1802.6 (66.5)	
2013	g0(.) σ(.)	4	1031.71	15.898	0	7.38 (1.22)	0.05 (0.004)		1823.9 (67.8)	
2014	g0(sex) σ(sex)	6	2082.18	0	0.722	7.22 (1.16)	0.05 (0.005)	0.04 (0.003)	1477.6 (67.3)	2176.7 (76.8)
2014	g0(.) σ(sex)	5	2084.09	1.909	0.278	7.22 (1.16)	0.04 (0.002)		1546.9 (63.9)	2123.1 (68.9)
2014	g0(sex) σ(.)	5	2121.88	39.697	0	7.17 (1.15)	0.3 (0.003)	0.04 (0.003)	1911.6 (53.0)	
2014	g0(.) σ(.)	4	2122.41	40.235	0	6.3 (1.01)	0.04 (0.002)		1909.0 (50.8)	

TABLE. S2 Survival rates of tigers (n=97) in Ranthambhore between 2006 to 2014.

Age class	Gender	Sample size	Average annual survival rate* ($CI_{95\%}$)	Average annual survival rate** ($CI_{95\%}$)
			Conservative	Optimistic
Cubs (< 12 months)	Male	39	85.35 (80.3 – 90.4) %	
	Female	35	85.40 (80.3 – 90.5) %	
Juveniles (1-2 years)	Male	33	97.05 (95.4 – 98.7) %	97.07 (95.4 – 98.7) %
	Female	26	97.06 (95.4 – 98.7) %	97.08 (95.4 – 98.7) %
Sub adults (2-3 years)	Male	28	96.46 (94.0 – 98.9) %	98.13 (96.1 – 1.0) %
	Female	19	96.49 (94.1 – 98.9) %	
Young adults (3-5 years)	Male	20	93.87 (88.0 – 99.8) %	99.14 (96.0 – 1.0) %
	Female	18	94.26 (89.0 – 99.6) %	
Prime adults (5-10 years)	Male	15	82.53 (74.6 – 90.4) %	
	Female	20	86.43 (80.7 – 92.1) %	
Old adults (> 10 years)	Male	3	82.78 (76.9 – 88.7) %	
	Female	12	84.52 (79.1 – 90.0) %	82.62 (77.3 – 87.8) %

** Conservative estimates, where we have considered seven 'missing' tigers as dead in a more likely scenario.*

*** Optimistic estimates reported for the stages where we have censored the seven 'missing' tigers: two juveniles, one sub adult male, one young adult male, and three old adult females.*

Connecting the cat: Modelling connectivity for tigers from dispersal data in dry forests of western India

A disperser's dilemma: *A sub-adult male at the edge of Ranthambhore tiger reserve, above the Ranthambhore-Kuno corridor; later on, it dispersed to Datia forest of Madhya Pradesh.*

Tiger's eye view: *The human-dominated landscape outside Ranthambhore. The photograph was clicked from the Khandar fort which acts as stepping stone corridor, connecting Ranthambhore with Kuno landscape. Chambal river can be seen at the horizon.*

1. Introduction:

Large carnivore populations are declining across the world (Ripple et al. 2014). Large carnivores need contiguous habitat patches with inviolate space and ample prey-base (Dinerstein et al. 2007), but attaining these requirements is challenging in the Anthropocene (Woodroffe 2000). Tiger (*Panthera tigris*, Linnaeus 1758) serves as the umbrella and a flagship for conserving the Asian forested ecosystems. However, the tiger populations experienced severe range loss and population decline in the recent times due to persecution, habitat loss, and prey depletion (Sanderson et al. 2010). Stringent law enforcement managed to secure tiger strongholds inside the protected areas (hereafter, PAs) (Panwar 1982), but many tiger populations exist as small insular populations within forested refuges (PAs) in hostile human-dominated landscapes (Jhala et al. 2020). Recent studies have found, due to poor landscape connectivity, high level of local structuring has occurred in these isolated tiger populations (Yumnam et al. 2014, Kolipakam et al. 2019). This emphasises the importance of protecting and restoring connectivity between the tiger populations and manage them as metapopulation in the larger landscape for their long-term persistence (GTRP 2010, Walston et al. 2010). Protecting the tiger populations inside PAs with existing administrative set up seems plausible and offers a pragmatic solution for conserving tigers; however, maintaining connectivity in the multiple-use landscape is a daunting task. The dispersal routes are situated outside the domain of legal protection, often on public or private lands which are exposed to land use changes pertaining to anthropogenic causes.

The dry deciduous forests consist one of the largest and highly productive tiger habitats in Indian subcontinent (Smith et al. 2011). These habitats, at the same time, are also the most vulnerable to habitat loss due to anthropogenic disturbances and climatic

stochasticity (Sharma et al. 2017). Extinctions of two tiger populations from the PAs in the last decade underlined the vulnerability of extant tiger population in the dry forest habitats (Check et al. 2006, Gopal et al. 2010). The westernmost tiger population of Ranthambhore landscape (hereafter Ranthambhore, consists of Ranthambhore National Park, Sawai Mansingh Sanctuary, and part of Kailadevi Wildlife Sanctuary) holds the last stronghold of tigers in the dry forest patches of western India (Jhala et al. 2020). Due to unregulated hunting, habitat loss, and prey depletion, tiger populations went locally extinct from the neighbouring patches of Ranthambhore in the recent past (Singh and Reddy 2017). Stringent law enforcement and habitat management over a decade resulted in the recovery of Ranthambhore tiger population from the initial low and reaching the carrying capacity threshold (Sadhu et al. 2017). Being a large-ranging carnivore, tigers need vast expanse of inviolate land to attain an ecologically sustainable population (Sanderson et al. 2010). The present size of the PAs in the dry forest habitats are too small to secure a viable tiger population (Seidensticker 2016). Therefore, it is imperative to manage these populations as metapopulation through maintaining landscape-level connectivity (Yumnam et al. 2014, Qureshi et al. 2014). When landscape connectivity persists, dispersing individuals from the 'source' population are likely to colonise and contribute to the recovery of 'sink' populations (Hanski 1998). Therefore, maintaining connectivity in the landscape is pivotal to prevent the decline of large carnivore population (Rabinowitz and Zeller 2010). In the dry forest habitats of western India, tiger dispersal events are few and sporadic, thus delaying the process of recolonization of sink habitats (Jhala et al. 2020).

Conserving connectivity in the landscape requires mapping of potential dispersal routes, mostly in human-dominated landscapes outside the PA network (Watson et al. 2015).

Modelling dispersal routes requires a resistance (cost) surface and a connectivity algorithm to model potential dispersal routes/linkages in the landscape. The resistance surface can be generated using species distribution modelling which has been used extensively and accepted as an important tool for delineating potential habitats to model the resistance surface (Elliot et al. 2014). Radio telemetry provides the most authentic data at the finest resolution on species occurrence and dispersal (Zeller et al. 2018). However, the scope of such studies are constrained by sample size, funding and logistics (Beier 1995, Fagan & Calabrese, 2006). Thus, presence information obtained from secondary sources (camera trap and indirect signs, genetics, and expert opinion) are often used as the closest proxies to model resistance surface in the landscape (Zeller et al. 2012). While using the secondary sources, careful assessment of the resistance surface needs to be done as resource selection of the dispersers are often different from the resident ones (Elliot et al. 2014). Moreover, the movement strategies of dispersing tigers traversing through human-dominated landscape will be different from that of the resident ones living inside the PAs (with least human disturbances).

In the present study, we presented the actual dispersal points recorded from six tigers dispersed from Ranthambhore to other parts of the landscape (Fig. 2.1). On the basis of these dispersal points which were outside the PAs, we have prepared the resistance surface using species distribution modelling (MaxEnt). Furthermore, we have generated resistance surfaces using tiger presence points obtained from only the PAs (PA models, details in the method section) and compared them with the resistance surface generated using the actual dispersal points (dispersal model). Our results indicated that the resistance surfaces generated from the PA models vary from the dispersal model. This highlighted the importance of using actual dispersal points for modelling landscape

resistance for dispersal over the presence points obtained only from the PAs. The resistance surface generated from dispersal model was further used for delineating potential habitat linkages in the landscape (CIRCUITSCAPE). The CIRCUITSCAPE delineated corridors showed potential for tiger dispersal in the landscape. The future conservation investments need to be focussed on the protection and restoration of these corridors. Our findings are crucial for maintaining metapopulation structure to ensure long-term persistence of tigers in the semi-arid landscape of western India as suggested by recent studies (Sadhu et al. 2017, Kolipakam et al. 2019).

2. Methods

Ethics statement

Permissions for capture and collar tigers were obtained under the Wildlife (Protection) Act 1972 from the Ministry of Environment and Forests, Government of India and the Chief Wildlife Warden, Government of Rajasthan. The technical committee of the National Tiger Conservation Authority which also considers the well-being of animals and ethics of research approved the research project. Tigers were anesthetized using standard drugs under supervision by qualified veterinarians. All tigers were observed from a safe distance till they fully recovered from the anaesthesia and walked away into the forest.

2. 1. Study area

The study was conducted as a part of the long-term ecological monitoring of tigers in Ranthambhore Tiger Reserve which began in 2006; 97 individual tigers were monitored

to record their life history events including dispersal (details in Sadhu et al. 2017). The dry deciduous forests of western India situated in the semi-arid bio-geographic zone of India (Rodgers and Panwar 1988). Two ancient mountains ranges surround the dry forest habitats of western India - the Aravallis, and the Vindhyas. The study area (27°35' to 24°21' N and 73°05' to 79°00' E, ~210000 Km^2) comprised of protected forests as well as forest lands outside the PAs (Fig. 2.1). PAs include national parks (Ranthambhore, Sariska, and Mukundara Hills, Kuno, and Madhav), and wildlife sanctuaries (Sawai Mansingh, Ramgarh-Visdhari, Kaila Devi, Bhainsrodgarh, Gandhi Sagar, Bassi, Sita Mata, Phulwari ke Nal, Kumbhalgarh, Van Vihar). While the forested habitats are now restricted mostly in the rugged and inaccessible terrain, since the flatter valleys being taken over by agriculture and pasture. In historical times, tiger presence was reported across the present PAs and beyond (Singh 1999, Singh and Reddy 2017). Ranthambhore is the only source population of tigers in the landscape, tiger presence in the rest of the landscape is due to dispersal or translocation of tigers from Ranthambhore (Fig. 2.1).

The area is rich in mineral depositions, especially limestone, thus mined extensively, which in terms causes destruction and fragmentation of wildlife habitats in the landscape. River Chambal and its tributaries are the main source of water in the landscape, however, most of these tributaries are seasonal. Extensive ravine network in the Chambal river catchment is infamous for illegal activities (dacoits), therefore, sparsely populated. These extensive system of ravine provides refuge habitat to wildlife in this landscape. The predominant climate of this region is Sub-tropical dry climate with three distinct seasons,

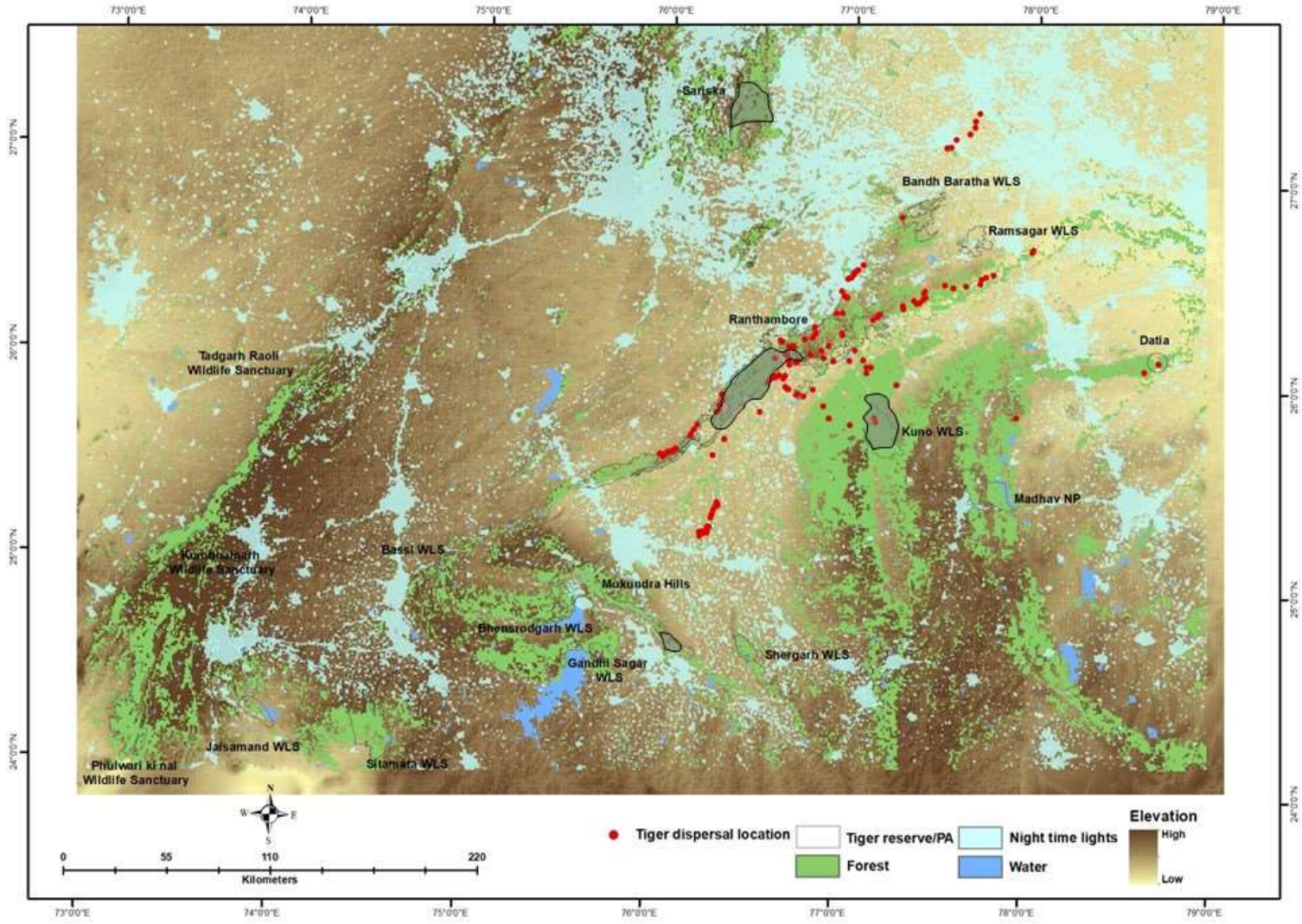


Figure 2.1: *The map depicting the tiger landscape of dry forest habitats of western India with present tiger distribution (shaded polygons) and dispersal points.*

dry winter (temperature <10°C, October-February), very hot summer (temperature >40°C, March-June), and hot and humid monsoons (temperature 30-40°C, July-September). The average rainfall is 800mm, and 90% of it happens in the monsoon months. Monsoon quickly transforms these dry forests into a lush green, and most of the tiger dispersal events happen during these time as the tall standing mustard crops provides refuge to the straying animals. The PAs in this landscape are dominated with northern tropical dry deciduous forests ($5B/C_4$) interspersed with scrubland (DS_1) and grassland ($5/DS_4$) habitats forming thinly wooded savannahs (Champion and Seth 1968). These PAs harbour rich biodiversity of wildlife, though many threatened species reside outside of the PA network. The large carnivores found in the landscape are - tiger (*Panthera tigris*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), striped hyaena (*Hyaena hyaena*), Indian wolf (*Canis lupus*). Presence of wild dogs was reported in a few pockets of the landscape, however, recent photographic evidence is lacking. Apart from the large carnivores, several small carnivore species are present in the landscape - golden jackal (*Canis aureus*), jungle cat (*Felis chaus*), desert cat (*Felis silvistris*), caracal (*Felis caracal*), rusty spotted cat (*Prionailurus rubiginosus*), honey badger (*Mellivora capensis*), Indian fox (*Vulpes benghalensis*), common palm civet (*Paradoxurus hermaphorditus*), small Indian civet *(Viverricula indica),* Indian gray mongoose (*Herpestes edwardsii*)*,* small Indian mongoose *(Herpestes auropunctatus),* and ruddy mongoose *(Herpestes smithii)*. Occasional records of fishing cat (*Prionailurus viverrinus*) were reported in few parts of the study area (Mukherjee et al. 2012, Sadhu and Reddy 2013).

2. 2. Collection of tiger presence points

2. 2. 1. Tiger dispersal data

We followed six dispersing tiger individuals (one female and five males) within a period of nine years (2006 to 2014) and recorded their presence points in the landscape. A team comprised of researchers and experienced field staff follow the dispersing individuals. Based on indirect evidences, information gathered from the local villagers (livestock depredation, pugmark, or direct sightings), camera-traps, the team validated tiger presence and recorded coordinates. Most dispersal events happened in the post-monsoon (September-October) to end of winter (February), when the agricultural fields were covered with crops that provided cover in an otherwise open and barren landscape. We recorded a total of 139 presence points from six dispersal events from the source population of Ranthambhore TR. These coordinates were plotted using a GIS platform (ArcMap, *ver*. 10.1) for further spatial analysis.

2. 2. 2. Tiger telemetry data

Eight tigers (three adult males, one adult female, three sub-adult males and one sub-adult female) were radio-collared and monitored between April 2007 to February 2011 (see Sadhu et al. 2017 for details). Tigers were collared with a duel transmitter system consisting of Very High-Frequency transmitter (Telonics, Arizona, USA) and in most cases with a Global Positioning System with ground download facility (HABIT, British Columbia, Canada). Radio-collared tigers were tracked and regularly monitored (>three times a week) from a four-wheel drive vehicle or on foot throughout the functional period of those collars. The presence points obtained from the radio-telemetry were used to generate resistance surface for the entire landscape (PA Model -1).

2. 2. 3. Camera trapping data

We have used the long-term camera trapping data from the PAs to generate resistance surface using the tiger detections in camera traps (PA Model -2). The camera traps were placed in strategic locations inside the PAs to estimate the number of tiger and leopards in a mark-recapture framework (see Sadhu et al. 2017 for details). Location of each camera trap was recorded by handheld GPS unit (Garmin 72™ and Garmin Etrex® 10, Kansas, USA) and used for geo-tagging the camera trap images. Each Camera was programmed with unique trap ID, time and date stamp on each photograph.

2. 2. 4. Tiger sign survey data

Tiger presence points obtained from carnivore sign survey data were used to generate the resistance surface for dispersal analysis (PA Model -3). Potential tiger occupied areas in the source population (i.e., Ranthambhore) were surveyed by searching the habitats frequented by tigers for indirect signs (pugmark, rake mark, scrape and scat, and vocalisation) (see Jhala et al. 2015 for details). Surveys were conducted by a team of trained researchers familiar with identification of signs of tigers and other co-predators.

2. 3. Modelling landscape resistance for tiger

2. 3. 1. Habitat suitability modelling for tigers

Often studies use data from telemetry or CT's obtained from within source areas of the target population to model resistance surfaces in the landscape. We believe that such models underestimate habitat permeability since all the "presence" locations are obtained from the most suitable habitats and not from habitats that permit animal dispersals but are not appropriate for residence or breeding. Therefore, we created habitat suitability model

for tigers using different sources of presence points – actual dispersal points vs. presence points from the source (details in the previous section, 2.2) to model the habitat suitability using program MaxEnt (*ver.* 3.4.1, Phillips et al. 2006). MaxEnt is a presence-only model which predicts species distribution using a set of suitable environmental variables drawn randomly from the background samples (Pearson 2007).

For building the model in MaxEnt, 70% of the present locations were used randomly for training the model. A different set of regularisation multiplier was used to address the overfitting of the model with 100 replicates (Bootstrap replication) to address the overfitting of the model (Marino et al. 2011). A different set of models (Linear, Quadratic, and Product – independently and in combination) suited for the data type were used, and the best model was selected using the AUC (Area Under Curve) value (Phillips and Dudik 2008). Contribution of each covariate was tested using Jackknife test for the best model (Phillips et al. 2006).

2. 3. 2. Preparation of environmental layers

From the ecological understanding and published literature, we used key habitat and anthropogenic factors likely to influence the habitat use by tigers in the landscape. Initially, we have considered four habitat layers- forest cover classes (non-forest, scrubland, open forest, moderately dense forest, dense forest), distance from drainage (river, rivulets, seasonal streams), elevation, and ruggedness; three layers depicting human disturbances – distance from night time visible lights (hereafter, nightlights), distance from human habitation, and distance from roads. We used only one variable from a pair of variables that were correlated (Pearson correlation, $r > 0.7$) and used five uncorrelated layers for the analysis- forest cover classes, distance from drainage,

ruggedness, distance from nightlights, and distance from the roads. The forest cover layer was classified as woodland (comprising of moderately dense and dense forest cover types) and scrubland (scrubland, grassland, and open forest type) layer to assess their independent influence on tiger dispersal. Forest cover, road, and drainage information was obtained from Survey of India (http://www.surveyofindia.gov.in/). Forest cover data was extracted using the LISS-III satellite at 23.5 m resolution (four multispectral bands). Elevation and ruggedness information was obtained from the Shuttle Radar Topography Mission (SRTM) available at 90m resolution. Human footprint data from Last of the Wild Project, Version 2, 2005 (LWP-2) representing the effect of human influence in each pixel was used. Information on nightlights was downloaded from the United States Air Force Defense Meteorological Satellite Program (DMSP) and the National Oceanic and Atmospheric Administration's (NOAA, http://www.ngdc.noaa.gov/dmsp/sensors/ols.html). Protected Area shape files were accessed from GIS Cell, Wildlife Institute of India. All the layers were resampled to 1Km^2 pixel size to maintain uniformity in the analysis. Calculation of Euclidean distances was done in Esri® ArcMap™ 10.1. using Euclidean Distance Tool in Spatial Analyst.

2. 4. Modelling potential corridors for tiger

We used program CIRCUITSCAPE to model the dispersal linkages in the landscape (McRae et al. 2008). The program uses circuit theory where PAs are considered as focal nodes (current source), and the probability of animal movement (current flow) was generated using the resistance surface (McRae et al. 2013). The MaxEnt generated output (dispersal model) was considered as resistance surface for tigers to delineate habitat linkages in the landscape. We have used the permeability (1- resistance) matrix where each cell/pixel was assigned the permeability value. Higher permeability (current flow)

values depicted areas preferred by tigers while dispersing from one PA to other (focal nodes) compared to lower-value areas. The CIRCUITSCAPE generated habitat linkages were classified into five classes using their current flow values (natural breaks): very low, low, moderate, high, very high. We have also highlighted bottlenecks on the corridors which need immediate conservation attention and losing out those crucial links are likely to hinder connectivity in the landscape. We have overlaid the tiger dispersal points on the CIRUITSCAPE delineated corridors to validate the model-based output with real-life data.

3. Results

Tigers in the dry forest habitats of western India dispersed long distances (~60 to 220 Km) traversing human-dominated landscapes. These long dispersal distances show the existence of connectivity and unavailability of suitable habitat patches in the vicinity of Ranthambhore. All dispersal events were from Ranthambhore, the only source population in the landscape.

3. 1. Modelling landscape resistance for tiger

The average Area Under the Curve (AUC) for the 'dispersal model' was 0.861 (SD 0.018), while AUC for 'PA model' 1, 2, and 3 was 0.950 (0.008), 0.943 (SD 0.008), and 0.882 (SD 0.021), respectively.

The Jackknife estimator depicted the relative importance of different covariates for modelling the suitability. In the 'dispersal model', scrubland-open forest habitats contributed the most (~45%) followed by woodland and distance to the road (Fig. 2.2). Distance to drainage, distance to night-time light, and ruggedness contributed much lower than the above (less than 10%). Presence of scrubland-open forest habitats and woodlands

in a pixel highly influence the tiger usage probability in a pixel compared to areas dominated with human land use (Fig. 2.3a, b). Moderately rugged terrain and the proximity of drainage (river, rivulets, seasonal streams) influenced the tiger usage probability in a pixel (Fig. 2.3c, d), however their contribution to the model was low (Fig. 2.2). In 'PA models' the relative contribution of woodland was the most followed by scrubland, drainage, and ruggedness (Fig. 2.2). Trends of the covariates' response to tiger permeability did not differ than those of the 'dispersal model', except for ruggedness (Fig. 2.4- 2.6). Therefore, using the actual dispersal points highlighted the importance of scrubland-open forest areas for tiger dispersal in the landscape, which was otherwise not highlighted in the PA Models. The MaxEnt outputs for 'dispersal model' and 'PA models' depicted the permeability for tiger movement in the landscape (Fig. 2.7a-d).

3. 2. Modelling potential corridors for tiger

The program CIRCUITSCAPE generated potential dispersal linkages in the landscape using the tiger resistance surface generated by program MaxEnt (dispersal model). The PAs were used as nodes and probability of dispersal between these nodes were modelled in CIRCUITSCAPE (Fig. 2.8). We have divided the dispersal probability (i.e., current flow) into five categories: very low (<0.5), low (>0.5 to 0.6), moderate (>0.6 to 0.7), high (>0.7 to 0.8), and very high (>0.8). The area under the very high probability class was ~3300 Km^2, less than 2% of the entire landscape. While area under the high and moderate classes were ~2900 and ~4800 Km^2, respectively. The 'pairwise' connectivity output estimated the potential resistance of current flowing (dispersal probability) in the landscape between the PAs (nodes) (Table 2.1). The modelled habitat linkages were used to identify connectivity bottlenecks in the landscape (Fig. 2.9). All the presence points were situated on the high connectivity areas apart from one individual which ventured

into the city of Mathura, returned back to the nearest habitat patches afterwards (Bharatpur, Fig. 2.8). In the absence of suitable habitats in the vicinity, the current flow was feeble and directionless.

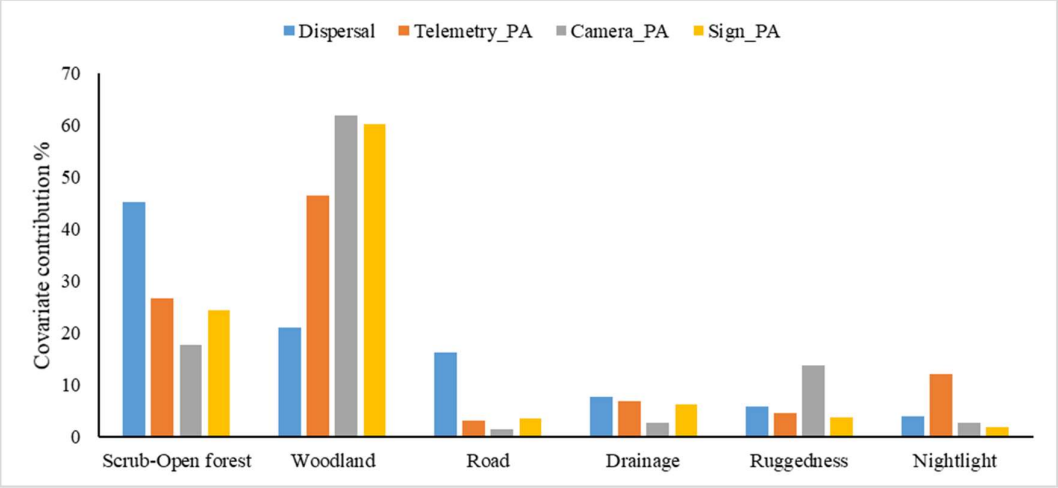
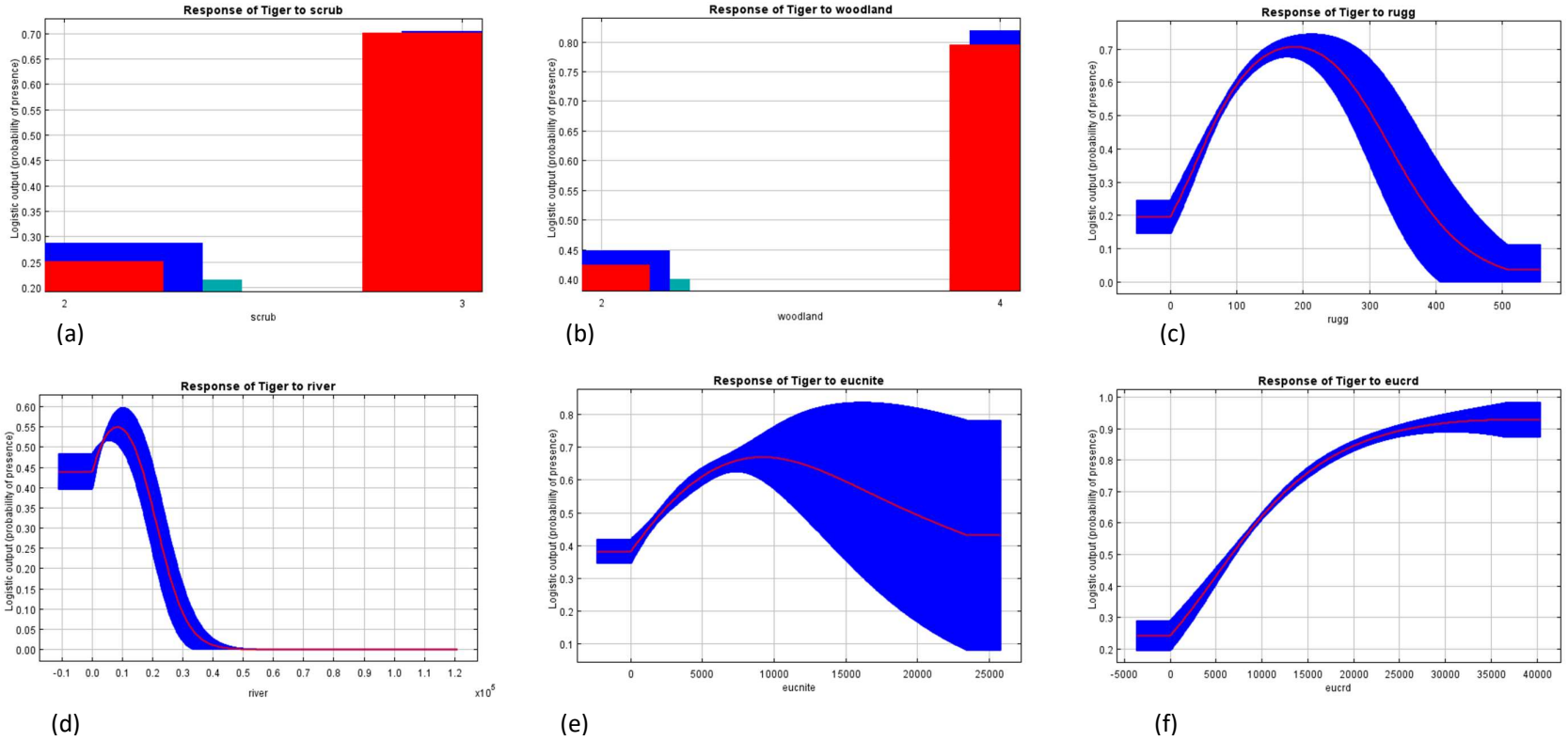


Figure 2.2: *Based on Jackknife estimates, percent contribution of different covariates for modelling tiger habitat suitability in the dry forest landscape of western India.*

The ravines (intricate gully network) of Chambal & its tributaries harbour rich biodiversity & act as dispersal corridors for the large carnivore in the semi-arid landscapes of western India. However, the rapid expansion of agriculture, developmental projects, and sand mining activities are destroying ravine habitats.

Table 2.1. Isolation by resistance (IBR) matrix between nodes generated by CIRCUITSCAPE. *Node names: 1: Ranhthambore TR, 2: Datia FD, 3: Shergarh WLS, 4: Jaisamand WLS, 5: Sitamata WLS, 6: Ramsagar WLS,7: Bandh Baretha WLS, 8: Kuno-Palpur NP, 9: Madhav NP, 10: Gandhi Sagar WLS, 11: Ramgarh Visdhari WLS, 12: Mukundara Hills TR, 13: Bhainsrodgarh WLS, 14: Bassi WLS, 15: Sariska TR, 16: Tadgarh Raoli WLS, 17: Kumbhalgarh WLS, 18: Phulwari ki nal WLS*

Nodes	***1***	***2***	***3***	***4***	***5***	***6***	***7***	***8***	***9***	***10***	***11***	***12***	***13***	***14***	***15***	***16***	***17***	***18***
1	0.00	2.44	1.97	3.92	3.14	1.53	1.10	0.51	1.29	1.53	0.10	1.14	1.46	2.01	1.70	2.55	3.03	4.65
2		0.00	4.09	6.54	5.77	2.84	2.85	2.51	2.43	4.15	3.86	3.73	4.13	4.69	3.78	5.13	5.63	7.27
3			0.00	4.92	4.05	3.56	3.21	2.25	2.63	2.18	2.45	1.46	2.25	2.97	3.53	3.74	4.15	5.70
4				0.00	2.06	5.81	5.36	4.70	5.26	3.25	3.90	3.32	3.24	3.10	5.21	2.84	2.30	2.15
5					0.00	5.06	4.62	3.93	4.47	2.24	3.10	2.40	2.27	2.25	4.53	2.76	2.64	3.38
6						0.00	1.28	1.86	2.26	3.48	3.13	3.07	3.45	3.98	2.72	4.36	4.88	6.53
7							0.00	1.54	2.07	3.07	2.70	2.67	3.03	3.54	2.05	3.89	4.42	6.08
8								0.00	1.15	2.30	1.96	1.87	2.28	2.84	2.20	3.31	3.81	5.44
9									0.00	2.82	2.56	2.37	2.81	3.38	2.80	3.89	4.37	5.99
10										0.00	1.49	0.45	0.26	1.19	3.12	2.37	2.67	4.09
11											0.00	1.11	1.36	1.90	2.75	2.60	3.05	4.65
12												0.00	0.13	1.22	2.78	2.28	2.63	4.13
13													0.00	1.11	3.06	2.31	2.62	4.07
14														0.00	3.48	2.19	2.46	3.92
15															0.00	3.57	4.16	5.89
16																0.00	0.16	3.19
17																	0.00	2.19
18																		0.00



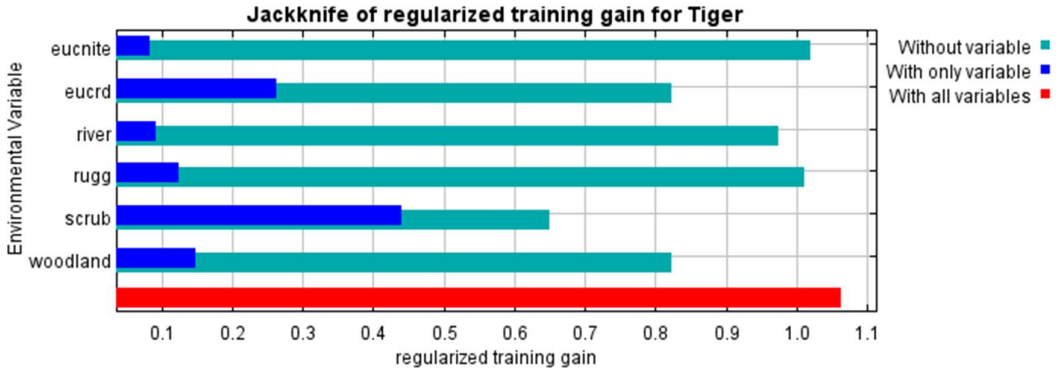
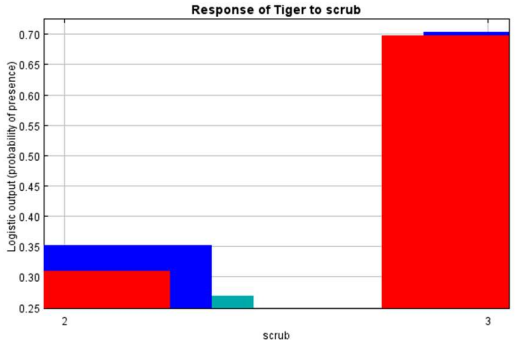
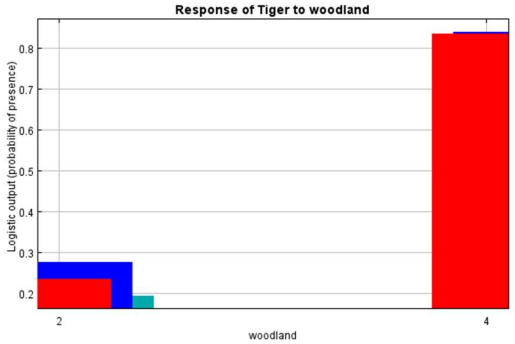


Figure 2.3: (a to f) *Response curve of independent covariates derived from MaxEnt (Dispersal model) while keeping all other variables at their average sample value; (g) Relative contribution of covariates.*

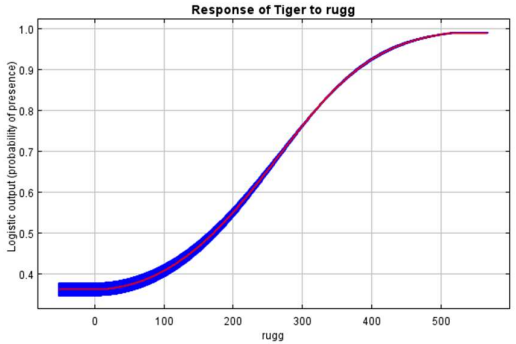
(eunite: Euclidean distance from nightlights, eurd: Euclidean distance from road, river: Euclidean distance from drainage, rugg: Ruggedness, scrub: Scrubland and open forest habitats, woodland: moderately dense and dense forest habitats)



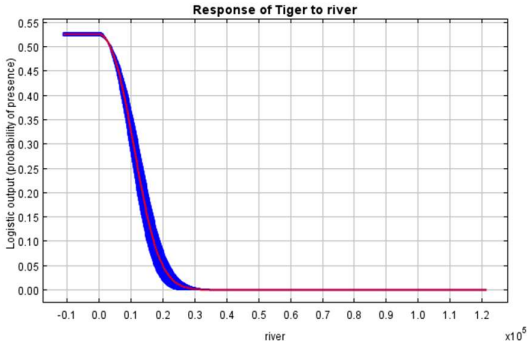
(a)



(b)



(c)



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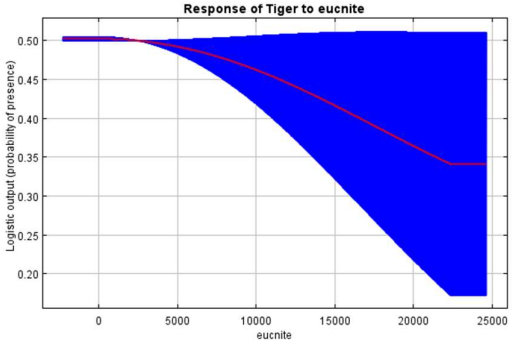
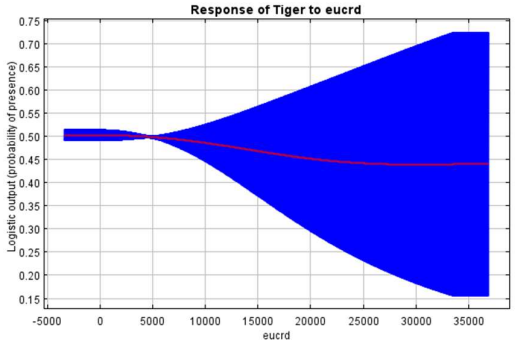


(e)



(f)

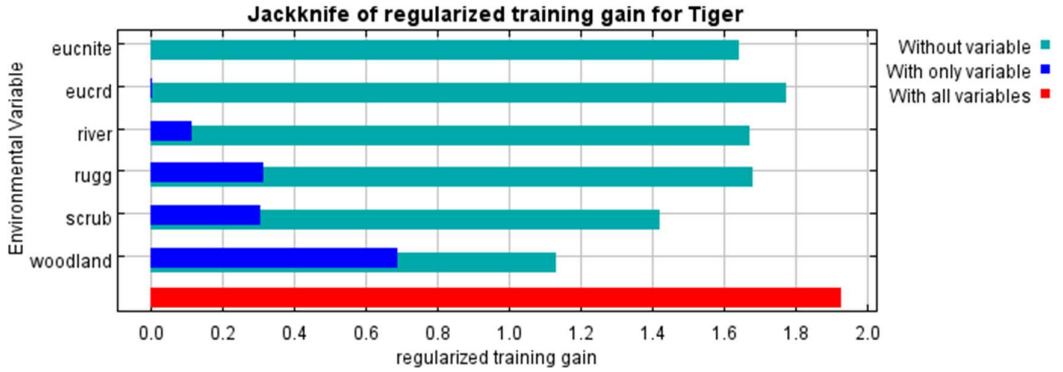
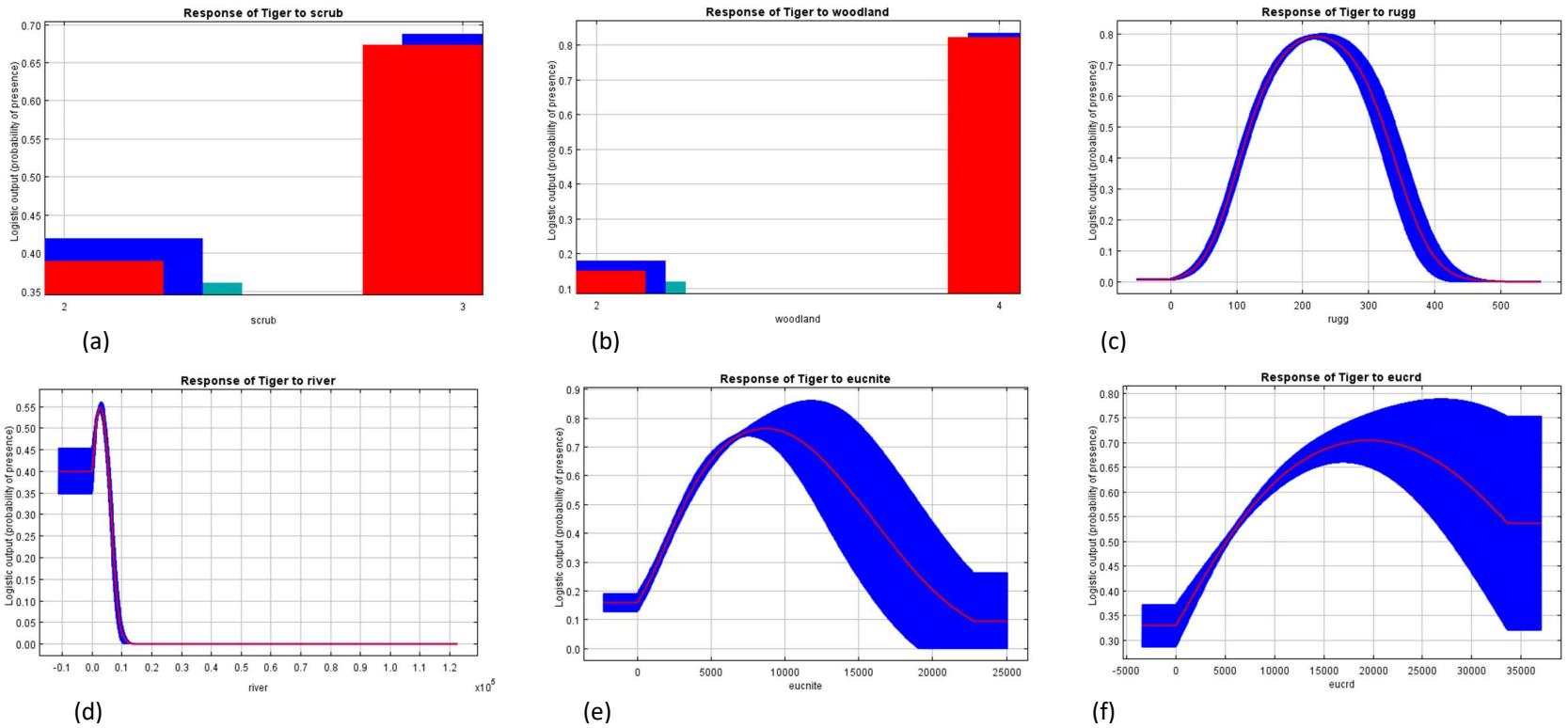


Figure 2.4: (a to f) *Response curve of independent covariates derived from MaxEnt (PA model 1- telemetry points) while keeping all other variables at their average sample value; (g) Relative contribution of covariates.*

(eunite: Euclidean distance from nightlights, eurd: Euclidean distance from road, river: Euclidean distance from drainage, rugg: Ruggedness, scrub: Scrubland and open forest habitats, woodland: moderately dense and dense forest habitats)



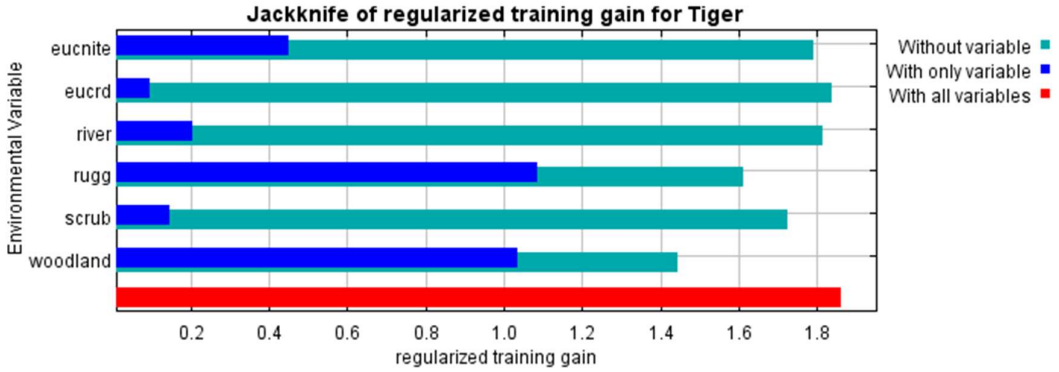
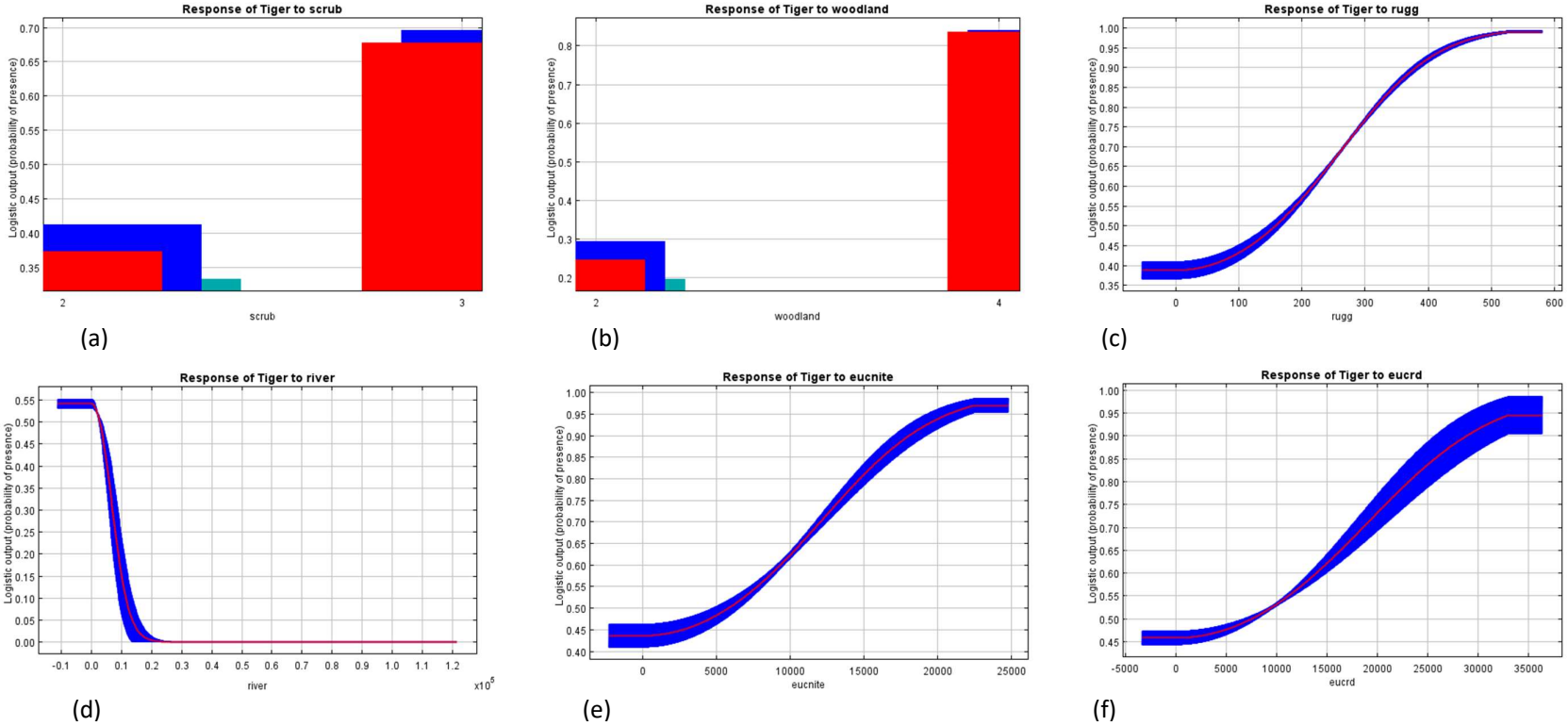


Figure 2.5: (a to f) *Response curve of independent covariates derived from MaxEnt (PA model 2 – camera trap points) while keeping all other variables at their average sample value; (g) Relative contribution of covariates.*

(eunite: Euclidean distance from nightlights, eurd: Euclidean distance from road, river: Euclidean distance from drainage, rugg: Ruggedness, scrub: Scrubland and open forest habitats, woodland: moderately dense and dense forest habitats)



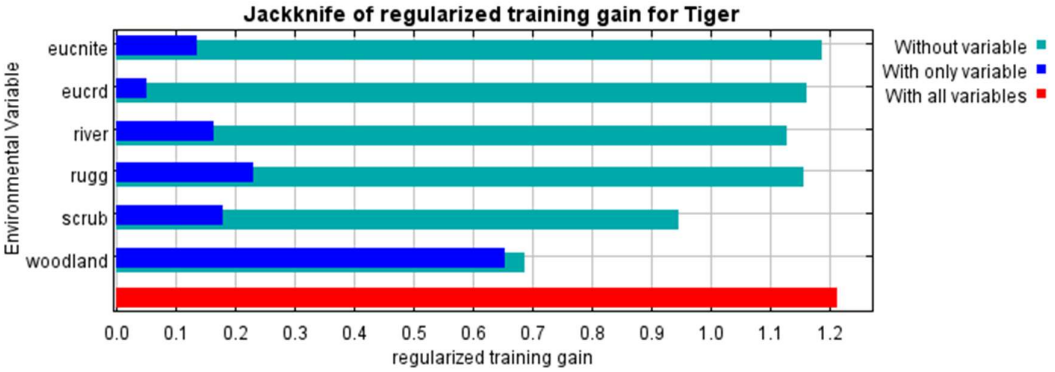
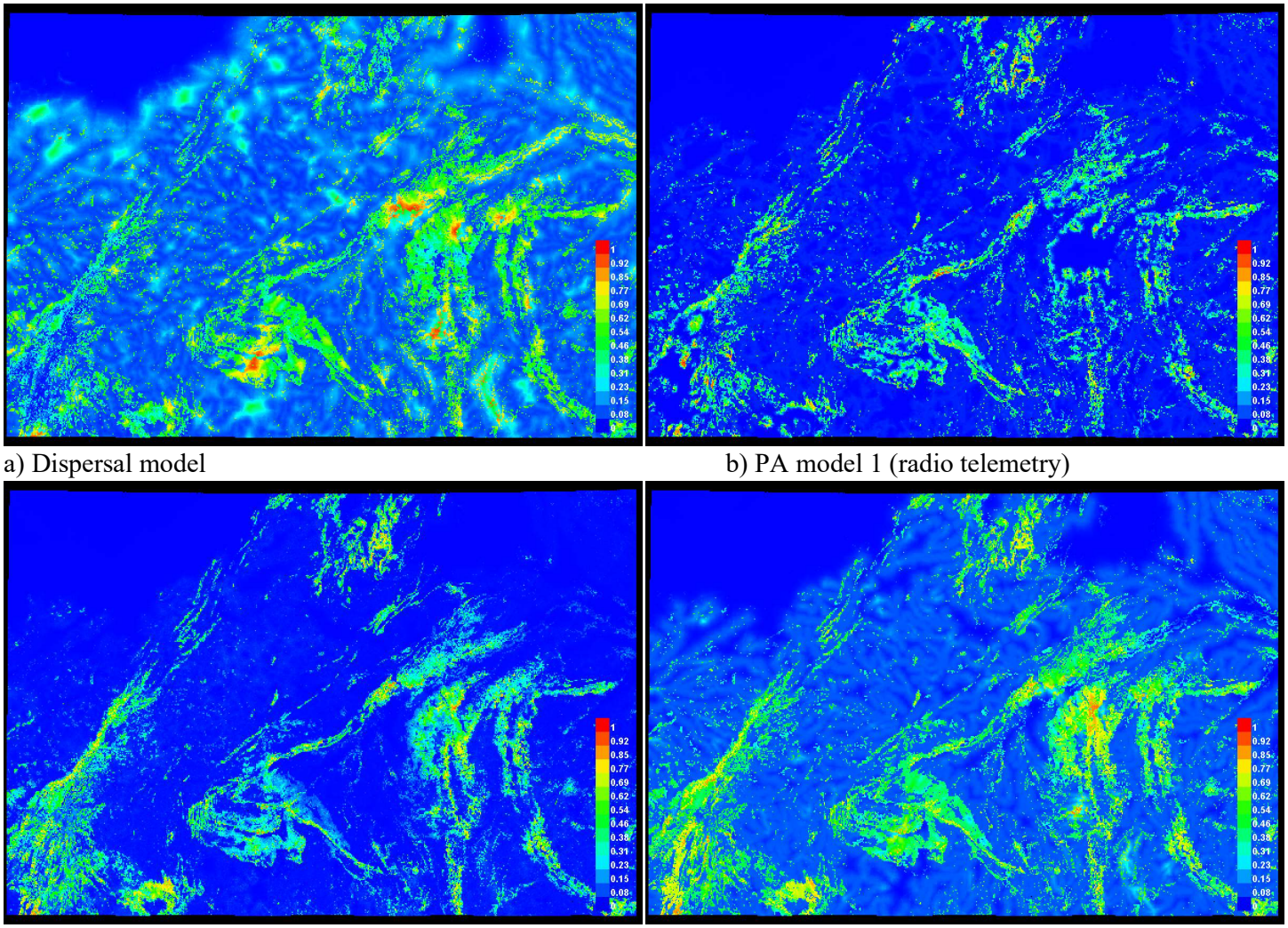


Figure 2.6: (a to f) *Response curve of independent covariates derived from MaxEnt (PA model 3 – sign survey points) while keeping all other variables at their average sample value; (g) Relative contribution of covariates.*

(eunite: Euclidean distance from nightlights, eurd: Euclidean distance from road, river: Euclidean distance from drainage, rugg: Ruggedness, scrub: Scrubland and open forest habitats, woodland: moderately dense and dense forest habitats)



a) Dispersal model b) PA model 1 (radio telemetry)

c) PA model 2 (camera trapping) d) PA model 3 (sign survey)

Figure 2.7: *The map showing probability of tiger usage (permeability to movement) derived from MaxEnt output using dispersal model, and PA models.*

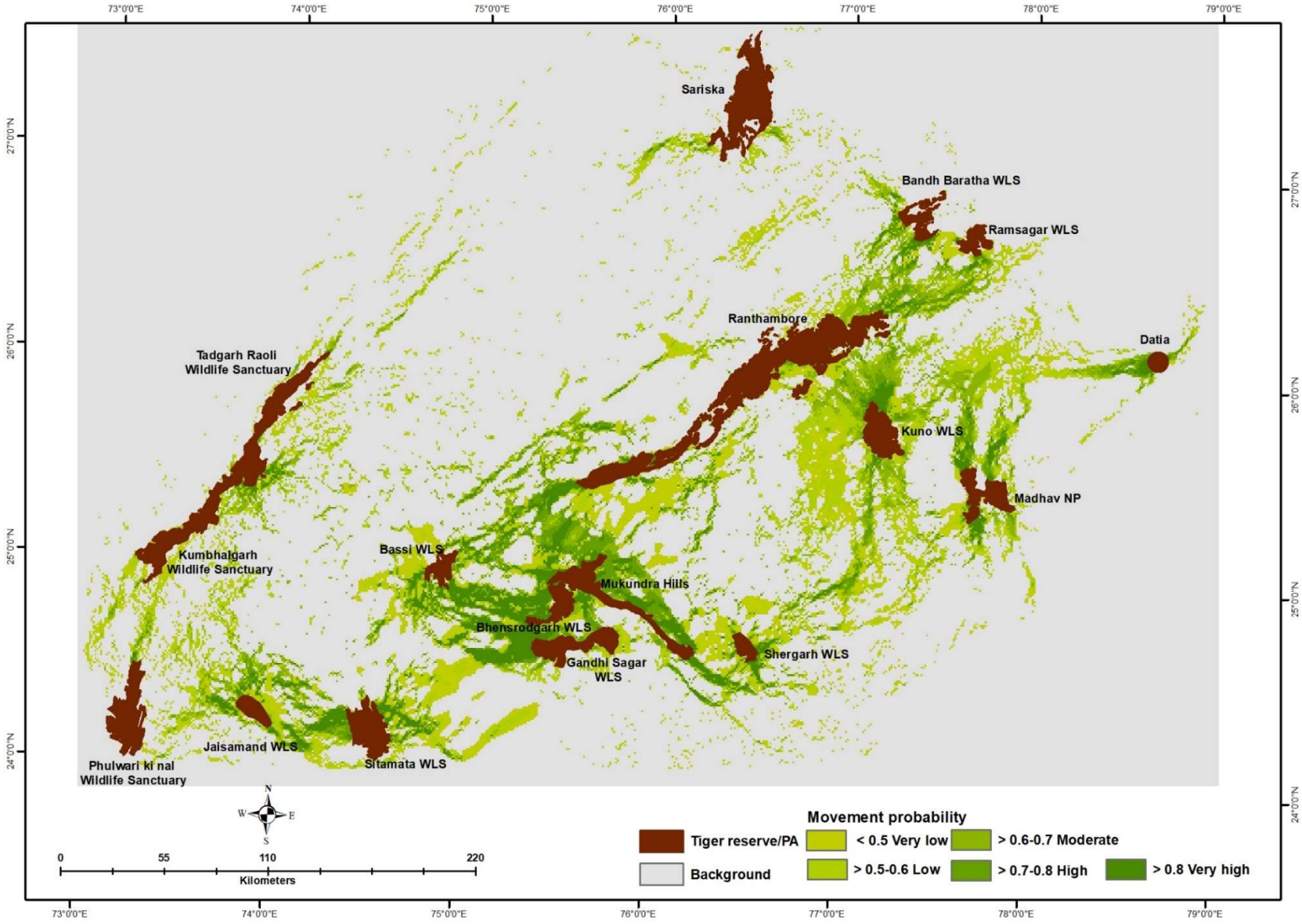


Figure 2.8: *CIRCUITSCAPE output map depicting potential dispersal linkages in the dry forest habitats of western India.*

4. Discussion

Conservation investments have protected India's tiger populations from imminent threats inside the PAs and contributed to substantial increase in tiger number over the years (Jhala et al. 2019). Yet, the tiger habitats outside the PAs are getting degraded and converted to human land use, limiting the dispersal in the landscape. Therefore, identifying potential tiger dispersal routes and understanding factors influencing dispersal are essential to plan future recovery of tigers.

Our results highlighted the importance of scrubland-open forest habitats to maintain permeability for tiger dispersal in the dry forest habitats of western India. These habitats are under immense anthropogenic pressures (grazing, resource dependency, burning), and often get converted to industry, plantation and agricultural land use to bolster local economy (Bhardwaj et al. 2011, Rawat and Adhikari 2015). The ravines of the Chambal and its tributaries comprised of a majority of tiger permeable areas in the landscape (Fig. 2.7). Due to low economic gain (unproductive for agriculture), inaccessibility, and notoriety, these ravines are considered as 'wastelands' (Wasteland Atlas of India 2019). Reclamation programs to convert these ravines into arable lands and plantation are destructing this wildlife haven. In the absence of field data to substantiate the importance of protecting these habitats for tiger conservation, the majority of conservation funds/efforts were invested on tiger strongholds. Consequently, the scrubland-open forest habitats remain ignored during policymaking.

Proximity to roads, which acts as barriers for dispersal (Proctor et al. 2005), were major deterrent for tigers in the landscape. Drainage systems consist of river, rivulets, and seasonal streams facilitated tiger dispersal in the landscape. All the dispersing individuals

in our study used these drainage network and associated habitats while dispersing through human dominated landscapes (Fig. 2.7). The drainage in the dry forest habitats are the crucial source of water and also provide refuge to the dispersing individuals. The highly rugged terrain in our study area were one of the most inaccessible areas as well, therefore spared from expansion of human land use and mostly protected under PA network. The moderately rugged terrain, therefore, available for the dispersing animals and facilitated dispersal.

From our observations, we did not find any evidence of tigers using large tract of agricultural fields devoid of suitable habitat fragments (ravines, hillocks, woodlands-degraded forest fragment). Agricultural lands with standing crop (mostly mustard crop and sugarcane) might be suitable for tiger dispersal, but cannot act as potential corridors without the presence of suitable patches in the vicinity. A similar observation was reported from Terai Arc Landscape, where tigers avoided agricultural fields during dispersal (Smith 1993). However, these findings may vary from landscape to landscape subject to the availability of preferred habitats and human density in the landscape.

In the absence of field-based tiger dispersal data, expert opinion, genetic data, and detection data from the protected areas were used for preparing the resistance surface for tiger dispersal (Areendran et al. 2012, Rathore et al. 2012, Joshi et al. 2013, Dutta et al. 2016, Thatte et al. 2018, but see Krishnamurthy et al. 2018). The resistance surface modelled based on the 'PA models' was different, and a subset of the resistance surface modelled from 'dispersal model' (Fig. 2.7). It seems likely as dispersing tiger individuals often move through degraded habitats in the human-dominated landscape, mostly at night, while resident tigers required inviolate areas to establish their territory (Smith

1993). Therefore, caution should be taken when presence points are borrowed only from resident individuals for modelling of dispersal corridors in the dry forest habitats.

Our findings identified the existence of connectivity and the potential areas permeable for tiger dispersal. However, the future of these potential habitat corridors is uncertain without law enforcement and effective management regime. Creating inviolate space to facilitate dispersal in the densely populated landscapes is an expensive and an irrational goal to achieve. Therefore, protecting the existing PAs along with maintaining connectivity in the landscape to facilitate gene exchange between sub-populations should be the desired conservation strategy. Strategies to conserve large carnivores in a human-dominated landscape involves major arguments over land sparing (Packer et al. 2013) versus land sharing (Carter and Linnell 2016). The land-sparing model ascribes the protection of inviolate area for large carnivores (devoid of humans), while the coexistence model emphasises on sharing lands between large carnivores and human in order to conserve them (Chapron et al. 2014). We have observed, in the absence of continuous habitat patches, tigers used the multiple-use landscapes while dispersing from Ranthambhore to other PAs, especially in the north-western and south-eastern part of the landscape. Therefore, dispersal friendly land use pattern (agro-forestry, and plantation) should be promoted in the CIRCUITSCAPE delineated priority areas (land sharing approach). At the same time, the existing PAs played a pivotal role to harbour the extant tiger population in the dry forest habitats (Jhala et al. 2020, in press). Therefore, restoring the prey base and creation of inviolate space by implementing Government incentivised voluntary village relocation program to eliminate human disturbances from the tiger bearing forests will secure the extant tiger populations (land sparing model).

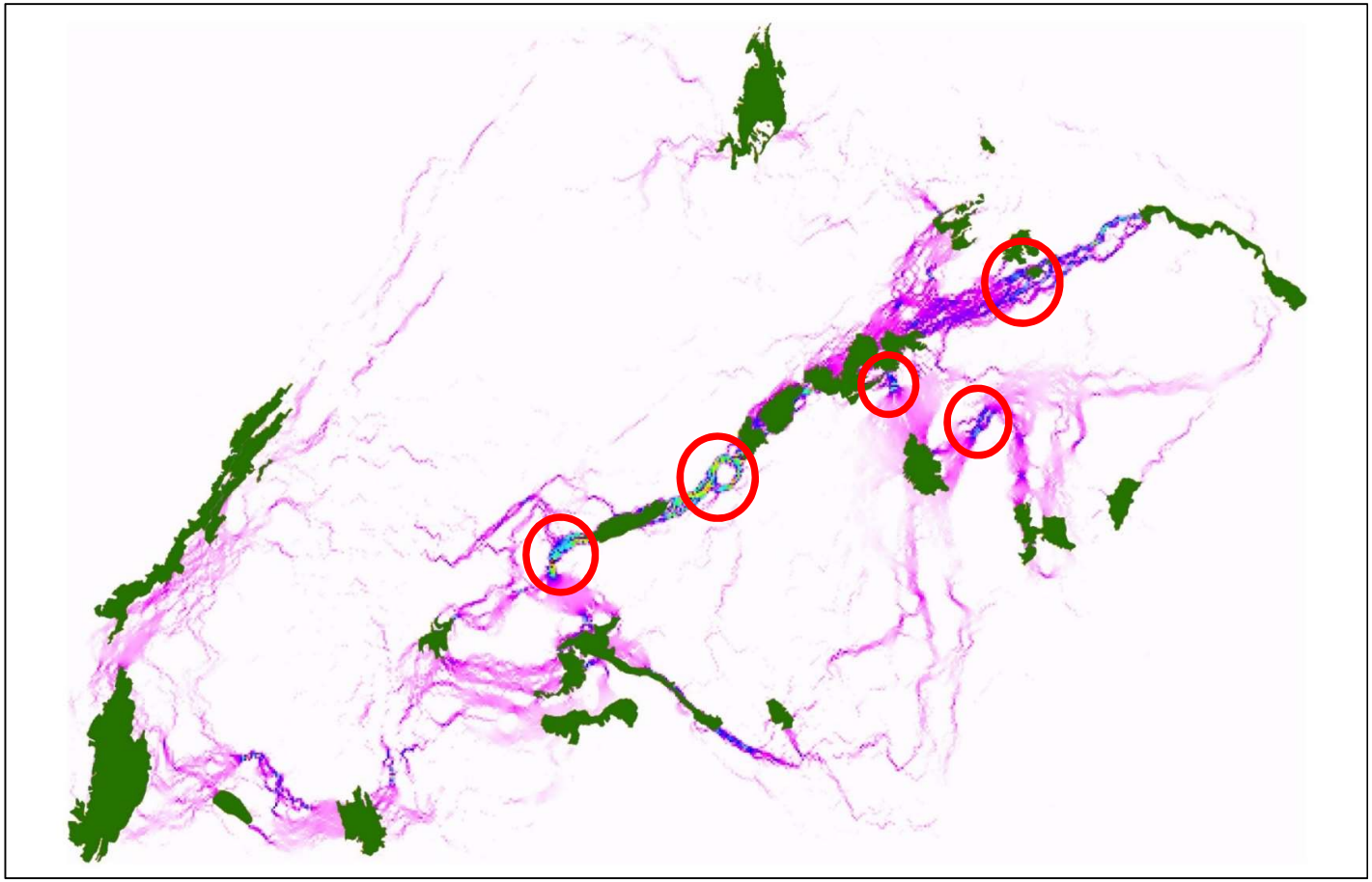


Figure 2.9: *Pinch point analysis showing bottlenecks/pinch points (marked here with red circles) in the landscape which need immediate conservation attention.*

Living on the edge: Evaluating the co-occurrence pattern of a high density leopard population in the tiger bearing forest of semi-arid landscape

Leopards in the tiger land: Leopards have adopted to take refuge or hide their kills on tree to avoid antagonistic encounters with tigers (the dominant predator).

1. INTRODUCTION

Interspecific competition plays a pivotal role in shaping and structuring species distribution, population, and behaviour of the competing species (Berger and Gese 2007). The competition can be resource-driven (exploitative competition, Creel and Creel 1996), or in the form of antagonistic interactions (interference competition, Fedriani et al. 1999). Outcomes of the competitive interactions between the dominant and subordinate predators are often asymmetric; ranges from spatial avoidance to interspecific killing and in extreme cases population decline of the subordinate competitor (Palomares and Caro 1999, Caro and Stoner 2003). However, in the habitats exposed to anthropogenic pressure, carnivores rarely reach their ecologically functional densities due to resource depletion and persecution (Kuijper et al. 2016). Thus, human disturbance and availability of inviolate space influence the behaviour and directs the magnitude of interaction between competing carnivores. Therefore, co-occurrence in small isolated patches is likely to escalate the intensity of interspecific competition which can affect the demography and behaviour of subordinate carnivores (Kumar et al. 2019). To avoid the negative consequences of interspecific competition, the subordinate species may adopt strategies to reduce niche overlap with the dominant competitor.

The leopard (*Panthera pardus fusca*, Linnaeus 1758) and tiger (*Panthera tigris tigris*, Linnaeus 1758) co-occur in most of their range in the Indian subcontinent (Nowell and Jackson 1996). Tiger being the dominant predator possesses competitive advantage over the leopard through intraguild predation, spatial exclusion, and kleptoparasitism (McDougal 1988). Thus, leopards are believed to avoid areas frequented by tigers to reduce agonistic interactions (Schaller 1967). However, spatial niche segregation between sympatric large carnivores occurs at large spatial scales. In India, the fast

growing human population restricts the range of large carnivores into small habitat fragments. In the semi-arid landscape of western India, tiger and leopard share spaces in protected areas (hereafter, PAs) which are small and surrounded by human land uses. The co-occurrence patterns in these fragmented habitats is likely governed by tiger abundance, prey availability, escape cover for leopards, and tolerance towards human disturbance. High level of dietary and temporal overlaps between tiger and leopards were recorded from across their overlapping ranges (e.g. Karanth and Sunquist 1995, Ramesh et al. 2009, Mondal et al. 2012a, b). These overlaps are likely to result in intense interspecific competition, especially when space and food are a limiting factor. Therefore, understanding the co-occurrence mechanism of these large carnivores within insular habitat patches is crucial to forming apt conservation strategies where the umbrella role of the dominant predator the tiger is harnessed to its maximum potential.

Radio telemetry provides fine-scale data on interspecific competition, especially on species behavioural response and spatiotemporal separation under the competitive pressure (Seidensticker 1976). However, radio telemetry studies are limited by their sample size (number of individuals), largely due to few permits for capture and collaring. To infer the competitive or coexisting mechanism operating at the population-level requires large (representative) number of animals tagged with telemeter, which is costly and often logistically unfeasible (Hebblewhite and Haydon 2010). In contrast, camera traps are easy to use and cost-effective tool to obtain authentic data on multiple species presence, intensity of spatial use, as well as temporal activity, all obtained from a single survey (O'Connell et al. 2010). Systematic camera trap sampling can generate information at the population scale to understand the mechanism of co-occurrence (Burton et al. 2015).

In the present study, we estimated the density of leopards (and tigers, Chapter 1) using camera trap based spatially explicit capture-recapture technique. From the same camera trap data, we examined the mechanism of co-occurrence between tiger and leopard with respect to their spatio-temporal behaviour. Furthermore, we tried to understand how anthropogenic interference influence the co-occurrence patterns where both the predators occurred at high density. Our results showed that the density of leopards remained constant over the years. However, the intensity of leopards' space use changed in response to tiger distribution and human disturbance.

2. Methods

2.1 Study area

The study was conducted in the core area of Ranthambhore Tiger Reserve (hereafter Ranthambhore, $25^0$41' N to $26^0$22' N and $76^0$16' E to $77^0$14' E) from 2012 to 2014. Ranthambhore is situated in the semi-arid zone of western India at the junction of two ancient mountain ranges, the Aravalli and the Vindhya. Ranthambhore experiences hot summers (March- June/July, average temperature 45˚C), dry winter (October-February, minimum average temperature 5˚C), and hot, humid monsoon (July/August- September, average temperature 30-35˚C).

Dry deciduous forests of Ranthambhore are dominated with *Anogeissus pendula* in association with *Acacia*, *Butea, Capparis*, *Zizyphus* and *Prosopis* species (5B/C_2-Northern Tropical Dry Deciduous forests. 6B/DS1-*Zizyphus scrub*, DS1-Dry deciduous scrub and 5/DS4-Dry Grasslands (Champion & Seth 1968). Ranthambhore comprises of steep hills, gentle slopes, plateaus, and narrow valleys dotted with shallow man-made

perennial lakes. Plateau tops are mostly dominated with open forest-grassland complexes (sparse canopy cover) while valleys are dominated with woodlands (Fig. 4.1). The peripheral habitats were exposed to biotic pressures from the local villages. Cattle grazing, fuelwood collection and illegal timber extraction (of *Anogeissus pendula*) have degraded the forests into thorny scrub. Most of these peripheral habitats are infested with invasive weeds (*Prosopis juliflora*, *Cassia tora, Cascuta* sp etc.). Areas 2-3 km away from the boundary of the Reserve were free from human disturbances. These inviolate areas are frequently used by tigers (*Panthera tigris*). The rugged terrain, especially the cliffs and slopes provide ample crevices, which are often inhabited by sloth bear (*Melursus ursinus*), leopards (*Panthera pardus*), and striped hyenas (*Hyaena hyaena*).

The mesopredator guild comprised of golden jackal (*Canis aureus*), caracal (*Caracal caracal*), fishing cat (*Prionailurus viverrinus*), jungle cat (*Felis chaus*, Schreber), desert cat (*Felis silvistris*), and honey badger (*Mellivora capensis*). Small carnivores present in the study area was rusty-spotted cat (*Prionailurus rubuginosa*), Indian fox (*Vulpes bengalensis*), common palm civet (*Paradoxurus hermaphorditus*), small Indian civet (*Viverricula indica*), Indian gray mongoose (*Herpestes edwardsii*), small Indian mongoose (*Herpestes auropunctatus*), and ruddy mongoose (*Herpestes smithi*). The ungulate prey comprised of chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelus*), chinkara (*Gazella bennetti*), and wild pig (*Sus scrofa*). Common langur (*Semnopithecus entellus*) and rhesus macaque (*Macaca mulata*) are the primate species present in the study area.

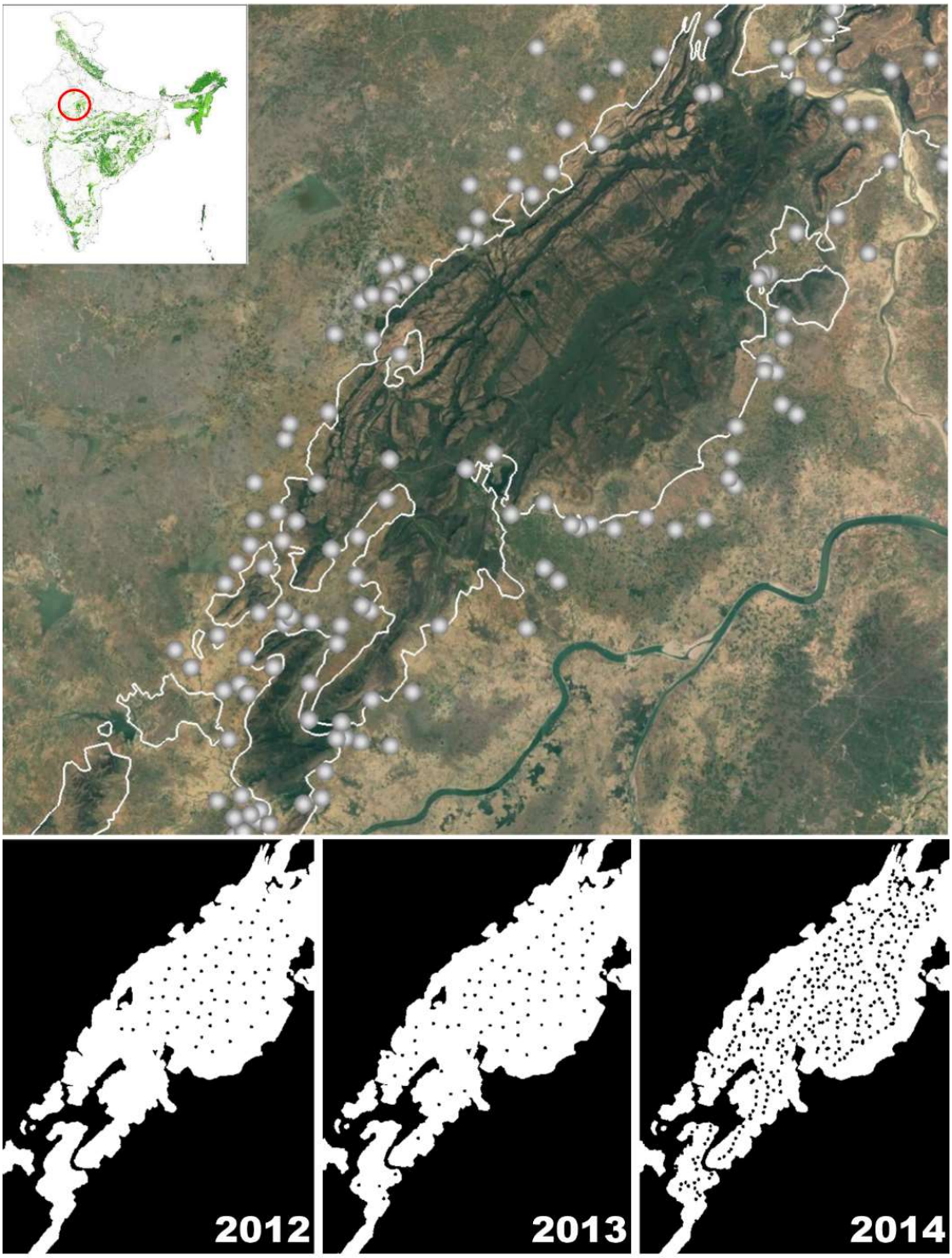


Figure 4.1: *Top: Location of Ranthambhore Tiger Reserve (core), the light green patches inside the reserve represent plateau tops with open forest-grassland habitats while the dark green depicting the woodland (Anogeissus pendula dominated patches). Villages situated immediate next to the Reserve are depicted with grey circle on the map; Bottom: Camera trapping coverage from 2012 to 2014. Inset: Location of the study area in India.*

2.2 Camera trapping

The study area was sampled using a systematic grid-based camera trapping survey (4 km^2 2012 and 2013, and 2 km^2 in 2014) for a duration of 45 to 51 days each year. The sampling coverage has increased from 2012 to subsequent years, while camera trap intensity was highest in 2014 (Table 4.1). A pair of camera traps were placed in strategic locations of the grids to maximise the detection probability of the target species (for details, please see Sadhu et al. 2017). Each camera was given unique IDs, and GPS location of the camera trap stations was recorded. Cameras were programmed to take photographs after every 5 to 15 seconds (depending on the use of white flash). Each photo captured leopard was manually identified to individual by comparing their rosette patterns and given a unique identity numbers (e.g. L1, L2, and so on).

2.3 Leopard density estimates

Leopard density was estimated using a likelihood-based spatially explicit capture-recapture (SECR, Borchers and Efford 2008) in package 'secr' on R platform (Efford 2020) (Table 4.1). SECR model is an extension of classical capture-recapture models where spatial capture locations were considered while estimating the population. The modelling framework of SECR comprised of two models, the distribution sub-model and the detection sub-model. The spatial point process model (the distribution sub-model) assumes the animal activity centres (or, home range centres) are distributed in the model space following prior distribution (e.g., Poisson distribution). The detection sub-model ($g(x)$) fits a detection function which started decreasing with the increasing distance from the animal's activity centre. The spatial scale of this detection function is parameterized by sigma (σ), which roughly represent the home range radius of the animal. A spatial capture history matrix and a camera trap operational matrix (1- working, 0- not working)

were prepared and used in SECR. A habitat mask was used to exclude large human habitations and water bodies from the model space. However, we did not remove agricultural fields adjacent to the reserve as leopards use these human land-use areas for foraging (Odden et al. 2014). Due to very few spatial captures of most of the individuals, we used the model with no heterogeneity in g_0 and σ to estimate leopard density. No cub/juvenile were photo-captured during the camera trapping sampling; however, lactating females were observed on a few occasions.

2.4 Spatial interaction between tiger and leopard

In areas used by sympatric carnivores, competitive pressure often resulted in spatial segregation (Fedriani et al. 1999). Therefore, we used the two-species occupancy model to assess the spatial co-occurrence pattern of tiger and leopard from the camera trap detections (MacKenzie et al., 2004). Input data for this model was the same as the single-species single-season occupancy model except for the detection histories of both the species were entered into a stacked manner (one below the other). For each year, spatial detection (1) non-detection (0) histories were prepared for each camera trap sites for both the species. The two-species approach estimates the species' conditional probability of occurrence given the other species is present (species interaction factor (φ) = $\psi_{\text{Tiger Leopard}}$ / $\psi_{\text{Tiger}} \times \psi_{\text{Leopard}}$). The parameters ψ_{Tiger} and ψ_{Leopard} are the probability that the area is occupied by tiger and leopard, respectively. The detection probabilities are computed for two different scenarios, a) the probability of detecting one species when both are present, ii) the probability of detecting one species when the other one is absent. The values of $\varphi < 1.0$ indicates the competing species avoids each other, while >1.0 indicates attraction.

2.5 Spatiotemporal separations between tiger and leopard

Sympatric large carnivores tend to avoid each other by minimising spatial overlap or adopting temporal separation in their overlapping ranges. Therefore, to understand the pattern of co-occurrence, both temporal and spatial separation need to be taken into consideration. We used the camera trap photographs to assess the spatiotemporal interactions of tiger and leopard in Ranthambhore for all three sampling sessions. The number of photographs for tiger and leopard was divided by the camera trap operational days to get the site use intensity (in terms of photo-capture rates, PCR) for each camera traps. In the case of multiple triggers, we have counted only the first capture for this analysis. The intensity values were subsequently plotted on GIS domain to get the spatial distribution of the PCR. The temporal activity of tiger and leopard were recorded from the camera trap photo-captures. The *EXIF* information of each independent photo-capture was extracted using ExifPro software (http://exifpro.com) and imported into program Oriana (*ver.* 4.0, Kovach 2011) to analyse the temporal activity pattern. To understand the mechanism of spatiotemporal separation in the overlapping sites, we calculated the time interval between a tiger and subsequent leopard detection. We assume that being the subordinate competitor, the leopard will avoid using the same area immediately after tiger detections. Furthermore, we have plotted the range of leopard capture intervals in a span of 24 hours (1 day) to see the immediate temporal avoidance by leopards when tigers were detected. Finally, we have plotted the leopard PCR (photo-capture rate) values against tiger PCR and human impact PCR to find out their influence on leopard distribution. For human impact, we considered the photo-capture rates of local villagers (non-forest department and not involved in research team) and their livestock (buffalo, cows, camel, goats, and sheep) in the camera trap sites. In many instances, villagers and

domestic dogs were seen accompanying the livestock, therefore, considered as single human impact events.

3. Results

3.1 Leopard density estimates

We have identified 23, 19, and 51 individual leopards from the camera trap photographs over the sampling years (Table 4.1). Sex ratio (Female to male) varies from 0.75 to 1, the total number of lactating females were reported as 2, 0, and 5 for 2012, 2013, and 2014 respectively. The likelihood-based leopard population density estimates were estimated at 9.4 to 10.4 for the sampling years (Table 4.1). Detection probability at home range centre (g (0)) ranges from 0.004 to 0.016, while the movement parameter (σ) was estimated lowest in 2013 (0.86 km) and highest in 2012 (1.6 km).

3.2 Spatial interaction between tiger and leopard

The number of camera trap with tiger captures was more than the camera traps with leopard captures (Table 4.2). The number of overlapped sites (both the species detected) were ~58% in 2012, and reduced to 38% and 35% in 2013 and 2014 respectively. For all three years, leopard detection probabilities were lower in the sites where tigers were detected than the sites where tigers were not detected (Table 4.2). Species interaction factor was estimated close to 1 for all the sessions, which suggests co-occurrence between two species at the camera trap scale.

Table 4.1: Camera trapping details and SECR parameter estimates (model used - $\widehat{D}$ *~1, g0(.), σ(.)*) for leopards in Ranthambhore from 2012 to 2014.

Year	Camera trap polygon (km^2)	Distance between neighbouring camera traps (SE)	Trapping efforts (days)	M (t+1)	Male	Female	Unidentified	$\widehat{D}$ (SE) /100 km^2	g0 (SE)	σ (SE)
2011-12	223	1.2 (0.22) km	2660	23	12	9	1	9.4 (2.37)	0.004 (0.001)	1607.27 (229.47)
2013	464	1.76 (0.34) km	3876	19	9	9	2	10.44 (3.74)	0.016 (0.007)	868.38 (168.38)
2014	492	1.09 (0.18) km	8736	51	23	21	7	10.44 (1.54)	0.006 (0.001)	1284.01 (80.88)

SE: Standard error $\hat{D}$ *SECR: Density estimate from Maximum Likelihood based spatially explicit capture recapture*
$\hat{\sigma}$ *(Sigma): Spatial scale of detection function,* $\hat{g}_0$*: Magnitude (intercept) of detection function*

Table 4.2: Details of leopard and tiger photo-captures details and occupancy estimates for 2012, 2013, and 2014 in Ranthambhore.

Year	Species detection in camera traps (%)			Tiger-Leopard interaction factor* *Avoidance <1.0* *No pattern = 1.0* *Attraction >1.0*	Leopard detection probability	
	Leopard	Tiger	Both		tiger not detected	tiger detected
2012	61.67	93.33	58.33	0.966 (0.026)	0.072 (0.056)	0.058 (0.022)
2013	40.79	88.16	38.16	0.907 (0.068)	0.092 (0.028)	0.064 (0.019)
2014	49.31	86.18	35.48	0.87 (0.038)	0.138 (0.017)	0.073 (0.018)

**derived from likelihood based two-species interaction model (MacKenzie et al. 2004);*

3.3 Spatiotemporal separations between tiger and leopard

A total of 92, 65, and 243 leopard detections and 580, 347, 822 tiger detections were recorded from camera trapping survey in 2012, 2013, and 2014, respectively. Tiger photographs were obtained across the park, however, the intensity of detection increases away from the periphery (Fig. 4.2). The intensity of tiger detection changes over the years, which most likely affected the use intensity of leopards in those habitats (Fig. 4.2). Both species were found to be nocturnal with less number of day time detections (but see 2012 leopard activity, Fig. 4.2). Although the temporal activity of leopard and tiger overlapped, their activity peaks were asynchronous (Fig. 4.2). The activity peak of tigers was observed after dusk (~1900 hrs) to late evening (2100-2200 hrs) with a smaller peak around the dawn (0600 hrs). In contrast, leopards were most active after midnight to before the sunrise (Fig. 4.2). We have reported 186 events where a leopard photo-captured after the tiger on the same site, and in 25% times leopards photo-captured within 24 hours of tiger detections (Fig. 4.3). When using the same site within 24 hours, in 75% of the cases, we observed an interval of five hours or more between the tiger and successive leopard photo-captures (Fig. 4.3).

We found a total of 77 camera points with photographs of human activity. Most of the human activity events were contributed from 21 cameras situated in the north-western and southern part of the reserve. Leopard PCR was observed higher in areas with moderate human activity and moderate tiger detections (Fig. 4.4), while leopards were observed to avoid areas with high tiger usage and high human activity.

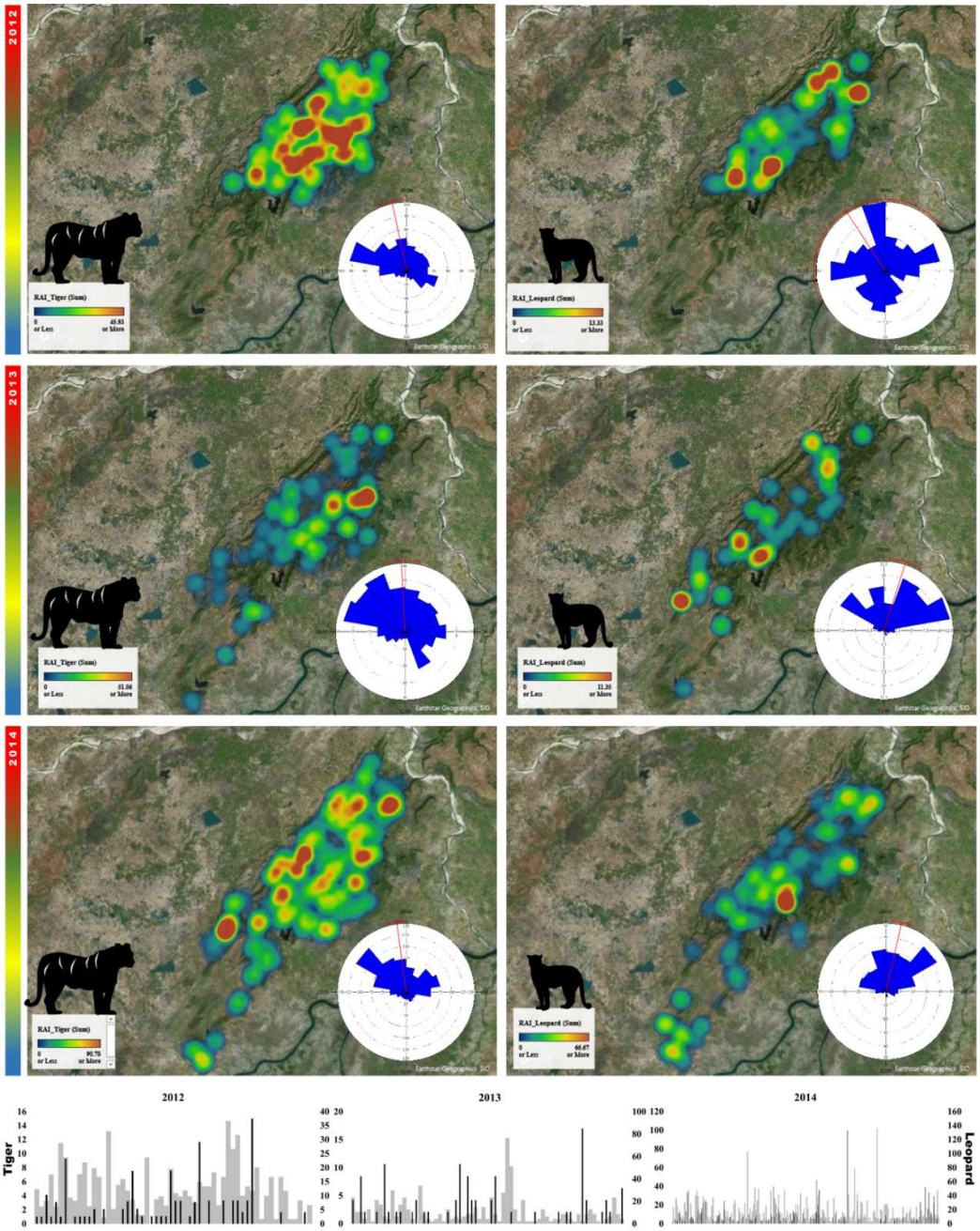


Figure 4.2: *Heat maps showing relative detection rates of tiger and leopards for all the survey years (2012 to 2014); warmer colour depicts higher detections. Temporal activities of tiger and leopard are depicted in the circular plots, the activity peaks for these sympatric carnivores were found mutually exclusive. Bar charts (at the bottom) depicting the capture frequency of tiger (thick grey bars) and leopard (black lines) in individual camera traps over the years.*

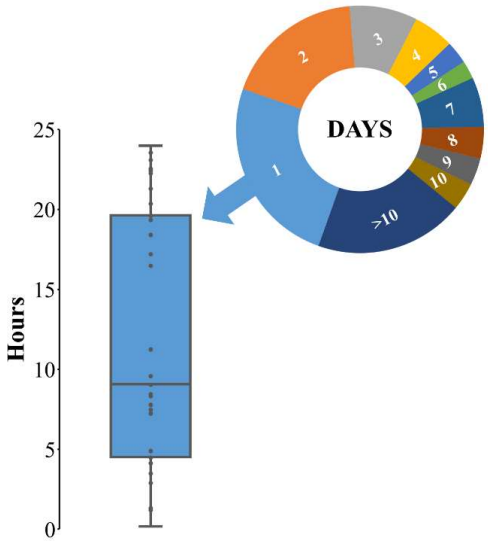


Figure 4.3: *The pie chart is showing the percent frequency of intervals (in days) between the tiger photo-capture and the successive leopard captures. The numbers within each colour classes in the pie chart depicting the number of days. The box-whisker plot is highlighting the range of capture intervals within one day (in hours).*

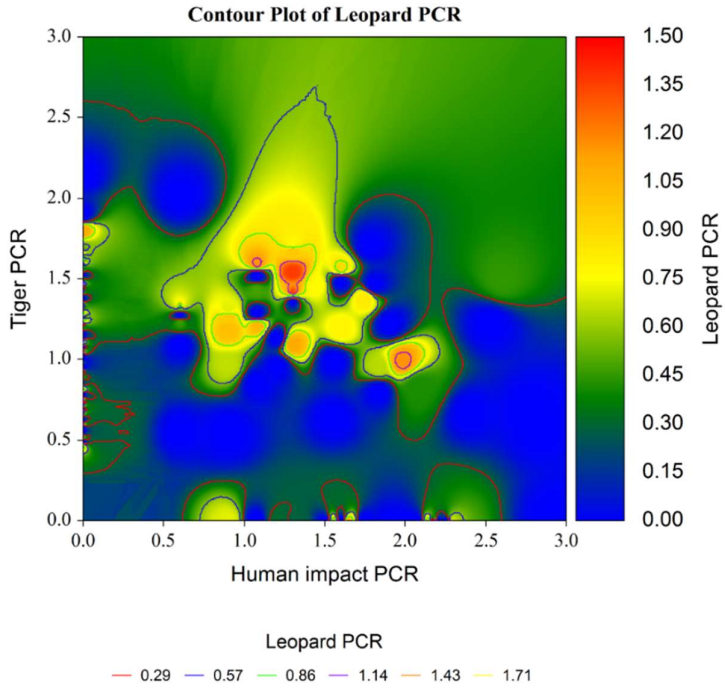


Figure 4.4: *The relationship between leopard photo-capture rate (PCR) with tiger PCR and human impact PCR depicted in the heat and contour map. The values of PCR were log-transformed for the analysis.*

4. Discussion

The leopard density estimated using maximum likelihood SECR models were constant over the years, 9-10 leopards per 100 km^2 (Table 4.1). The number of individual leopard photo-captured in camera traps was highest in 2014 and lowest in 2013. Its noteworthy to mention even with larger camera trap coverage, the number of leopard individuals were

less in 2013 than 2012. Also the number of recaptures was far less in 2013 compared to other years, resulting in a higher variance in the density estimate (Table 4.1). The leopard density of Ranthambhore was reported higher than most areas of the Central Indian Landscape (Mondal et al. 2012, Jhala et al. 2015, Kumar et al. 2019). The sex ratio of leopards was marginally male-biased (Table 4.1). The movement parameters (σ) known to vary between sexes as females restricted themselves in smaller areas compared to males (Kumar et al. 2019). However, due to less number of spatial recaptures of leopards throughout the sessions, we could not run heterogeneity models (as these complex models did not converge for our dataset). The less number of recaptures could be explained by the placement of the camera traps on large trails and mud roads which are frequently used by tigers. To avoid antagonistic encounters with tigers, leopards use smaller trails and take refuges on big trees, on the cliffs. In a few instances, we have photo-captured leopard individuals using narrow trails situated adjacent to the large animal trails/mud roads regularly used by tigers (Fig. 4.S1). The number of leopard photo-captures and recaptures per individuals increased substantially in 2014 when camera trap intensity was highest and more number of camera traps were placed on narrow trails.

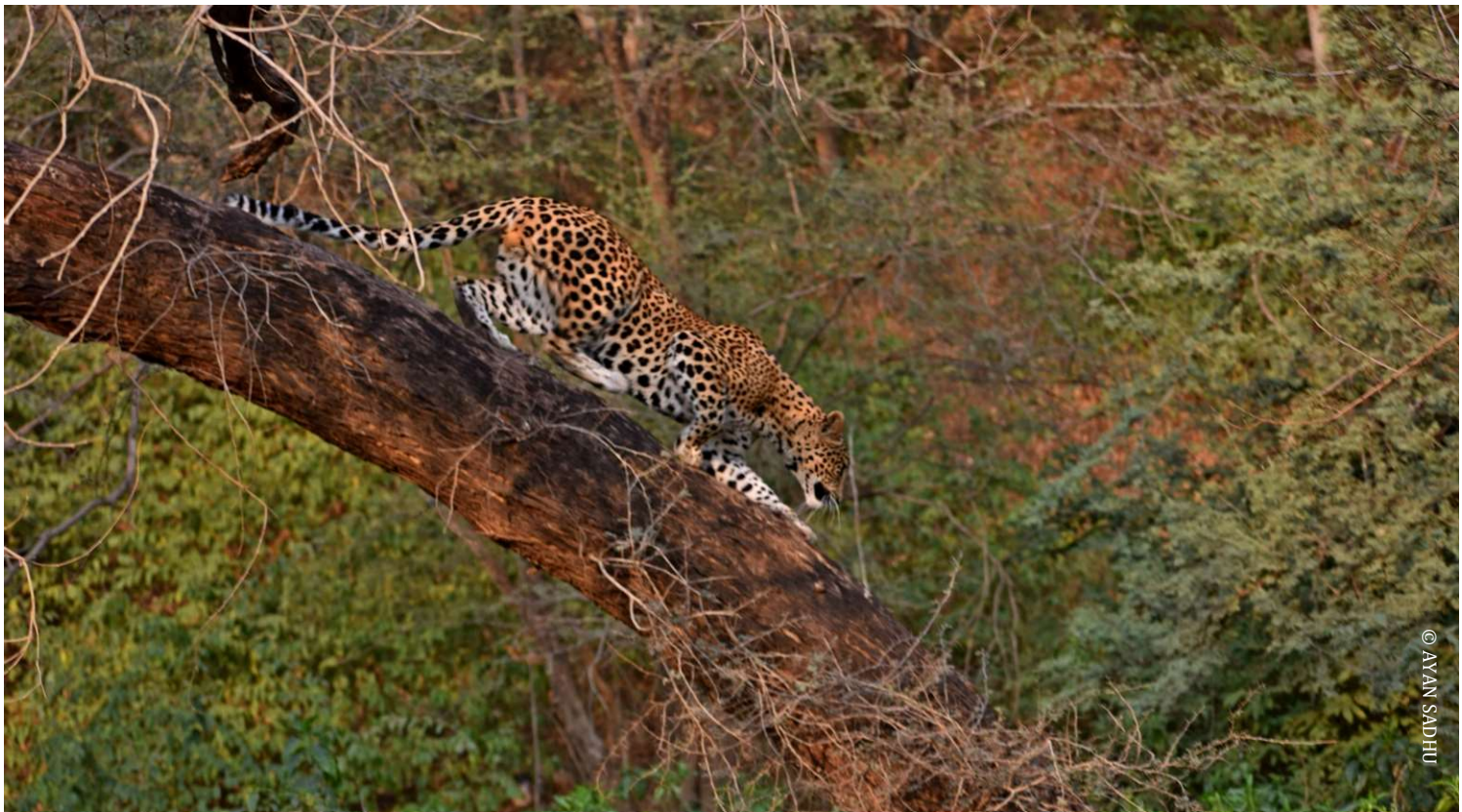
The presence of tigers influenced leopard's occupancy in Ranthambhore. The outcomes of the two-species occupancy (co-occurrence) model did not depicted strong spatial avoidance between tiger and leopards. Detection probability of leopard was higher in areas with no tiger presence than areas where tigers were detected (Table 4.2). Similar avoidance interactions have been reported from similar prey-predator systems in the Indian subcontinent (Kafley et al. 2019, Kumar et al. 2019).

The activity patterns of tiger and leopard depicted substantial overlap in their activity while their activity peaks were different. When we assess the activity of leopards with

respect to tiger detections, we observed that leopards were avoiding sites by five hours or more immediately after tiger detection (Fig. 4.3). These results suggested that although the activity time of leopard and tiger overlaps for the sampling area, the leopard did avoid tigers in the overlapping sites. Radio collared leopards in Royale Chitwan National Park in Nepal were observed to avoid tiger by temporal separation when both of the competitors were in proximity (<1 km) (Seidensticker 1976). However, these evasion distances may vary from landscape to landscape depending on the vegetation structure and topography of the site. In two instances, after the photo-capture of an old age female (>12 years), leopards used the camera trap station within an hour interval. Interestingly, the same site was not used by leopards for more than 7 hours when an adult male was photo-captured on a different occasion.

Photo-captures of leopards were obtained from almost 50% of the camera traps deployed during the camera trapping surveys (Table 4.2). The leopard photo-capture rates were higher in areas less frequented by tigers, especially the peripheral areas (Fig. 4.2). Males were captured more on the edge of the reserve boundary than females. The habitats in the periphery of Ranthambhore were mostly degraded due to long exposure to human disturbances, and less used by tigers. However, leopards can tolerate moderately disturbed habitats with less availability of large prey species (Athreya et al. 2013). We found that leopards were using areas with moderate human disturbances; however, highly disturbed areas were avoided by leopards in Ranthambhore (Fig. 4.4). Thus, by selecting edge habitats, leopards were minimising the chance of lethal encounters with the tiger (Seidensticker 1976). At the same time, they used the edge of the PA as a refuge to avoid the hostile human-dominated areas just outside Ranthambhore.

Our results showed that edge habitats, low tiger density areas with moderate human disturbance, are used mostly by the leopards. At present, Ranthambhore does not have a buffer surrounding the core tiger habitats of the reserve, and the protected area boundary delineates the sharp edge between human habitation and wildlife habitats. With an increase in tiger density over the years (Sadhu et al. 2017, Jhala et al. 2020), leopard population are likely to be pushed along the edges as observed in other areas (Harihar et al. 2011, Mondal et al. 2012b). Therefore, it is crucial to conserve thees habitats at the periphery of the reserve in its present form by adopting a core-buffer strategy (Gopal et al. 2007). The tiger-centric conservation goals resulted in habitat manipulation, and human intervention to aid orphan tiger cubs or injured tigers affected the demographic regulation of tigers. Therefore, formulating conservation action plans for leopards considering their habitat preferences, interactions with sympatric carnivores, and tolerance towards anthropogenic interferences, is the need of the hour to safeguard the leopards living on the edge.



Factors influencing distribution of large ranging carnivores in the semi-arid landscape of western India

Are we ready to shift the focus from tiger-centric conservation to biodiversity conservation under the ambit of tiger conservation?

1. Introduction

Carnivores are one of the most charismatic yet most vulnerable taxa, experiencing range loss and population decline because of human-caused habitat loss, poaching, and prey depletion (Crooks 2002, Chapron et al. 2014). Due to their inherent k-selected traits (small population, low-density occurrence, low reproduction rate, and high energy diet), carnivores are sensitive to rapid changes in their habitat and prey (Ripple et al. 2014). The impacts of local extinction or population decline of carnivores' ripple through trophic levels, disrupting the stability of the ecosystem (Beschta and Ripple 2009). Thus, carnivore conservation is crucial to safeguard the integrity of the ecosystem. To develop suitable conservation strategy, understanding on the status, distribution, and factors influencing the population are necessary (Geese 2001). However, with studies focussed primarily on large charismatic carnivores, their non-charismatic counterparts remain comparatively understudied (Brooke et al. 2014).

Protected areas (hereafter, PAs) are the cornerstone of biodiversity conservation and crucial for maintaining the integrity of ecological processes (Rodrigues et al. 2004). However, in India, especially in the semi-arid landscape, PAs are mostly small, isolated and surrounded by human land uses. Often these PS's are too small to contain the home ranges of some wide-ranging carnivores exposing them exposing them to anthropogenic threats, which makes their populations vulnerable to extirpation (Woodroffe and Ginsberg 1998). The semi-arid landscape of western India is home to 18 species of mammalian carnivores including five large carnivores (>20 kg, Table 5.S1). However, with conservation measures largely focussed on tigers, our understanding of other carnivore species remains limited and inadequate to develop apt conservation strategies for the remaining species. Moreover, habitats devoid of tigers get very less conservation

attention irrespective of the presence of other carnivores and conservation dependent species.

Reliable status assessment of wildlife populations, especially carnivores, is challenging due to their elusive nature and low-density occurrence (Geese 2001). In recent times, camera traps have been widely used for estimating the abundance and documenting the presence of elusive and nocturnal species (O'Connell et al. 2011). Majority of the camera trapping studies focussed on the abundance estimation of naturally marked species using the capture-recapture framework. However, there is a growing interest to assess the population of species that cannot be identified using their natural markings (Burton et al. 2015). Thus, focus shifted from the number of individuals to the number of sites occupied (Occupancy framework, Mackenzie et al. 2002). The occupancy framework provides the scope to model species distribution while taking care of imperfect detection (Mackenzie et al. 2017). Moreover, occupancy framework allows evaluating the effects of different covariates on the species occurrence, this is extremely important while formulating species conservation plans.

Mapping and management of the key habitats are important for formulating conservation program for threatened species (Gaston 1996). In human-dominated landscape, carnivores use protected areas and remaining patches of natural vegetation and cover as a refuge during times of peak human activity while foraging in the larger landscape at other times. By adopting this strategy, they reduce lethal encounters with humans and domestic dogs and at the same time exploiting easily accessible meals (livestock carcasses and garbage) in the human-dominated landscape (Jhala 2015a, b). Therefore, conserving these small refuges are important in order to secure the future of these carnivores in the human-dominated landscapes. Rapid increase in human population and expanding land

use altering are degrading habitat patches that are without any legal protection status. Therefore, identification of these areas, and devising strategies to arrest their degradation is essential for the conservation of carnivores in the landscape.

In this paper, we used systematic camera trapping survey to estimate the status and distribution of large-ranging carnivores in the semi-arid landscape of western India. We used occupancy framework to evaluate factors responsible for species' distribution. Subsequently, we used the camera trap presence points to model and characterise suitable areas within the landscape for the large carnivores. We believe our findings are pertinent and timely to evoke conservation attention to safeguard the future of undervalued large carnivores in the landscape.

2. Methods

2. 1 Study area

The dry deciduous forests of western India situated in the semi-arid biogeographic zone of India (Rodgers and Panwar 1988). Two ancient mountains ranges are situated in the dry forest habitats of western India - the Aravalli and the Vindhya. The study area (27°35' to 24°21' N and 73°05' to 79°00' E, ~210000 km^2) comprises of protected forests as well as forest lands outside the PAs (Fig. 5.1). PAs include tiger reserves (Ranthambhore, Sariska, and Mukundara Hills), national parks (Kuno, Madhav), and wildlife sanctuaries (Ramgarh-Visdhari, Kaila Devi, Bhainsrodgarh, Gandhi Sagar, Bassi, Sita Mata, Phulwari ke Nal, Kumbhalgarh, Van Vihar). Wildlife habitats outside the PAs were mostly located in the rugged terrain, rest of the areas were dominated with human habitations and agro-pastoral lands. Mining, especially for limestone and marble, is one of the major threats to this fragile ecosystem. Extensive network of ravines (gullies) along

the river Chambal and its tributaries are sparsely populated due to its arduous terrain and low productivity. These ravines provide cover and act as a major wildlife refuge in the landscape. Unfortunately, much of these ravines have been (and are being) flattened to create arable lands for agricultural to meet the burgeoning food demand and bolster the backward economy of this region. This is a major threat to wildlife using these habitats.

The predominant climate of this region is Sub-tropical dry climate with three distinct seasons, dry winter (temperature <10°C, October-February), very hot summer (temperature >40°C, March-June), and hot and humid monsoons (temperature 30-40°C, July-September). The average rainfall varies from 400 to 1600mm, most of the rainfall happens during the monsoon season. The PAs in this landscape are dominated with northern tropical dry deciduous forests ($5B/C_4$) interspersed with scrubland (DS_1) and grassland ($5/DS_4$) habitats forming thinly wooded savannahs (Champion and Seth 1968). The dominant tree species are *Anogeissus pendula* (Dhok), *Butea monosperma* (Dhak/Cheela), *Acacia catechu* (Khair), *Acacia leucophloea* (Ronjh), and *Acacia nilotica* (Babul). The scrublands are dominated with *Ziziphus* spp, *Grewia* spp, *Capparis* spp. In the past few decades, the rapid spread of *Prosopis juliflora* (mesquite) an exotic invasive has degraded the habitat quality inside several PA's.

This area harbours a rich diversity of wildlife, including 18 species of carnivores with 5 large carnivores (> 20 kg, Table 5.S1). Tiger (*Panthera tigris tigris*) is the largest of the carnivores followed by sloth bear (*Melursus ursinus*), leopard (*Panthera pardus fusca*), striped hyena (*Hyena hyena*), Indian wolf (*Canis lupus pallipes*), and honey badger (*Mellivora capensis*). Presence of wild dogs (*Cuon alpinus*) was common in the past; but there is no photographic evidence to confirm their occurrence in recent times. The ungulates found in this landscape were, chital (*Axis axis*), sambar (*Rusa unicolor*),

Barking deer (*Muntiacus muntjak*), nilgai (*Boselephus tragocamelus*), chinkara (*Gazella gazella*), four horned antelopes (*Tetracerus quadricornis*), and wild pig (*Sus scrofa*). Due to severe habitat loss in the past, Asiatic cheetah (*Acinonyx jubatus*) has gone extinct from this landscape (Divyabhanusinh 1995). Fates of many other species in this landscape are dwindling due to human-caused habitat loss and persecution- the fate of the great Indian bustard (*Ardeotis nigriceps*), caracal (*Caracal caracal*) and Indian wolf (*Canis lupus*) are precarious (Dutta *et al.* 2011, Divyabhanusinh 1995, Jhala 2015a).

2.2 Field survey

2.2.1 Camera trapping

Four PAs – Ranthambhore National Park and Kailadevi Wildlife Sanctuary, Kuno-Palpur Wildlife Sanctuary, and Mukundara Hills National Park (and adjoining Jawahar Sagar Wildlife Sanctuary) were surveyed from April 2014 to March 2015 (Table 5.1). Camera trapping was done in a systematic grid-based manner, where each grid cell of 2 km^2 was surveyed for 35 to 51 days. Digital camera traps (Ambush, Cuddeback™, Green Bay, USA) were set up in selected locations. Before the deployment of camera trap reconnaissance surveys were conducted to find out locations frequently used by the target species (based on direct/indirect evidence). This increased the probability of photo-capturing the target species. We have found that mud roads, animal trails, fire lines, and dry river beds were most used by large and medium-sized carnivores. In human-dominated areas, we operated the camera traps from late evening to early morning to avoid theft. Each camera trap was set up to record the camera trap ID, date, and time label on the photographs. The camera traps were deployed at a height of 30-45cm above the ground to ensure photo-capture of carnivores of varying body sizes. After every 2–3 days,

field teams visited the camera trapping station to download data and to check battery status. The photographs obtained from the camera traps were tagged with geo-coordinates and EXIF information. Subsequently, these geo-tagged photographs were manually segregated to up to the species level for further analysis.

2.3 Analytical methods

Among the 18 species of carnivores, we used occupancy models to generate species distribution for striped hyena, leopard, sloth bear, and honey badger in the protected area extent. Furthermore, we used MaxEnt to identify landscape scale factors associated with the presence of striped hyena, leopard, sloth bear, Indian wolf, and honey badger and develop species distribution models at landscape-scale.

2.3.1 Occupancy of large carnivores

Wildlife species, especially carnivores, are rarely detected with 100% probability due to their secretive nature and low-density occurrence. Occupancy models predict species occurrence from the detection-non-detection data (Mackenzie et al. 2017). To address this problem of under detection, occupancy models use information from repeated surveys at each site to estimate the detection probability. The detection-non-detection history (H_i) for each site can be written as probability functions as follows (1 = detected, 0 = not detected):

$$Pr\,(H_i = 1001) = \psi * p_1\,(1\text{-}p_2)\,(1\text{-}p_3)\,p_4$$

Not detecting the target species during the entire survey ($H_i = 0000$) means, either the species was not present at that site or the species was present but not detected:

$$Pr\,(H_i = 0000) = (1 - \psi) + \psi * (1\text{-}p_1)\,(1\text{-}p_2)\,(1\text{-}p_3)\,(1\text{-}p_4)$$

These equations of all detection histories are combined into model likelihood:

$L(\psi, p \mid H_i) = \prod_{i=1}^{n} \Pr(H_i)$

The maximum likelihood techniques are used in program PRESENCE (*ver.*4.1) to estimate the ψ and *p*. We have used single season single species occupancy survey to estimate occupancy of large and medium sized carnivores. We believe the systematic camera trap placement and the sampling duration (20-35 days) met assumptions (independent detections and 'closed' occupancy state of the sites) of the survey (Mackenzie et al. 2005). Studies on species occurrence and distribution often seek the relationship between species presence and the covariates responsible for the pattern. Occupancy framework can relate site occupancy (ψ) with habitat covariates using logit-link function. We have used habitat covariates to establish species-habitat relationship and estimate ψ across the sites.

2.3.2 Species Distribution Modelling at landscape scale

The species distribution models depict a spatial map of suitable environmental conditions where species can potentially occur along with its likelihood of being present; thus it has often been used for selection of conservation priority areas (Pearson 2007). We used program MaxEnt (ver. 3.4.1) to map potential areas for the large carnivores in the landscape. MaxEnt is a presence-only model, i.e., it considers only the presence locations while predicting and uses set of background samples (randomly drawn) to contrast the spatial distribution of the presence points along with environmental layers (Phillips et al. 2006). Due to its predictive accuracy and easy to use user interface, MaxEnt is the most used software to carry out species distribution modelling (Renner and Warton 2013).

We used the camera trap photo-captures as presence points for the target species, i.e., striped hyena (n = 323), leopard (n = 199), sloth bear (n = 196), honey badger (n = 92),

and wolf (n = 21). The predictor variables were tested for collinearity (Pearson's $r > 0.7$), and if found correlated, we used one of them for the final run (Phillips and Dudik 2008). We tested different combinations of feature type (auto, linear, quadratic, and product) and regularization multipliers (0.5, 1, 1.5, 2). Due to the small number of sample size (<50) for the wolf, we have only used linear and quadratic feature types (Phillips and Dudik 2008). The index of habitat suitability ranges from 0 (least suitable habitat) to 1 (most suitable habitat). We have used a threshold for defining suitable habitats, where suitability value of 0.6 considered as the threshold. The choice of the threshold value for the selection of suitable habitats depends on the minimisation of the false negative or false positive errors. A threshold value set too high (close to 1) minimises the number of false positive sites (unsuitable sites predicted as suitable) and increase the number of false negative sites (suitable sites predicted as unsuitable). While a low threshold value will result in lower false negative but higher false positive sites. We assess the model performance using Akaike Information Criterion (corrected for small sample size, AICc) in the ENMTools (ver. 1.3, Warren et al. 2010) as the reliability of the area under the receiver operating characteristic curve (AUC) has been criticized for its unreliability (Lobo et al. 2008, Warren and Seifert 2011).

2.3.3 Environmental covariates

We used vital habitat and anthropogenic factors for modelling species distribution based on ecological understanding and published literature. For occupancy analysis, we extracted variables using the PA extents (area of extrapolation, Fig. 5.2), while for species distribution modelling using MaxEnt, extrapolation was done at the landscape scale. The ruggedness index was calculated from the DEM layer following the equation used by Riley et al. 1999. The forest cover classes were reclassified as woodland (dry deciduous

forest patches with a few of moist deciduous patches in the southern and eastern side of the landscape) and open forest-scrubland (open forest and scrubland areas) habitats. Apart from Ranthambhore, all other PAs in the study sites had human settlements inside. Therefore, we considered the protected habitats as one of the predictor variables (protectedness). A buffer of 1.5 km from the settlements (inside PA) and an inward buffer of 1.5 km from the PA boundary was considered as least protected areas, and the Euclidean distance from these habitats were calculated. Details of these predictor variables are mentioned in supplementary Table 5. S2. Calculation of Euclidean distances was done in Esri® ArcMap™ 10.1 using Euclidean Distance Tool in Spatial Analyst. All the layers were resampled to 1km^2 pixel size. Protected Area shape files were accessed from GIS Cell, Wildlife Institute of India.

The bear & the tiger: *Tigers often harass & kill sloth bears, especially the younger ones.*

Table 5.1: *Sampling details of the camera trap study conducted in different protected areas in the western India landscape from April 2014 to March 2015.*

Name of the Protected Area	**No of camera traps**	**Total effort**	**Species detected**					**Tiger population during the survey***	**Human settlements (inside)**
			Striped hyena	Leopard	Sloth bear	Indian wolf	Honey Badger		
Ranthambhore NP	359	8159	Yes	Yes	Yes	***No***	Yes	39	No
Kailadevi WLS	72	1245	Yes	Yes[#]	Yes	Yes	***No***	1	Yes
Kuno NP	117	2438	Yes	Yes	Yes	***No***	Yes	1	No
Mukundara Hills TR	106	1771	Yes	Yes	Yes	Yes	Yes	0	Yes

*All India Tiger estimation, Jhala et al. 2014
#only one photocapture

Table 5.2: *Depiction of suitable area derived from MaxEnt for the study species in the semi-arid landscape of western India. The threshold for predicted suitability value was kept at 0.6. TR – Tiger Reserve, PA – Protected area.*

Species	**Home range (km^2)**	**Total area (km^2)**			
		Total	**Under PA**	**Under TR**	**Outside PA**
Striped hyena	~30-60[1]	3160	964	477	2196
Leopard	13-48[2]	2184	773	333	1411
Sloth Bear	9.4 – 14.4[3]	1576	570	216	1006
Honey Badger	~200 & more[4]	1966	648	267	1318
Indian wolf	~150 & more[5]	4213	383	144	3830

[1]*Wagner 2006; Bopanna 2013* [2]*Mondal et al. 2013* [3]*Joshi et al. 1995* [4]*Begg et al. 2005* [5]*Jhala 2015*

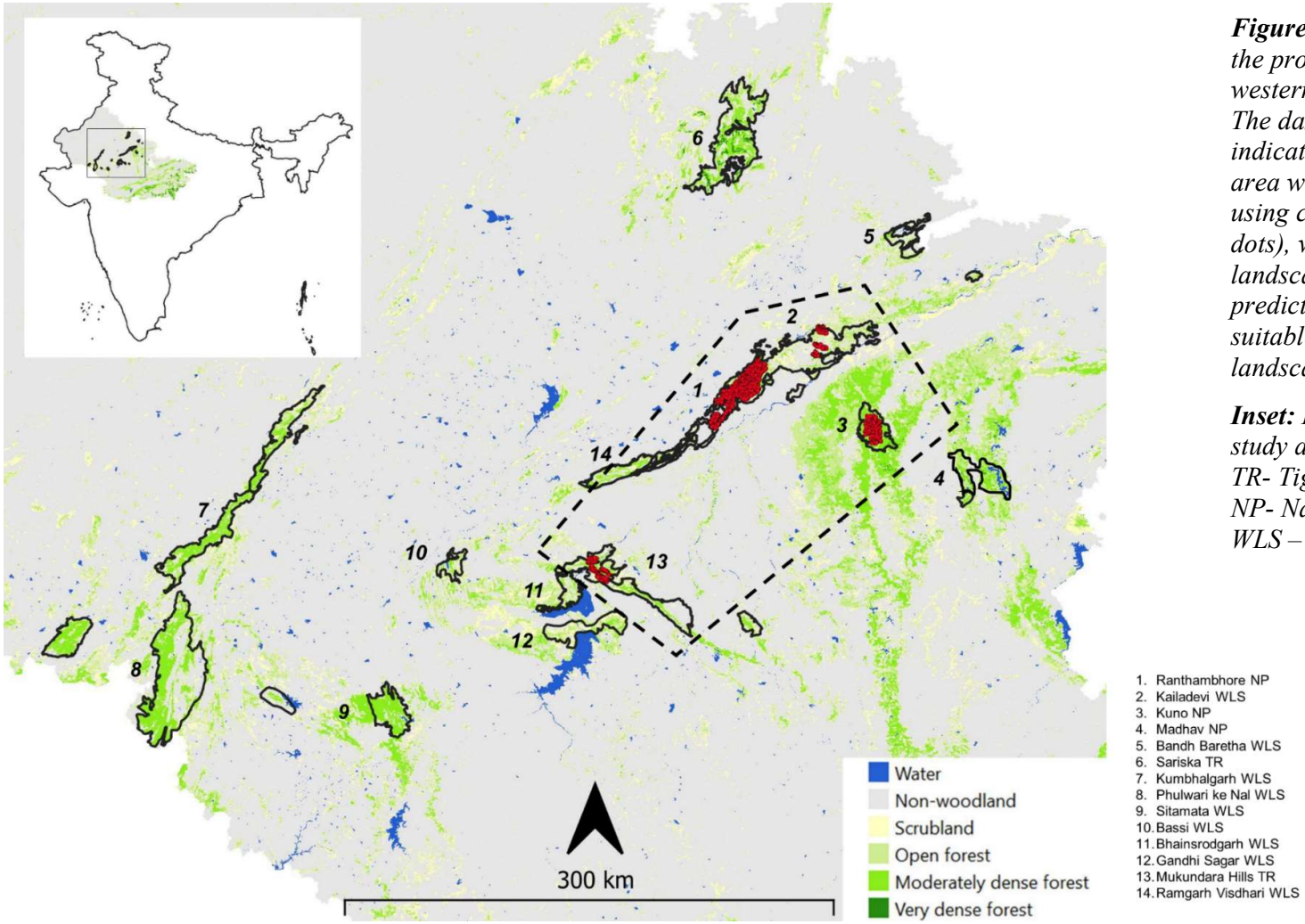


Figure 5.1: *Location of the protected areas in the western Indian landscape. The dashed line indicating intensive study area which was sampled using camera traps (red dots), while the larger landscape was used for predicting the potential suitable habitats in the landscape.*

Inset: *Location of the study area in India*
TR- Tiger Reserve
NP- National Park
WLS – Wildlife Sanctuary

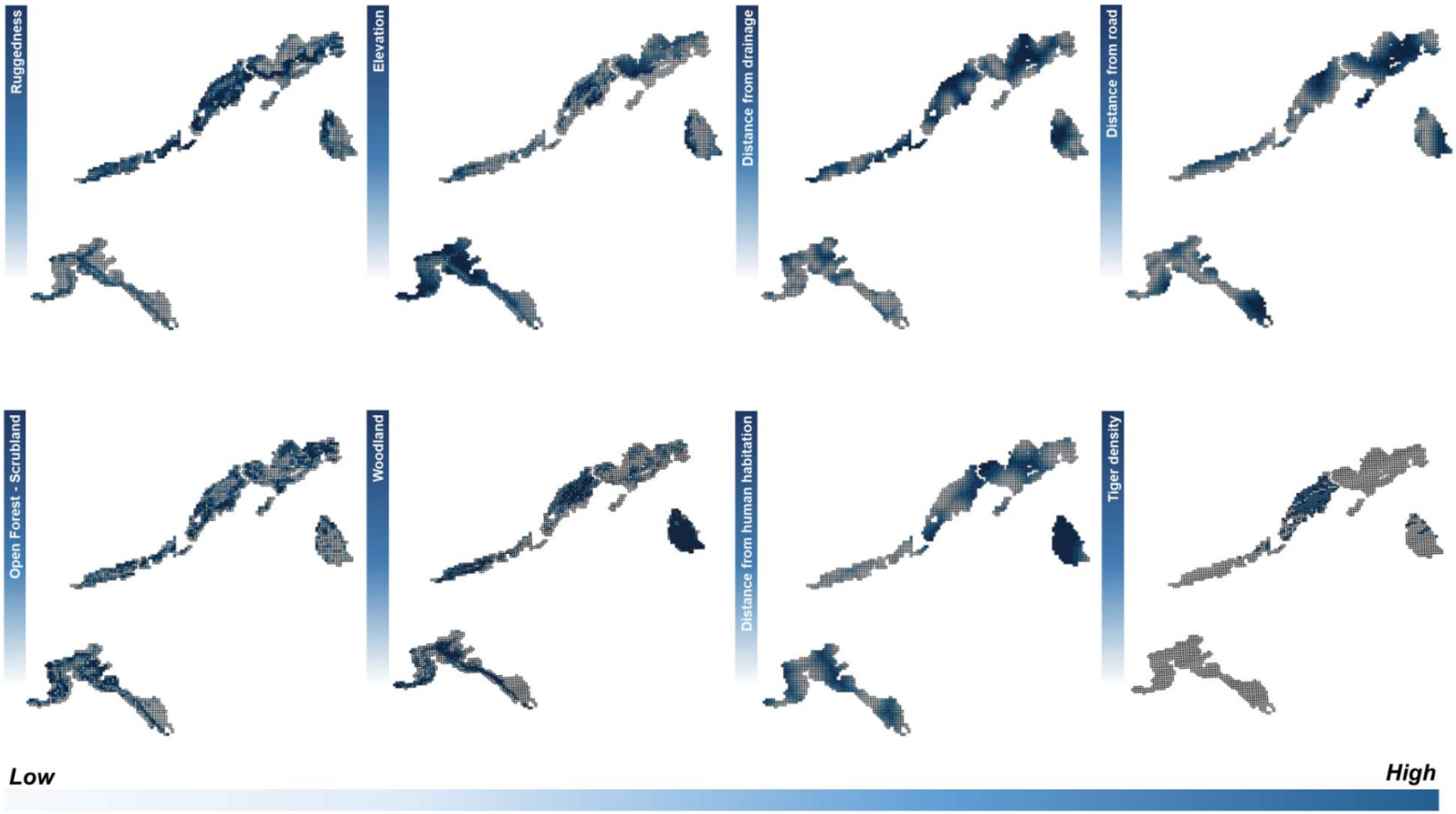


Figure 5.2: *Distribution of covariates used for occupancy analysis in the sampling sites.*

3. Results

Occupancy of large carnivores

Striped hyena presence was reported from across the study sites with higher occurrence observed in Mukundara Hills TR (Fig. 5.3). The occupancy probability ranged from 0.018 to 0.830 (ψ – 0.598, SE 0.005) with detection probability (p) 0.1106 (SE 0.0037). Occupancy analysis showed the importance of drainage, road, protection, and the influence of tiger presence on hyena occupancy (Fig. 5.3). As the distance from drainage and road increases, the occupancy probability decreased. Sites with high protection, the core areas of the PAs have lower occupancy probability than the sites near to human habitation (Fig. 5.3). Tiger occupancy also influenced hyena occurrence; hyenas avoided sites frequented by tigers. Leopard presence was reported from all the surveyed area. However, most of the captures were obtained from Ranthambhore NP and Kuno NP (Fig. 5.3). Leopard occupancy probability ranged from 0.124 to 0.987 (ψ – 0.661, SE 0.004) with detection probability (p) of 0.0488 (SE 0.0031). The occupancy model with predictor variables -availability of woodland, distance to drainage, and tiger presence was the best fit model according to the AIC_c score. Leopard showed preference for woodland habitats. However, areas far from the drainage and areas frequented by tigers were avoided by leopards. Sloth bear and honey badger were recorded from across the study sites. However, the Ranthambhore and Kuno NP had a greater number of detections than other sites. Sloth bear occupancy was best explained by distance to human settlement, distance to drainage, and scrubland-open forest habitat in the best fit model. The occupancy probability ranged from 0.144 to 0.755 (ψ – 0.496, SE 0.002) with detection probability (p) 0.0609 (SE 0.0034). Sloth bear preferred lands which far from human disturbance and close to drainage and avoided open forest-scrubland areas. For honey badger, the model

with drainage, human disturbance, and protected ness of the site was selected as the best fit model. The occupancy probability ranged from 0.08 to 0.79 (ψ – 0.394, SE 0.003) with detection probability (p) 0.0248 (SE 0.0033). Honey badger preferred sites which were far from human disturbance and well protected.

Species Distribution Modelling at landscape scale

The species distribution modelling for striped hyena shows human habitation, rugged terrain, presence of open forests and woodlands have highest influences on suitable sites (Fig. 5.5). Moderately rugged open forest-scrubland and its adjacent woodland habitats with intermediate human disturbance were identified as most suitable habitats for striped hyenas. The total area under suitable category (>0.6 suitability value) for striped hyena was 3160 km^2 in the landscape, out of which 964 sq. Km comes under the PA network (Table 5.2). Species distribution modelling for leopard and sloth bear shows significant influence of human settlements, presence of woodlands and rugged terrain on species occurrence (Fig. 5.5). Suitable areas for these two large carnivores in the landscape comprised of moderately rugged woodland habitats with intermediate human disturbance. The total suitable area (>0.6 suitability value) for leopard and sloth bear were 2184 and 1576 km^2, respectively (Table 5.2). Out of these highly suitable areas, 773 and 570 km^2 area comes under the PA coverage. The species distribution model for honey badger shows the highest influence of human disturbance, woodland, and ruggedness (Fig. 5.5). The species distribution model for wolves in the study area showed the highest influence of scrubland-open forest areas and distance from human settlement. The suitable habitats for wolves mostly comprised of open forest-scrubland areas in human-dominated landscapes. The total suitable area (>0.6 suitability value) for wolves and honey badger

were 4213 and 1966 km^2, respectively, and only 383 and 648 km^2 area comes under PA coverage (Table 5.2).

DISCUSSION

The decline in world's carnivore populations emphasises the need to develop conservation strategies for landscapes that have already been altered to accommodate anthropogenic requirements (Moilanen et al. 2005). It is essential to understand the population parameters, status assessment and factors affecting species for the sake of conserving them (Gese 2001), however, often the knowledge on these aspects are limited and sparse for many of the carnivores. In the present study, single season single species occupancy was used to depict the influence of site level covariates on the species distribution inside the PA. The MaxEnt modelling predicted the species distribution in the landscape scale (the semi-arid landscape of western India) and identified potential factors governing the distribution. Large scale conversion of wildlife habitats to human land use restricted the area used by large-ranging carnivores into a few pockets of the landscape. Therefore, most of the extant large carnivore populations in the semi-arid landscape are found in PAs and areas with low human disturbances. Although, we have sampled representative habitats and gradient of human-disturbed areas inside the PAs (Fig. 5.2), our camera trapping array did not cover habitat matrices outside the PAs due to logistical constraints. Therefore, the relationships with species distribution with covariates derived from occupancy analyses are most relevant for the PAs.

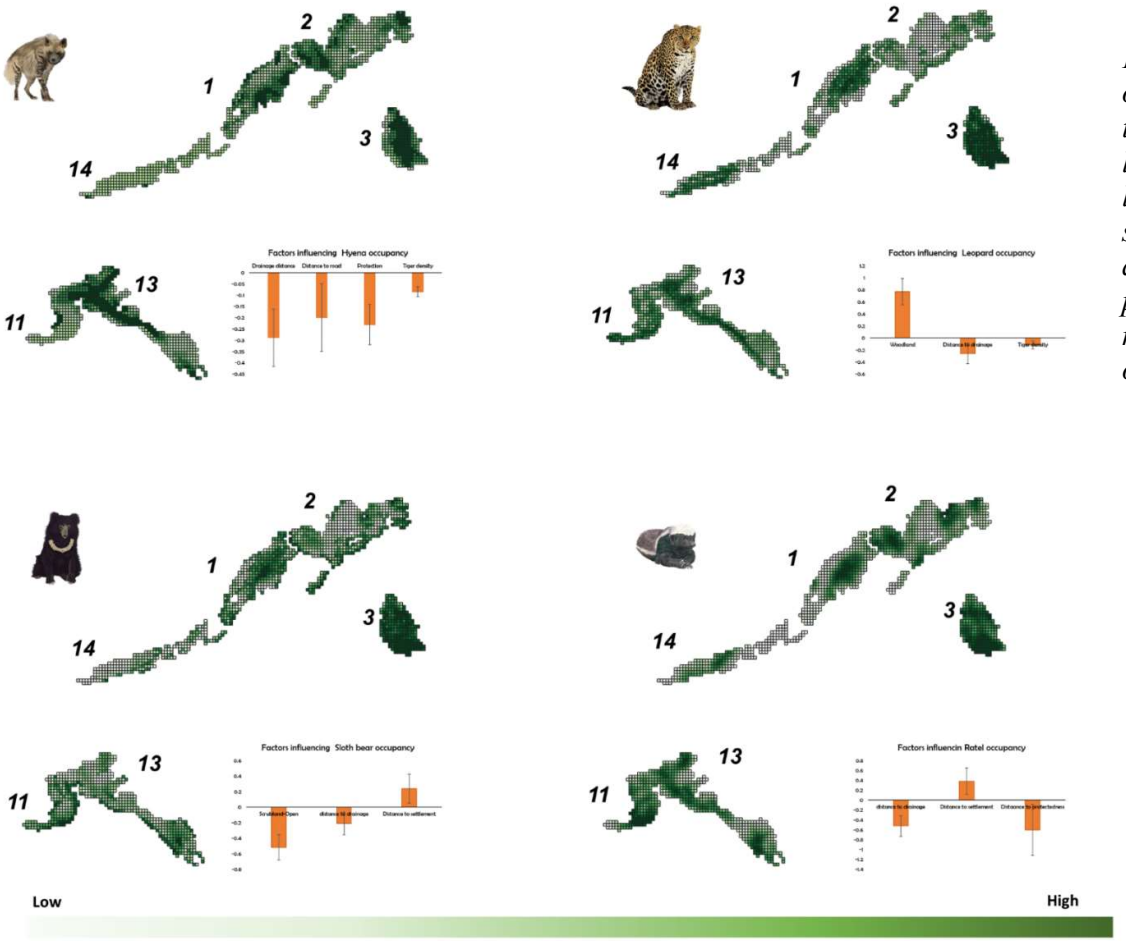


***Figure 5.3**: Predicted occupancy estimates across the study sites for (from top left, clockwise) striped hyena, leopard, honey badger, and sloth bear. The graphs are depicting the influence of each predictor variables (best fit mode) in the species occurrence.*

1. Ranthambhore NP
2. Kailadevi WLS
3. Kuno NP
11. Bhainsrodgarh WLS
13. Mukundara Hills TR
14. Ramgarh Visdhari WLS

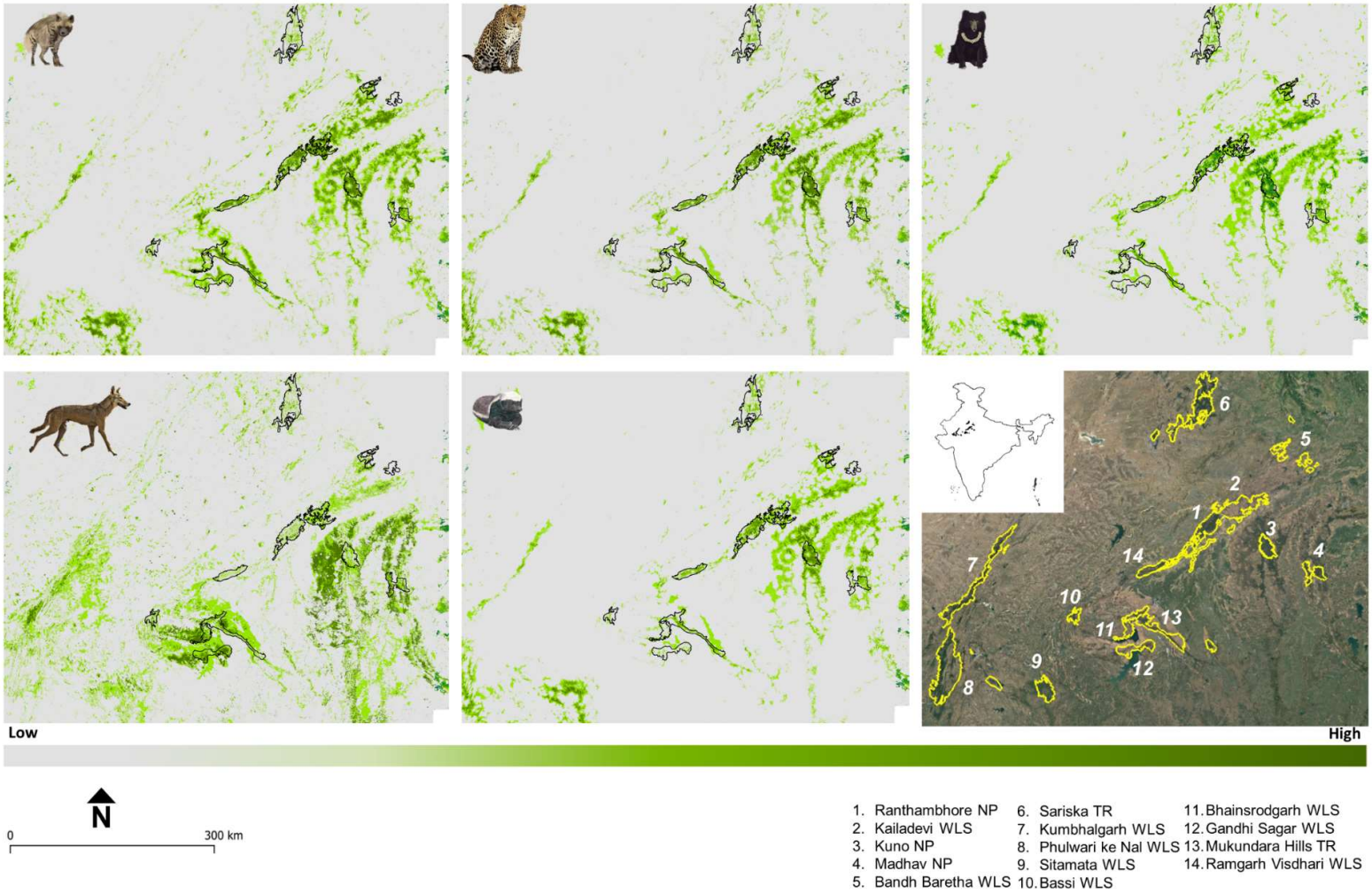


Figure 5.4: *MaxEnt predicted distribution maps for target species (top row, L to R: Striped hyena, Leopard, Sloth bear, bottom row, L to R: Indian wolf, Honey badger).* ***Inset:*** *Location of the study sites with reference to India.*

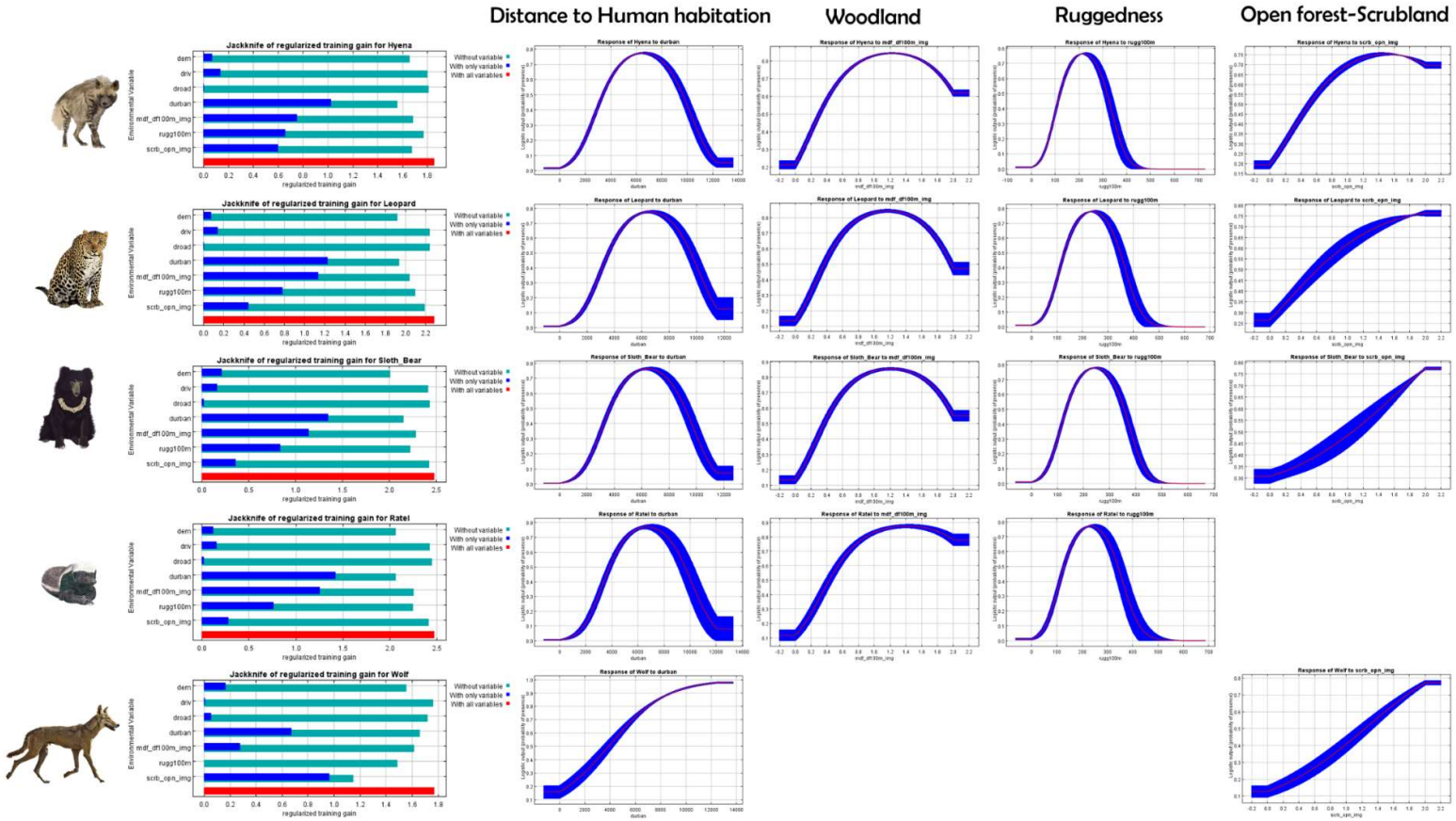


Figure 5.5: *Effects of the most important covariates on species distribution. The Jackknife test showing the relative importance of the predictor variables when used in isolation (dark blue bars) and when omitted from the prediction model (sea green bars). The response curves on the right hand side are showing how individual variables effected the MaxEnt prediction when used in isolation (only the most meaningful variable responses are included here).*

The occupancy estimates of striped hyena showed its preferences towards the availability of drainage (river, rivulets, seasonal streams), while negatively impacted by human habitation and decreasing level of protection (Fig. 5.3). Striped hyenas frequently use gullies, river and stream bed with vegetation cover while going from the den site to the foraging sites (in human-dominated landscape). Interestingly, striped hyena occupancy showed a positive relationship with the presence of roads (village and state highways). Striped hyenas are mostly scavengers; therefore, roadkills and availability of carcasses dumped by local villagers attract hyenas, and they forage on these human-dominated areas at night (Jhala 2015b). However, during the day they took shelter on refuges available nearby to avoid encounters with the human. Thus, striped hyenas in the landscape are using the PAs, especially the edge of the PAs, as a refuge. These edge habitats provide the perfect opportunity for foraging, shelter and less competitive pressure from tigers, the dominant competitor. Leopards in the study sites showed preference for woodlands (dry deciduous forests) and availability of drainage, while avoided areas frequented by tigers (Fig. 5.3). Leopards are known to use a diverse array of habitats. However, they attain higher densities in the inviolate forested habitats with ample prey. Very few photocaptures of leopards in the plateau top areas of Kailadevi and Mukundara (northern tip) suggested their low-density occurrence in those disturbed habitats with sparse tree cover. Forested areas with no tiger (Ramgarh and Mukundara during the period of study) or 1-2 tigers (Kailadevi and Kuno) showed higher leopard occupancy probability (Fig. 5.3). In areas where leopards cooccur with tigers, the latter dominates the former (Karanth and Sunquist 2000, Odden et al. 2010). In chance encounters, tigers were observed to kill leopards, similar observations were reported from Royale Chitwan National Park, Nepal (McDougal 1988).

Sloth bear occupancy in the study sites was influenced by habitat type, availability of drainage, and human disturbance. Undisturbed dry deciduous forest patches (woodlands) of Ranthambhore and Kuno showed the highest probability for sloth bear occurrence along with rugged terrain in the landscape (Fig. 5.3). Radio telemetry studies on sloth bear from central India (Yoganand 2005) and lowland Nepal (Garshelis et al. 1999) reported the preference of woodland habitats over open-grassland. Sloth bears avoid the human presence and preferred inviolate habitats (Yoganand et al. 2015), even in the resource-rich areas where human disturbance is high, sloth bear avoided using those areas (Garshelis et al. 1999). Predicted occupancy for honey badger (ratel) was patchy, unaffected by forest types. However, they were influenced by the presence of drainage (Fig. 5.3). Honey badger uses the streams and seasonal river beds (with boulders) and rugged terrain (e.g., ravines) for denning purposes (Prater 1980). The predicted occupancy for honey badger in the study area was also influenced by human disturbance and protectedness of the sites. The habitat suitability study on the species from Sariska showed human disturbances to negatively impact honey badger distribution (Gupta et al. 2012).

Species distribution modelling of the striped hyena and leopards showed avoidance towards areas with intense human habitations (townships and cities), while their predicted distribution probability has shown highest in areas with intermediate disturbances. These areas comprised mainly of the peripheral habitats of the PAs or habitat fragments surrounded by human land use (Fig. 5.4). The edges of the PAs in the semi-arid landscape are exposed to heavy biotic pressure from the nearby villages. Intensive grazing, fuelwood extraction from these forests degraded the woodlands into scrubland and open forest areas around the PAs. Due to disturbances and less availability of large-bodied

prey, these edge habitats are rarely inhabited by tigers. Thus, striped hyenas and leopards exploit the niche with less competitive pressure from the dominant predator, at the same time, stay close to the adjacent human land use (foraging ground) (Jhala 2015a). The probability of hyena and leopard distribution was predicted more in areas dominated with woodland-open forest clusters and with moderately rugged terrains. These habitats mostly cover woodland habitats of the PAs and the ravine areas of Chambal and its tributaries (Fig. 5.4). Almost 65-70% of the suitable habitats for striped hyena and leopard come outside the boundary of Pas (Table 5.2).

The predicted distribution of sloth bear and honey badger was mostly influenced by the presence of woodland habitats, human disturbances, and ruggedness. The woodland areas of Ranthambhore, Kuno, and Mukundara was showed highly suitable for these two species (Fig. 5.4). However, the contiguous chunk of woodland habitats outside of Kuno was predicted as highly suitable in the landscape. Less human disturbance and large size of the patch are likely to influence the higher suitability value of these species. The predicted high suitability areas of Indian wolf were comprised of primarily open forest-scrubland habitats with moderately rugged terrain and intermediate human disturbance. The plateau-top mesic savannah habitats adjacent to Kailadevi, Kuno, and Mukundara, and the ravines along the Chambal were depicted as highly suitable areas for these species. More than 90% of the suitable habitats for wolves were predicted outside the boundary of PAs (Table. 5.2).

Large ranging carnivores living in small protected areas use the habitat matrices (mostly agro-pastoral land uses) quite frequently, thus experiencing major challenges caused by the rapid alteration of land uses in human-dominated landscapes (Wolf and Ripple 2017). In the semi-arid region of western India, suitable habitats of the large-ranging carnivores

comprised of habitats patches outside the existing PA network (Table 5.2, Fig. 5.4). In these fragmented landscapes, long-term conservation planning needs to secure areas large enough to sustain the species over long-run (Cabeza and Moilanen 2001). Along with protecting vital habitat patches, connectivity between these patches needs to be restored/conserved in order to conserve the populations in a metapopulation framework (Hanski & Ovaskainen 2000). Our results of the species distribution modelling predicted the suitable habitats (or, already there) in the landscape (Fig. 5.4), and also identified the drivers which can influence their distribution (Fig. 5.5). These outcomes will be instrumental for the policy formation and conservation planning of priority areas to secure the fate of large carnivores.

In India, tiger serves as a good umbrella for conservation in the forest ecosystems, and since its inception, the PA formulation has largely been influenced by the presence of charismatic species or historical relevance of the place. However, the present PA coverage is not sufficient to conserve the diverse array of habitat used by other carnivores. Our study showed that the majority of the potential habitat for large carnivores were situated outside the protected area boundary (Table 5.2). However, the conservation requirements of these non-tiger bearing habitats often get subdued under the course of tiger conservation. In the semi-arid landscape of western India, the large expanse of suitable habitats outside PAs depicted the pressing need for increasing the existing PA network coverage (Table 5.2). These habitats were primarily comprised of open forest-scrublands (with semi-arid grasslands) and ravine areas. The 'treeless' semi-arid grasslands, scrublands, and ravine habitats are considered as 'wastelands' due to their agricultural unsuitability and low economic gain. These habitats, especially the ravines, harbour the majority of the potential large carnivore habitat and also act as dispersing

corridors for tigers (Chapter 2- tiger dispersal). Large chunks of these crucial wildlife habitats were converted to human land use under the 'wasteland reclamation' program (https://dolr.gov.in/documents/wasteland-atlas-of-india) (Parandiyal et al. 2018). Myriads of developmental projects are coming up in these areas to bolster the economy and socio-economic growth of the local people. Most of these unforeseen developmental activities are not sustainable for these fragile ecosystems and could lead to habitat loss and population decline of the large-ranging carnivores. Immediate recognition of these areas as conservation priority landscapes and direct conservation investments from the federal and state government is the need of the hour.

***A ghost of twilight**: Hyenas started their activity in the twilight hours, remain active throughout the night & take refuge in undisturbed patches during the day. Habitat patches like Mukundara provide safe haven for these animals in human-dominated landscapes.*

Table 5.S1: *Names and conservation status of carnivore species found in the semi-arid landscape of western India. Body weight are obtained from IUCN (https://www.iucnredlist.org/), Johnsingh & Manjrekar 2015. WPA – Wildlife Protection Act 1972; IUCN Status: LC – Least Concern, VU – Vulnerable, NT – Near Threatened, EN- Endangered*

Species name	Scientific name	Family	WPA Status	IUCN Status	Weight (Kg)	Category
Golden jackal	*Canis aureus*	Canidae	Schedule II	LC	4.5-15	Medium
Indian fox	*Vulpes benghalensis*	Canidae	Schedule II	LC	1.8-3	Small
Indian wolf	*Canis lupus*	Canidae	Schedule I	LC	15-25	Large
Caracal	*Caracal caracal*	Felidae	Schedule I	LC	6-10	Medium
Desert cat	*Felis silvestris*	Felidae	Schedule I	LC	3-4	Small
Fishing cat*	*Prionailurus viverrinus*	Felidae	Schedule I	VU	6-12	Medium
Jungle cat	*Felis chaus*	Felidae	Schedule II	LC	4-6	Small
Leopard	*Panthera pardus*	Felidae	Schedule I	VU	30-75	Large
Rusty spotted cat	*Prionailurus rubiginosus*	Felidae	Schedule I	NT	1-2	Small
Tiger	*Panthera tigris*	Felidae	Schedule I	EN	100-250	Large
Indian grey mongoose	*Herpestes edwardsii*	Herpestidae	Schedule II	LC	1.5-2	Small
Ruddy mongoose	*Herpestes smithii*	Herpestidae	Schedule II	LC	2-2.5	Small
Small Indian mongoose	*Herpestes auropunctatus*	Herpestidae	Schedule II	LC	0.5-1	Small
Striped hyena	*Hyaena*	Hyaenidae	Schedule III	NT	25-40	Large
Honey badger	*Mellivora capensis*	Mustelidae	Schedule I	LC	7-13	Medium
Sloth bear	*Melursus ursinus*	Ursidae	Schedule I	VU	80-150	Large
Common palm civet	*Paradoxurus hermaphroditus*	Viverridae	Schedule II	LC	1.4-5	Small
Small Indian civet	*Viverricula indica*	Viverridae	Schedule II	LC	2-4	Small

* Mukherjee et al. 2012, Sadhu and Reddy 2013

Table 5.S2: *Name, description, and source of predictor variables used for both occupancy and species distribution modelling (SDM) analysis. 'Yes' under the Occupancy/SDM columns depicted the use of that particular variable for Occupancy/SDM analyses.*

Predictor variables	**Description**	**Occupancy**	**SDM**	**Source**
Woodland	Comprised of moderately dense and dense forest classes	Yes	Yes	http://www.surveyofindia.gov.in/
Open forest	Comprised of open forest and scrublands classes	Yes	Yes	http://www.surveyofindia.gov.in/
Digital Elevation Model (DEM)	Elevation from mean sea level	Yes	Yes	http://bhuvan.nrsc.gov.in
Ruggedness	Rugged terrain complex	Yes	Yes	Calculated from DEM layer using Riley et al. 1999
Euclidean distance from drainage	Euclidean distance from river, rivulets, and streams	Yes	Yes	http://www.surveyofindia.gov.in/
Euclidean distance from road	Euclidean distance from roads (national, state, village highway)	Yes	Yes	http://www.surveyofindia.gov.in/
Night time lights	Euclidean distance from night time visible lights	Yes	Yes	http://www.ngdc.noaa.gov/dmsp/sensors/ols.html
Euclidean distance from urban settlements	Euclidean distance from human habitations/settlements	Yes	Yes	https://www.dlr.de/ (Esch et al. 2011)
Protectedness	As a surrogate of protection measures	Yes	No	Calculated from the boundary of PA & settlements
Tiger presence	Photographic rate of tigers in each occupied grids	Yes	No	Sadhu et al. 2017

Conservation Implications

Successful conservation efforts over the years have resulted in an increasing tiger population in Ranthambhore, which is nearing its carrying capacity. Lack of dispersal opportunity reduces the probability of natural dispersal in the landscape. At present, the surplus population has started venturing out in human-dominated areas outside the reserve.

Conservation implications

Ranthambhore tiger reserve (hereafter, Ranthambhore) along with the sink habitats in the western Indian landscape demarcates the western limit of tiger distribution in the world. Presence of tigers was reported from much of this semi-arid landscape (erstwhile state of *Rajputana*) in the past century (Singh and Reddy 2017). However, tiger populations went locally extinct from many of these areas due to persecution, habitat loss, and prey loss. With the local extinction of tigers from nearby forest patches, Ranthambhore became the last remaining tiger population in the entire semi-arid landscape of western India. With stringent law enforcement and protection, the tiger population of Ranthambhore has revived from its initial low density and reached near carrying capacity during the study period (Chapter 2 – Tiger Demography). At present, Ranthambhore harbours the highest density of tigers in the central Indian landscape, but it remains relatively small and isolated (Jhala et al. 2020). These isolated populations are susceptible to lose out genetic variation caused by inbreeding and genetic drift, which reduce their ability to cope with a changing environment. However, the demographic parameters of Ranthambhore tigers did not show any manifestation of inbreeding depression in the population during the period of study. The vital rates of Ranthambhore tigers were comparable to other tiger populations which are larger and well connected. With the high density of tigers (and >20 breeding units) along with their high survival rates (Chapter 2 – Tiger demography), there is no imminent threat of extinction (Fig. 6.1). Hence, there is no current need for genetic rescue for reviving the 'vigour' (Pimm et al. 2006) of Ranthambhore tigers. However, management actions in terms of medical interventions to treat injured/ailing tigers or interfering with the natural population regulation mechanism like infanticide is not

desirable and are likely to have a detrimental effect on the long-term persistence of the population. Such well-intended but short-sighted action can hinder the process of natural selection by keeping 'unfit' individuals in the population who were destined to be eliminated (Keller and Waller 2002) thus purging the recessive deleterious alleles from the population. Therefore, management should refrain from treating those sick/injured individuals based on the emotional grounds and focus on principles of conservation biology for the management of the tiger population. As a long-term conservation strategy, the Ranthambhore tiger population needs to be managed as metapopulation by restoring the sink habitats and conserving their connectivity with the source (i.e., Ranthambhore). The identified corridors (Chapter 3 - Tiger dispersal) need to be conserved as a buffer or eco-sensitive zone (ESZ) of the existing PAs. The ravines of river Chambal and its tributaries showed high potential for facilitating tiger dispersal in this semi-arid landscape. Recent tiger dispersal events from Ranthambhore to nearby sink habitats established the importance conserving these habitats along with the scrubland-open forest habitats in the landscape. The recent surge of developmental activities and 'reclamation' programs, which are major threats for these corridor habitats, need to be stopped/regulated.

Ranthambhore harbours a high-density leopard population (9-10 leopards/100 Km^2) as estimated using the spatially explicit capture-recapture method. Although the leopard density showed no significant change over the years, but their space use patterns changed with response to that of the tigers (Chapter 4 – Interactions between leopards and tigers). The results showed areas which were less visited by tigers and exposed to low to medium human disturbances, mostly the edge of the reserve, was frequented by leopards. Thus,

the edge habitats of Ranthambhore need to be protected following a core-buffer strategy to endorse leopard conservation in the reserve.

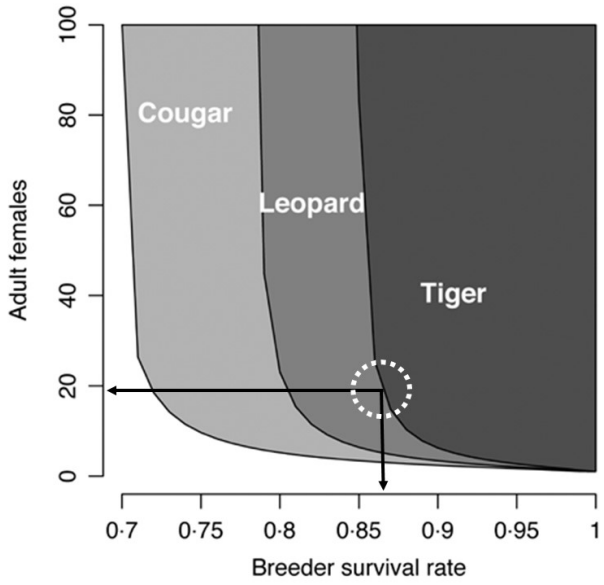


Figure 6.1: *Requirement of adult females (y-axis) in a population predicted as a function of breeder survival rate (x-axis) (reproduced from Chapron et al. 2008) showed with the present population and survival rate of the breeders in Ranthambhore tiger population (white dotted circle, Chapter 2- tiger demography), there is no imminent threat of extinction (extinction probability <1%).*

Species distribution modelling for large carnivores done in this study has identified potential habitats and likely drivers influencing their distribution. The MaxEnt output showed suitable areas for hyenas, leopards, and wolves, comprised of habitat patches outside the extent of the existing PA network (Chapter 5). Amongst the PAs, the open forest-scrubland habitats of Kaila Devi wildlife sanctuary, Mukundara Hills tiger reserve, and Kuno, showed high potential for harbouring these large carnivore populations. The ravine habitats, especially the contiguous patch stretched from Mandrayal (northern tip of Kailadevi WLS) to Dholpur-Morena region (Fig. 6.2), were depicted as highly suitable areas for most of the large carnivores in the landscape. The open forest habitats adjacent to Kuno national park (Sheopur forest division) was also suitable habitat for large carnivores. These areas were also found permeable to tiger dispersal, thus crucial for maintaining connectivity between sink habitats and with the source (i.e., Ranthambhore). At present, these habitats lack legal sanctity. Thus, prompt conservation investments

should be directed to protect these habitats from future destruction to facilitate tiger dispersal in the landscape as well as to conserve the habitats for other large carnivores. The dry deciduous forests patches have faced severe habitat loss and fragmentation for widespread mining activities, and 'wasteland' reclamation programmes. Local extinction events of large carnivores (the tiger, Chundawat et al. 2016, and the cheetah, Divyabhanusinh 1995) from this landscape has highlighted the importance of conserving these habitats.

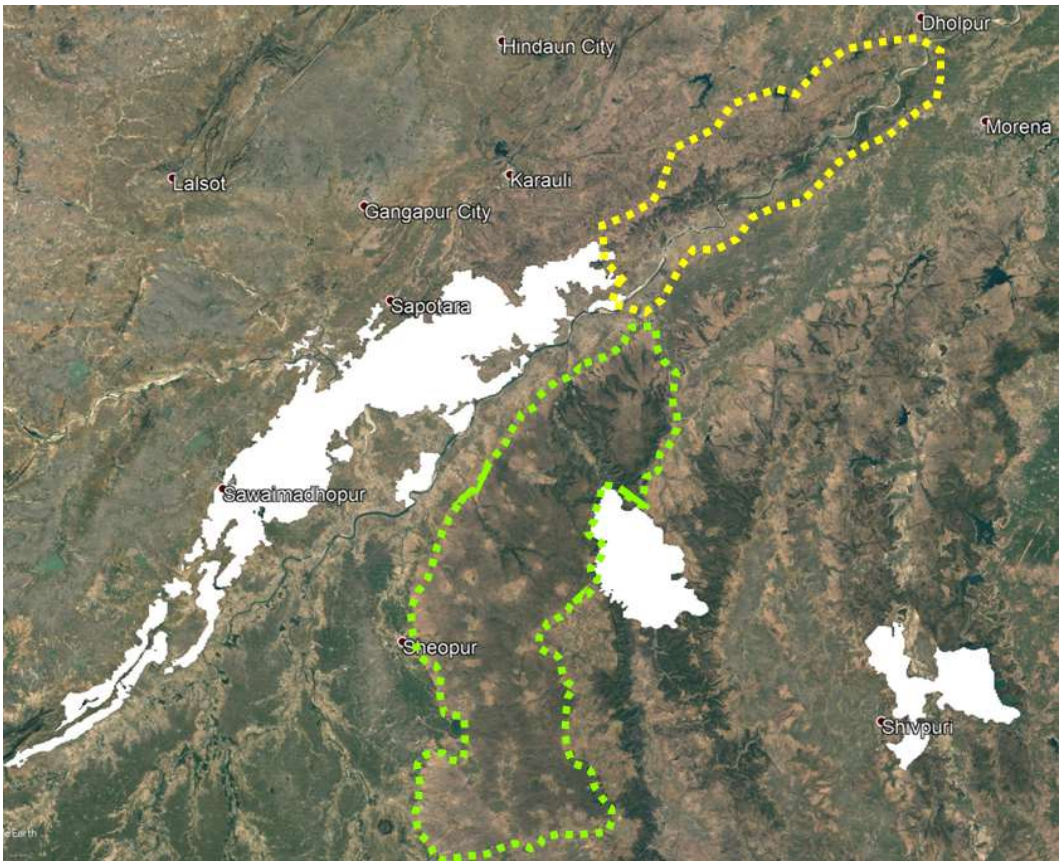


Figure 6.2: *The map of the greater Ranthambhore landscape showing two important areas for conservation investments- the ravine complex of river Chambal stretched from Karauli to Dholpur-Morena (the yellow dotted line), and open forest clusters of the Sheopur forest division (green dotted line) adjacent to Kuno National park.*

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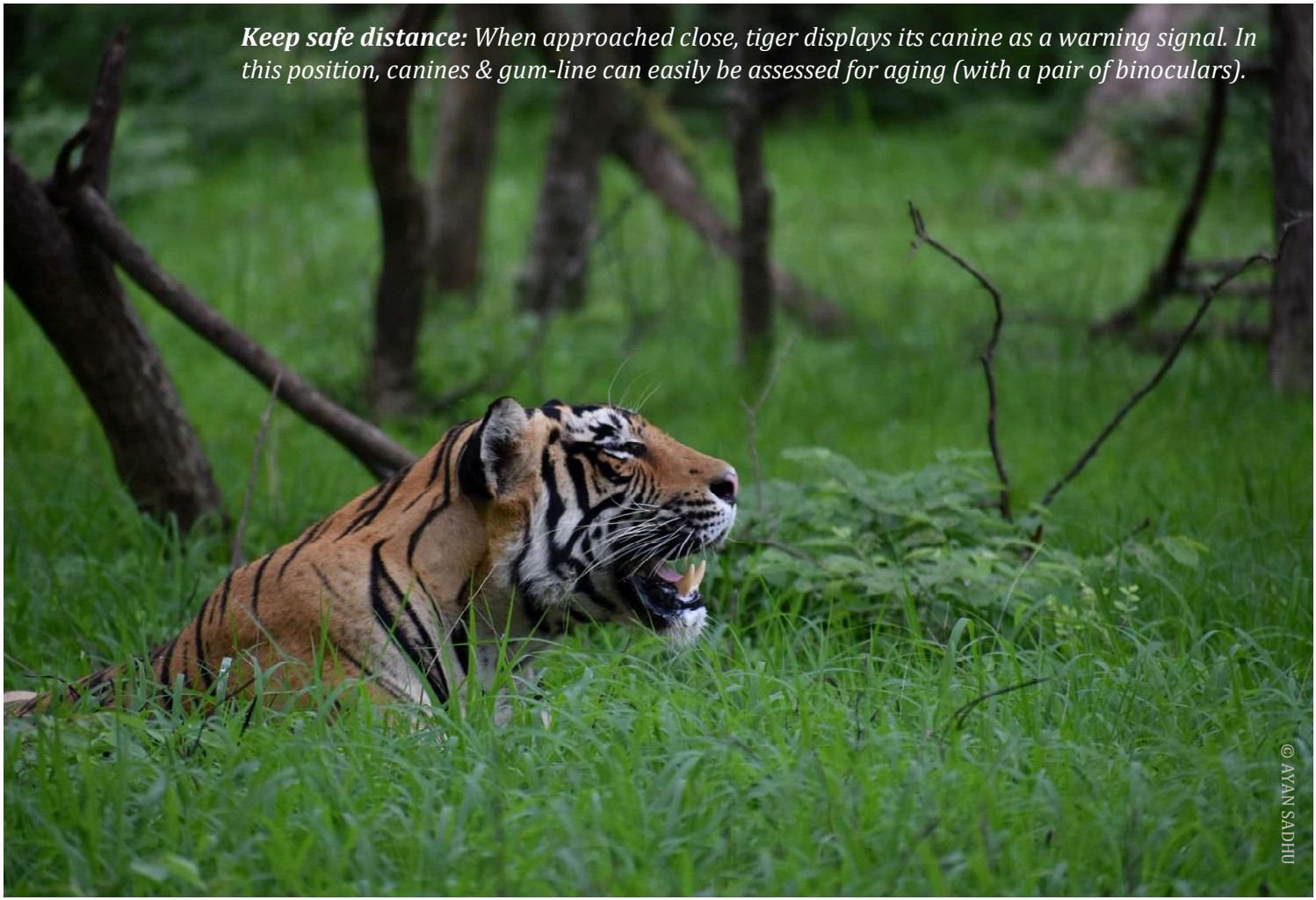

Keep safe distance: *When approached close, tiger displays its canine as a warning signal. In this position, canines & gum-line can easily be assessed for aging (with a pair of binoculars).*

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We have recorded GPS location of the dispersing tigers by observing their fresh pugmarks, livestock kill/attack (along with other signs), and by interrogating the local villagers.

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Supplementary material(s)

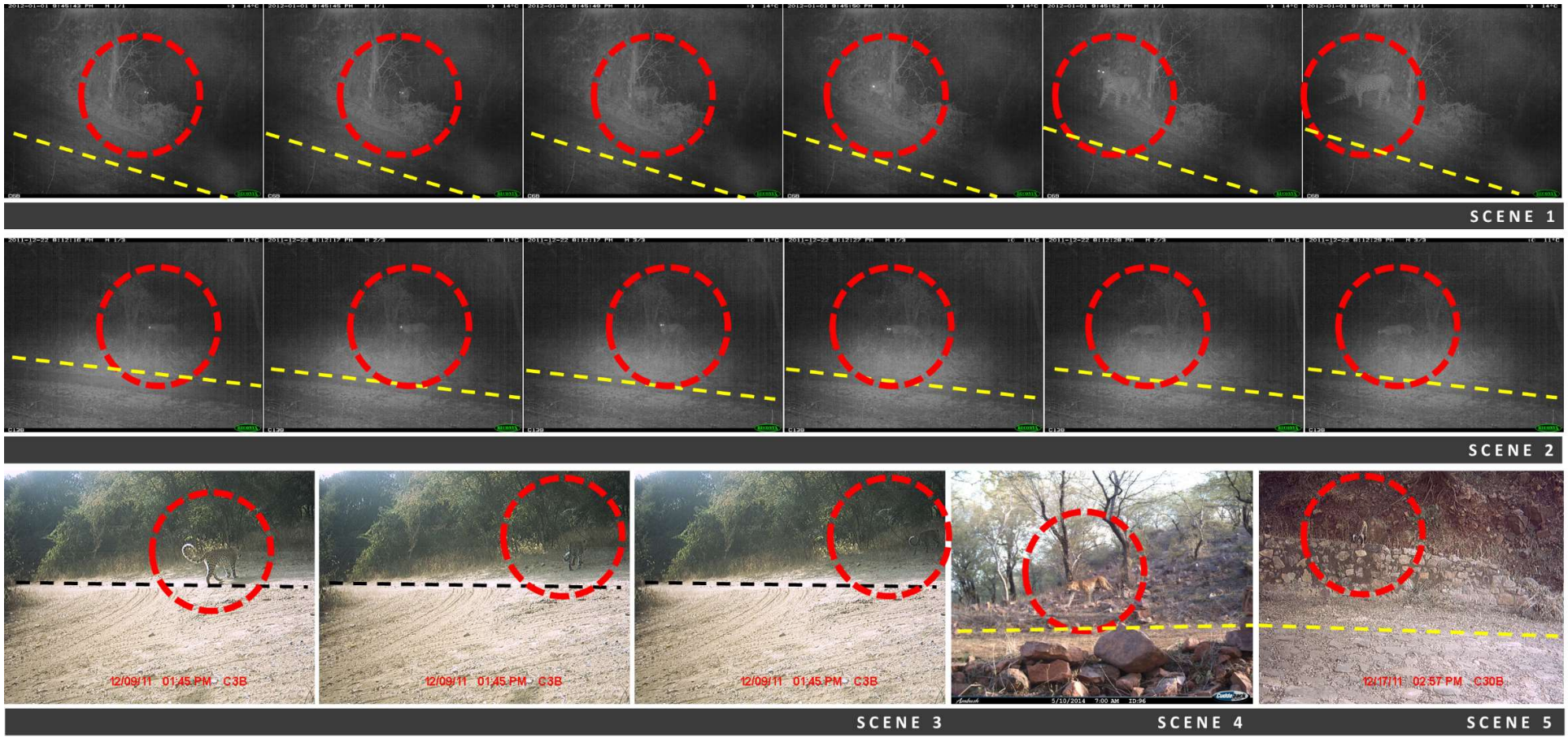

Figure 4.S1: *Camera trap photographs of leopard individuals (red dashed circles) from different detection events recorded how leopards were using the small/narrower trails over the large animal trails/mud roads (yellow dashed line). Different scenes are depicting different series of event.*

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