PLAYING IT SAFE? TIGER MOVEMENT AND LIVESTOCK DEPREDATION PATTERNS IN PANNA TIGER RESERVE, CENTRAL INDIA

A THESIS

Submitted by

MANU MOHAN K

For the award of the Degree of
MASTER OF SCIENCE
IN
WILDLIFE SCIENCE

Under the guidance of
DR. K RAMESH
&
DR. S SATHYAKUMAR

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

SAURASHTRA UNIVERSITY
RAJKOT- 360 005

JULY - 2021

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DECLARATION

I, **Manu Mohan K**, hereby declare that the research work entitled **"Playing it safe? Tiger movement and livestock depredation patterns in Panna Tiger Reserve, Central India",** carried out in partial fulfilment of M.Sc. (Wildlife Science) degree of Saurashtra University, Rajkot is an original piece of research. This research work was carried out under the supervision of **Dr. K Ramesh** and co-supervision of **Dr. S Sathyakumar**, at the Wildlife Institute of India from December 2020 to July 2021. I hereby declare that this work has not been submitted in any form for any other degree or diploma at any university or other institution.

Date: 16th July 2021

Place: Dehradun

Mr Manu Mohan K

(XVII M.Sc. Wildlife Science)

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
इ.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई–मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

CERTIFICATE

This is to certify that Mr. **Manu Mohan K** has carried out an original piece of research in partial fulfilment of Master's Degree in Wildlife Science of the Saurashtra University, Rajkot, Gujarat. The topic of his dissertation was "**Playing it safe? Tiger movement and livestock depredation patterns in Panna Tiger Reserve, Central India**". The study was carried out under our supervision from December 2020 to July 2021. We hereby certify that this work has not been submitted for any degree to any university.

K Ramesh, PhD
(Supervisor)
Scientist-E,
Department of Landscape Level Planning and Management,
Wildlife Institute of India
Chandrabani, Dehradun
Uttarakhand, India -248 001

S. Sathyakumar, PhD
(Co-supervisor)
Scientist-G,
Department of Endangered Species Management,
Wildlife Institute of India
Chandrabani, Dehradun
Uttarakhand, India -248 001

Date: 16th July 2021

Place: Dehradun

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई-मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

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(Sunita Agarwal)
Librarian
Wildlife Institute of India
Dehradun

Dr. K Ramesh
Supervisor

पत्रपेटी सं० 18, चन्द्रबनी, देहरादून – 248 001, उत्तराखण्ड, भारत
Post Box No. 18, Chandrabani, Dehradun - 248 001, Uttarakhand, INDIA
ई.पी.ए.बी.एक्स : +91-135-2640114, 2640115, 2646100 फैक्स : 0135-2640117
EPABX : +91-135-2640114, 2640115, 2646100 Fax : 0135-2640117
ई–मेल/E-mail : wii@wii.gov.in वेब/Website : www.wii.gov.in

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Manu Mohan

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EXECUTIVE SUMMARY

The movement of large carnivores in human-dominated landscapes is not uncommon anymore. While their presence is superficially tolerated or ignored, it is a consistent cause of concern to the people living in its proximity, due to competing interests in sharing of resources and direct threat to human lives. Carnivores incur energetic costs in the form of restricted activity and having to make spatial and temporal activity adjustments. Humans, on the other hand, face losses from livestock depredation and/or loss of lives. Depredation patterns of livestock by carnivores are associated with a variety of factors including habitat structure as well as movement patterns of carnivores in relation to anthropogenic and livestock activity. Hence, deducing movement patterns of the groups in conflict is an important step in understanding the dynamics of conflict patterns at fine scales. Supplemented by models to predict the probability of conflicts spatially which delineates conflict hotspots, site-specific mitigation measures could be devised.

To understand such patterns of carnivore movement and relation to livestock depredation events, I conducted this study in a human-dominated region adjacent to the Critical Tiger Habitat of Panna Tiger Reserve in central India from December 2020 to April 2021, within an area of 200 km^2. The broad objective was to model the conflict probability based on the proportion of the human-dominated area used by tigers, its intensity of use and spatio-temporal activity within the area, in response to human disturbances. For this, I used intensive camera trap sampling at fine-scale within grids (1 km x 1 km) across the entire study area. Movement parameters of tigers such as displacement and distance to villages in day and night were also analysed by monitoring two GPS-collared tigers in the study area. Occupancy estimates showed 74% of the sampled area being used by tigers, with the relative abundance of a large-

bodied wild prey (sambar) as the strongest predictor. In addition, a clear positive trend in the relative abundance index of tigers with distance to villages was observed. The temporal activities of the tigers also showed a significant difference in median activity time, shifting towards the night along with moderate diurnal activity at higher distances from villages. The tigers exhibited both crepuscular and nocturnal activity at close distances to villages.

The movement range analyses of the tigers using camera traps showed the study area being used by 17 tigers, with 9 of them being adults (>3 years of age). Fixed Kernel Density home-range estimates of the two GPS-collared tigers showed a considerable proportion of their home range areas falling within village boundaries (10%) and an average of 16% of all GPS locations of the tigers fell within 0-100 metres from villages. Despite such high exploratory use of areas within and close distances to villages by sub-adults, there were relatively low incidences of conflict between the tigers and villagers in the study area. Finally, to assess the extent of risk and predict the probability of livestock depredation in the area, Generalized Linear Models were used. The best-fit model indicated a significant negative effect of distance to villages and highway to the probability of livestock depredation. Linear intrusions through highway and forest trails from villages allow easy access to livestock and herders for the utilization of the multi-use buffer areas of the Reserve as well as the tigers to come in proximity to settlements. Corralling of livestock in the night, avoiding free-ranging and grazing of livestock in the identified conflict hotspots, incentivisation of alternate source of livelihood by strengthening the institutions such as Eco-Development Committees, along with continuous monitoring of tigers which range close to human settlements are discussed as some of the important measures which can be adopted to decrease the interfaces leading to tiger-human conflict in Panna Tiger Reserve.

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INTRODUCTION

Over the years, there has been a drastic decrease in the available forested habitat worldwide and as a result, a major section of wildlife is facing severe resource scarcity. Due to this, a host of species have witnessed a decrease in their distribution range as a consequence of extirpation from some of their natural habitats. Competing interests for resources by humans and wildlife acts as the driver for such processes and could unfold in a multitude of ways including habitat loss and fragmentation of the wild species as well as their persecution when they come in close contact with humans (Inskip and Zimmermann, 2009; Treves and Karanth, 2003). Large carnivores are especially susceptible to such conditions and are prone to negative interactions with humans due to their role as top predators in the ecosystem and are perceived as direct competitors (Sillero-Zubiri and Laurenson, 2001). The instances of fatality are not restricted to just either one of the two groups. Humans incur the costs in more than one way, which includes opportunity costs arising due to limited access to resources, loss of livestock through depredation, and even loss of human lives in extreme cases (Herrero et al., 2013). Such a complex suite of interactions further puts the already declining carnivore population under pressure leading to their extirpation even from protected habitats. Nevertheless, efforts are being made to revive the population of several carnivore species through an array of conservation strategies. In India, the conservation and recovery of the tiger population is a prime example (Jackson, 2010; Jhala et al., 2019). The recovery of population and range extension of tigers and other large carnivores through such conservation tools could also give rise to conflicts and manifest as a restrictive conservation measure disturbing the livelihood and economic development of the native communities (Breitenmoser, 1998). The first-ever large carnivore reintroduction for conservation purposes occurred in Białowieża Forest of

Poland in 1937 where Brown bears were reintroduced (IUCN 2013). Although such a conservation approach was far ahead of its time, one of the weaknesses of the undertaking was that the local people were not sensitized about the ways to coexist with a reintroduced carnivore and this lead to casualties involving both humans and animals (Samojlik et al., 2018). The support of local communities is imperative in the success of any such conservation effort (Tilson and Nyhus, 1998).

Reviving large carnivore populations in a habitat is an extended and expensive process. A consequence of rising large carnivore numbers in protected areas is the spill-over of individuals from the prime habitats to the peripheries of a Reserve, where the resource abundance in human-altered environments also inducing the drive (Bunnefeld et al., 2006). With a highly fragmented and isolated protected area network of the country, the movement of such spilling over of individuals to the adjoining human-dominated areas is inevitable. Such a human-wildlife interface furthers occurrences of conflict between the two groups. However, it is only when the trade-offs the animal makes between risks and resources associated with an area is quantified, would enable understanding the degree of conflict or a potential landscape of co-existence (Gehr et al., 2017; Oriol-Cotterill et al., 2015). A variety of biophysical variables affect how a large carnivore behaves with respect to its movement and choice of resources in human-dominated areas (Wilkinson et al., 2020), which includes geographical and habitat factors such as elevation, slope, vegetation cover (Rostro-García et al., 2016), proximity to human infrastructures (Michalski et al., 2006) among others. Conflict mitigation efforts, even when concentrated in time and space would only be effective once such ecological mechanisms are empirically understood (Goswami et al., 2015; Miller, 2015).

Literature Review

With the rise in anthropogenic pressures across the globe, conflicts with wild animals have become more common in the recent past and are more so the case with carnivore species (Treves and Karanth, 2003). Such circumstances arise when humans and wildlife have to negotiate to live in close proximity to each other, competing for food resources and space (Inskip and Zimmermann, 2009). Large carnivores are one such extremely vulnerable group of animals that are subject to direct persecution, habitat loss and fragmentation which leads to a decrease in their overall range (Ripple et al., 2014). Such a reduction of the area of their natural habitat causes them to venture into human-dominated areas in search of prey and new territories (Chapron et al., 2014; Ripple et al., 2014). As a result, humans also face losses in the form of livestock depredation, which in some cases affect the daily sustenance and livelihood of people (Herrero et al., 2013).

Livestock depredation by large carnivores is the reason for over 40% of conflicts with humans (Sillero-Zubiri and Laurenson, 2001). Such negative interactions serve as the root cause hindering large carnivore conservation (Thirgood et al., 2005). More than 75% of the world's felid species are affected by conflict with humans and the severity increases with an increase in body mass of the felid (Inskip and Zimmermann, 2009) which exemplifies the threat that big cats such as tigers the face.

In India, recovery and conservation of large carnivore population, specifically, that of tigers has gained much momentum compared to other carnivores and tiger-range countries owing to proactive management efforts (Jackson, 2010) backed by the

Wildlife (Protection) Act, 1972 which was instrumental in setting up of protected areas, curbing hunting and other activities which would affect the healthy population of the big cats. According to Jhala et al., (2019), tiger numbers have shown a 42% rise from the population estimates of 2010, towards achieving the TX2 goal of the St. Petersburg Declaration (Nyhus and Tekancic, 2010). The population rise is also attributed to conservation programmes such as reintroduction. In India, few protected areas have witnessed successful reintroduction of tigers (Ramesh et al., 2015; Sankar et al., 2010; Sarkar et al., 2016). Through active protection and augmentation leading to population growth, tigers are now seen in areas where they were not able to thrive before. Through the course of the establishment of a viable population and as it increases further, the risk of negative interactions with the adjacent local community (where human population density increases simultaneously) also tends to increase.

Animals adapt differently to anthropogenic disturbances with respect to their space use and time of activity (Tuomainen and Candolin, 2011). The animals would either learn to avoid areas of high risk and disturbance according to the risk-disturbance hypothesis (Frid and Dill, 2002) or get habituated to the alternate resource along with the moderate risks associated with it (Lima and Bednekoff, 1999) and adopting either one of the behaviour depends on the extent of threats and resources present. In line with the former, the concept of landscape of fear (Laundré et al., 2001) has been widely used in analysing the behaviour of prey in the prey-predator system. However, in the framework of human-wildlife conflict, the concept can also be applied to carnivores in human-dominated areas due to the risk of persecution. Valeix et al., (2012) tested such behaviour and found that carnivores avoided spatial and temporal overlap with humans and had a high rate of movement when in human-dominated

areas. ‘Nocturnal refuge’ of a wide array of mammals due to predominant diurnal human activity is also well-established around the world (Gaynor et al., 2018). In situations where the activity of humans are lethal, such as areas that witness high poaching, nocturnal behaviour of animals are associated with increased survival probability (Murray and St. Clair, 2015). Human-induced fear or disturbance have also been associated with the surplus killing of wild prey as, at times, the predators have to abandon the kills made near human settlements (Smith et al., 2015) as well as higher kill rate of livestock by large carnivores, especially in low-density wild prey areas (Khorozyan et al., 2015) and in areas where the lower density of wild prey is due to their illegal hunting practices (Soofi et al., 2019). Surplus kills are known to be behavioural trade-offs that the predator makes to satisfy opposing environmental factors (Kruuk, 1972).

On the other hand, large carnivores which acclimate to such conditions due to abundant resources might not exhibit the fear or avoidance behaviour with respect to human activities and hence turn into bold individuals (Bombieri et al., 2021; Tuomainen and Candolin, 2011). Such individuals have a higher chance of coming into conflict and direct competition with humans and as a result, generate a negative attitude towards their conservation (Johansson et al., 2016).

Technological advancements such as the application of GPS in animal movement tracking studies have allowed us to understand the behaviour of wild animals in varied conditions at much finer scales than before (Kays et al., 2015). It also allows us to identify individual variations within species in response to gradations in resources or disturbance (Spiegel et al., 2017). Coupled with conventional animal

movement monitoring techniques through camera traps and application of appropriate spatial risk prediction models (Miller, 2015; Treves et al., 2011) would make for effective tools in the suite of human-carnivore conflict mitigation measures.

India, with the second-highest human population density in the world with 1.37 billion people (Department of Economic and Social Affairs, 2019) where the human-dominated landscapes also supporting a variety of adaptable large carnivore occurrences due to the presence of domestic prey (Athreya et al., 2016; Majgaonkar et al., 2019), conflicts duly ensues. In parts of the country, it has been shown that over 50% of livestock depredation by large carnivores occur within villages and an annual loss of 16% of average household income is incurred as a result (Madhusudan, 2003). Hence, understanding the spatio-temporal dynamics of large carnivore movement in human-dominated landscapes is imperative for effective management and conservation of the species and to promote a landscape of co-existence. Therefore, this study was carried out in the human-dominated buffer zone area of Panna Tiger Reserve, Madhya Pradesh from December 2020 to April 2021 with the following objective.

OBJECTIVE

To assess the spatio-temporal patterns of tiger movement and model its conflict probability in the human-dominated region of Panna Tiger Reserve.

Research Questions

1. What proportion of the human-dominated area is used by tigers and what is the frequency of occurrence?
2. Where are the activity centres of tigers in time & space? Is it influenced by proximity to human settlements?
3. What are the movement and ranging patterns of tigers? Does the movement rate change to negotiate areas close to human settlements?
4. Where are the hotspots of livestock depredation and what are the strongest predictors of depredation probability within the study area?

THE STUDY AREA

General Description

The study was carried out in Panna Tiger Reserve (PTR), which spans across the districts of Chhatarpur, Damoh and Panna, northern-central Madhya Pradesh, Central India. The extent of the reserve is between 79° 45' to 80° 09' E longitudes and 24° 27' to 24° 46' N latitudes and located in the Biogeographic Province 6A Deccan Peninsula - Central Highlands (Rodgers et al., 2002) (Figure 1). Topographically, PTR is divided into the Ken river valley, where the Ken river cuts through the reserve (Mandla and Chandranagar Ranges), Hinnauta plateau (Hinnauta Range) and the Talgaon plateau (Panna Range) of the Vindhyan Range. The Reserve has an area of 1598 km^2 of which 576 km^2 is core (Critical Tiger Habitat) and 1022 km^2 is the buffer zone (Multiple Use Area) (Murthy, 2018).

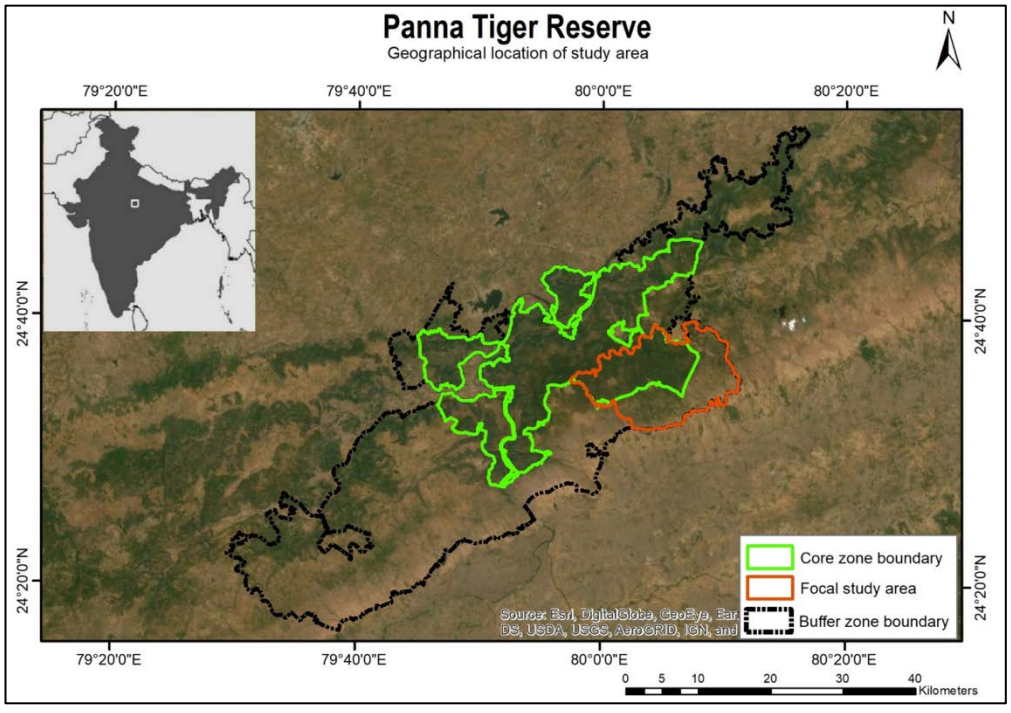

Figure 1. Geographical location of the study area showing core, buffer and the focal area of study

Flora and Fauna

The vegetation type includes Northern tropical dry deciduous mixed forest, Southern tropical dry deciduous teak mixed forest (with the northernmost natural distribution of teak), Dry deciduous scrub forest, *Boswellia* forest, *Anogeissus pendula* forest (easternmost natural distribution) and dry bamboo brakes (Champion and Seth, 1968). Along with *Panthera tigris* (The Tiger), other mammal life of the reserve includes *Panthera pardus* (Leopard), *Melursus ursinus* (Sloth bear), *Hyaena hyaena* (Striped hyaena), *Cuon alpinus* (Wild dog), *Felis chaus* (Jungle cat), *Canis aureus* (Golden jackal), *Rusa unicolor* (Sambar), *Axis axis* (Chital), *Boselaphus tragocamelus* (Nilgai), *Gazella bennettii* (Indian gazelle), *Tetracerus quadricornis* (Four-horned antelope), *Sus scrofa* (Wild pig), *Semnopithecus entellus* (Northern plains gray langur) and others. The Reserve also consists of over 150 bird species, 50 species of fishes, 10 species of reptiles among others. (Ramesh et al., 2013).

Tiger extirpation and anthropogenic pressures: A brief history

The tiger population of PTR was functionally extinct in 2009. To recover the population, tigers were translocated from adjacent Reserves, with an initial founder stock of 6 individuals which were reintroduced between 2009 and 2014, three tigers (2 females and a male) from Bandhavgarh Tiger Reserve, Kanha Tiger Reserve and Pench Tiger Reserve. In 2011, two more captivity raised female tigers were released as experimental addition and in 2014, one more tigress was translocated from Pench Tiger Reserve (Sarkar et al., 2016). The number has now grown to more than 50 individuals in the reserve (Phase IV monitoring, 2020). Simultaneously, livestock depredation events have also been on the rise (Kolipaka et al., 2017).

With an increase in tiger population, the younger generations move out in search of new territories and resources. The later generations of reintroduced tigers in PTR have been seen to frequent human-dominated landscapes and the outer reaches of buffer areas (Kolipaka et al., 2018). Studies have also shown that the home ranges of tigers in PTR are three to four times larger than those known in other tropical habitats and is significantly exposed to anthropogenic edge effects (Chundawat et al., 2016; Sarkar et al., 2016). Between the years 2005 and 2007, 11 villages were relocated from inside the core area of the reserve. However, anthropogenic pressures are still considerably high, with the buffer zone of the Reserve housing an estimated human population of more than 43,000 along with approximately 25,000 cows, 15,000 goats, and 5000 domestic buffalo in the 42 villages (Kolipaka et al., 2015; Srivastava, 2014). The local community regularly use and have traditional rights to access the buffer forests which are regulated informally than through government channels.

Previous studies in the Central Indian landscape have assessed patterns of conflicts and its hotspots (Miller et al., 2016) and those based on incident site characteristics and social surveys/ interviews, analysing the dynamics of conflict from the people's perspective (Karanth et al., 2012). The proposed study in PTR allows us to look at the dynamics of conflict from the perspective of the conflict animal by utilizing fine-scale movement data available from GPS-collared tigers and intensive camera-trapping surveys. With increasing tiger population on one hand and consistent anthropogenic disturbance on the other, the Reserve grants us an opportunity to study the potential conflict between humans and a large carnivore, as a response to its growing population.

METHODS

Focal area of the study

The study was designed and executed in an area of about 200 km^2 in the south-eastern part of the Reserve, consisting of 3 ranges: Panna range of the core zone, Panna and Amanganj range of the buffer zone, was selected as the focal study area (Figure 2). The area was selected due to the following reasons:

- Intensive use and movement of collared as well as non-collared tigers.
- An area surrounded by human settlements and villages, with regular movement of humans and livestock within (Plate 5).
- 42% (107 out of 253) of all livestock depredation events by tigers according to the compensation records in Panna Tiger Reserve since 2018 occurred in the chosen area.

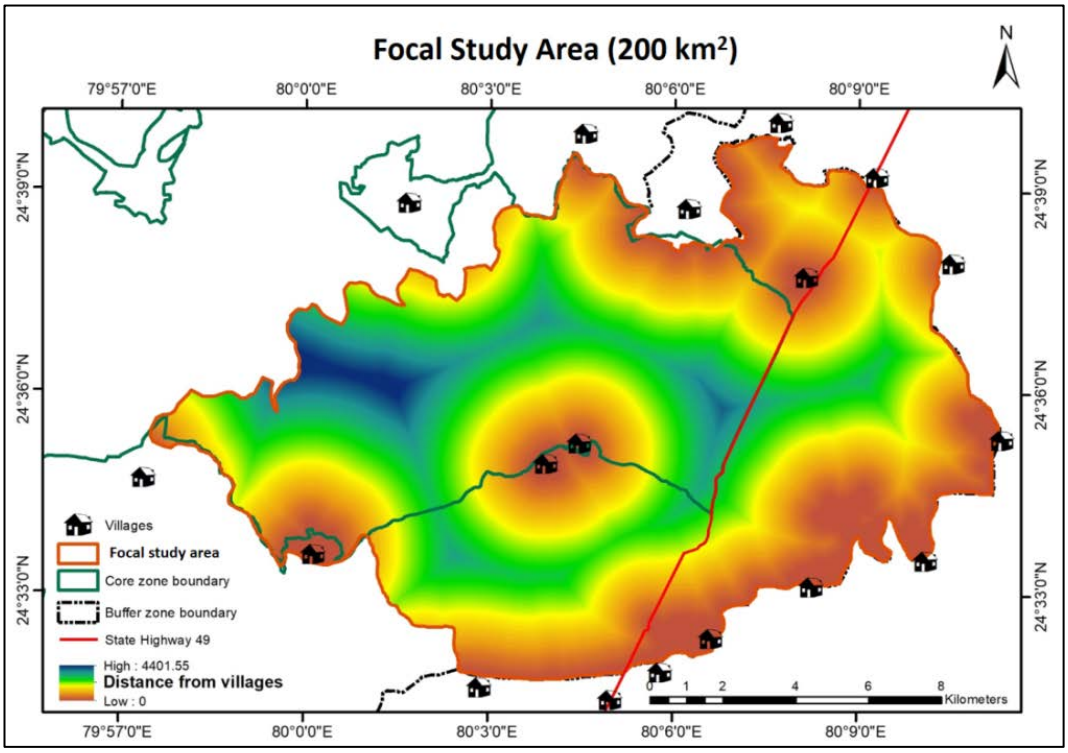

Figure 2. Focal area of the study showing the location of villages and the areas of anthropogenic influence around them.

Field Methods

The study was carried out from December 2020 to April 2021. The basecamp was located near the Hinauta gate of PTR. Field working schedules involved covering the study area regularly in a systematic manner. For logistic support, a jeep was available. The majority of the fieldwork effort was for the deployment and checking of camera traps. Equipment used during fieldwork included GPS (Garmin Etrex 10x), range finder, smartphone (and applications such as Locus Map) for various activities during camera trap sampling session and livestock kill site inspections.

Camera trap surveys

To understand the spatio-temporal movement and space use of animals, camera traps were deployed intensively throughout the study area evenly on the most suitable animal trails or forest paths and as close to the centroid of the representative grids as possible. Each camera trap represented a grid of 1 km x 1 km. The cameras were fixed at a height of 0.5-1 metre depending on the terrain, so that the plane of the photograph was parallel to the trail, to capture the flank region of all animals and enable individual identification of tigers. Few areas within or very close to human settlements were avoided to prevent theft and vandalism. Cuddeback C-1 camera traps with white flash were used for the survey. Each camera was set to capture photographs at an interval of 5 to 15 seconds based on the openness of the area as well as the intensity of anthropogenic movement in the day and Fast-As-Possible (FAP mode) at night. Each camera was checked for vandalism, malfunction or battery drainage and data was

collected at least once every 2 weeks (Plate 4). Damaged cameras were replaced wherever possible.

Monitoring GPS-collared tigers

Two GPS-collared tigers were available in the study area during the period of study to understand the fine-scale movement of tigers (Plate 1). Tigers were selected based on their movement outside the core areas of the Reserve, which ranged regularly near human settlements. Both tigers were collared in the winter of 2020-2021. The first to be collared was a tigress (P213-63), 27 months of age at the time of collaring and the second, a male tiger (P234-31), with an age of 14 months. Both the animals were fitted with a GPS/Satellite/VHF (Vetronics Vertex) radio collar and were set to transmit location data at 1-hour intervals to understand their movement at fine scales. The tigers were regularly monitored, especially during livestock depredation events and when locations were recorded close to villages through VHF-receivers.

Livestock-kill/GPS-cluster site inspection

To understand spatial patterns of livestock depredation, the site inspection was conducted at clusters of GPS fixes of collared tigers, as well as known locations of livestock depredation events during the study period. Clusters for inspection was based on concentrated GPS fixes in an area spanning 2 or more days, within a radius of 50-100 metres, since the average drag distance of livestock kills by tigers were known to be around 50 ± 54metres (Miller et al., 2015) in the Central Indian landscape. The sites were inspected only after the tiger had moved away from the suspected kill sites. Apart from GPS coordinates of confirmed kill sites, ocular estimates of other characters such

as canopy cover, horizontal visibility, shrub cover, presence of water source, distance to nearest forest roads/trails were also recorded (Plate 6). Livestock kill compensation records were also accessed from the forest department and all the locations within the season (late November to early April) of the study period, since 2018 were used for the analysis of livestock depredation patterns and model the conflict probability.

Analytical Methods

Processing of camera trap data

Camera trap data management and processing were done using R package: camtrapR (Niedballa et al., 2016). Consecutive capture at an interval of 30 minutes was considered as an independent capture for each species. Relative Abundance Index (RAI) of species in consideration were calculated as independent captures per day, scaled to 100 trap nights (O'Brien et al., 2003). Camera trap operation matrix and detection histories of species were also created for further analyses.

Processing of spatial data

Multiple raster layers were created for the extraction of different covariates within the study area. Sentinel-2 MSI: MultiSpectral Instrument, Level-2A (ESA, 2021), with a spatial resolution of 10 metres was used as the base satellite imagery for calculating various indices such as NDVI, NDWI and preparation of Land Use Land Cover layer. CartoDEM (ASST, 2008) was acquired from Bhuvan portal (NRSC) for extraction of elevation and slope. Villages and roads in the study area were digitized from Google Earth Pro (ver. 7.3.3.7786). All raster calculations and processing were done in Google Earth Engine (Gorelick et al., 2017) and ArcGIS 10.6 (ESRI, 2018).

Q1. Proportion of human-dominated area used by tigers and frequency of occurrence

The proportion of area occupied by tigers or probability of space use was estimated using an occupancy framework (MacKenzie et al., 2002) using the tigers' detection history with camera trap data, along with site covariates derived from camera trap and remotely sensed data in the Program PRESENCE (version 2.13.11) (Hines, 2006). The output gave the probability of space use with predictive habitat covariates corrected for detection probability. The occupancy model estimates two variables– ψ (psi), which is the probability of occupancy of a species at a site, and ρ (phi), which is the probability of detection of a species if it is present. Occupancy was estimated by keeping the probability of detection constant. The best fit model and model averaging of the top models were used to estimate the overall proportion of area occupied by tigers. The best models were chosen based on the lowest AIC values and the c-hat value was estimated through bootstrapping 1000 iterations to check for overdispersion.

To represent the frequency of occurrence, ordinary spherical kriging, a spatial interpolation method (Childs, 2004) was performed to produce a raster surface representing a continuum of areas between high and low space utilization of tigers with RAI as the variable for interpolation using Spatial Analyst tool in ArcGIS 10.6 (ESRI).

Q2. Activity centres of tigers in time & space and its variation with proximity to human settlements

The entire study area was graded into distance class of 1 km width based on distance from villages, resulting in 4 classes: 0-1 km, 1-2 km, 2-3 km and 3-4 km (hereafter referred to as distance class) to understand how the spatio-temporal use of animals

differed with varying proximity to human settlements. The distance classes were fixed at an interval of 1 km as it was known that humans used areas of the Reserve for fuelwood and fodder collection within a radius of 2 km from the village boundary and livestock herders grazed their animals till a distance of 5 km from the core of villages, with one of the highest travel distance seasons as winter (Kolipaka et al., 2017). This was also confirmed by observation during field-work. The camera trapping session started in late December 2020 and extended till early April 2021 and hence included the majority of the winter season. To discern the variability in their intensity of space use and movement, sampling at least at 1 km distance interval was essential. It was then compared to the tigers' activity for deduction of selection or avoidance. Accordingly, over 90% of all deployed camera traps were within 0-3 km distance from village boundaries (Table 3).

Spatial activity

Camera trap data across each distance class were pooled in to understand the variation in RAI in the respective groups. Variation in unique individual tiger captures as well as the capture rates of proportion of male and female tigers at increasing distances from villages were also diagnosed. This was done to eliminate any bias in the calculated relative abundance in each distance class due to difference in behaviour of males and females. Females tigers have smaller home ranges compared to males and hence, the number of captures at intensive camera trap sampling at 1 km x 1 km grids would result in higher captures of females. With larger home ranges, male tigers could have relatively higher captures in areas abutting villages and hence, there could also be variation in proportion of male and female captures at increasing distance from villages. Box-whisker plots were used to show differences and trends in abundance as

well as number of unique individual tigers detected at each distance class. Non-parametric Kruskal-Wallis test was used to test whether the difference between each group is statistically significant. To check for other significant predictors of tiger RAI, independent captures of tigers were modelled in a Generalized Linear Models framework. Capture rates were standardized for varying sampling periods of camera traps by using the number of sampling days as the offset variable in the GLM models. Model fit was checked both with Poisson and negative binomial family. Finally, the modelling was done with negative binomial due to its better model fit, correcting for overdispersion. The best model was selected based on the lowest AICc criteria, without any uninformative parameters. All modelling was done in R (Core Team, 2020) and RStudio (Team 2019), negative binomial GLM and model selection using R package: MuMIn (Barton and Barton, 2015) and data visualization using R package: ggplot2 (Wickham, 2011).

Temporal activity

Similar to the procedure to understand variation in spatial activity, the temporal activity of tigers was also calculated for each distance class separately. The diel activity patterns were estimated using a non-parametric method of kernel density (Worton, 1989). To determine whether there was a shift in tiger activity at each distance class and if it was significant, Fisher's Nonparametric Test for common median direction was used. A non-parametric test for the median shift was used instead of a parametric test since each set of samples were checked for uniformity and if the samples represented von Mises distribution with bias-corrected concentration parameter greater than 1. None of the four sets of samples had fit the criteria (Table

16). All circular statistical tests were performed using R package: circular (Agostinelli and Lund, 2013) and methods and functions described by Pewsey et al., (2013).

To explain the shifts in temporal patterns with respect to anthropogenic disturbance, activity density curves of humans and livestock were overlaid with that of tigers'. To discern the degree of activity overlap of the tiger, livestock and humans, the coefficient of overlapping, Δ was used, which uses kernel density fitted to the given data so as to represent the true density. Since the number of all the samples used for activity overlap were > 50, $\widehat{\Delta}_4$ was used as the estimator (Ridout and Linkie, 2009; Schmid and Schmidt, 2006). All temporal pattern analysis of kernel density and activity overlap was done using R packages: camtrapR (Niedballa et al., 2016) and overlap (Meredith and Ridout, 2014).

Q3. Movement patterns of tigers and variation in movement rate to negotiate areas close to human settlements

To understand general ranging patterns of tigers in the study area, tigers were individually identified from photographic captures of camera trap and individual ranges were estimated with 100% Minimum Convex Polygon.

To determine finer movement parameters, GPS locations of collared tigers were acquired from VECTRONIC Aerospace, Inventa WebApp Version: 1.1.116 (Inventa Wildlife Monitoring) for the period of study (January to April 2021). All GPS fixes at irregular intervals were omitted from the analysis. 95% fixed kernel density estimates were used to determine the home range of animals. 95% was used to exclude

occasional exploratory movements of the animals (Burt, 1943). Home ranges were created and estimated using R package: adehabitatHR (Calenge, 2011).

To determine how the animals' movement pattern changes to negotiate areas close to human settlements, the displacement (step-length per unit time) was determined for day and night separately as well as the average distances of the animals' location to human settlements in day and night. The step-length is the Euclidean distance between two consecutive GPS fixes of the animal's trajectory. The displacement for both the subject animals in the study is specified in metre/hour (m/hr). Due to the highly skewed nature of the distribution of step-lengths, median and median absolute deviance (MAD) was used to understand the spread of the data instead of mean and standard deviation. For the same reason, Mann-Whitney U test, a non-parametric test for significance was used to compare the medians displacement of animals as well as their distances to human settlements in night and day. All locations recorded between and including 06:30 hours to 18:30 hours were classified as day-time activity and others as in the night-time.

Q4. Conflict probability prediction and risk mapping

Livestock kills sites information recorded during the study period as well as from the forest department compensation records were converted to presence-absence format, in which each 1 km x 1 km grid cells with at least one depredation event was given a value of 1 and those without an occurrence was given a value of 0. Logistic regression models were then run with site-specific covariates (binomial GLM). A total of 14 variables were initially considered for the model based on field observations which were thought to be associated with depredation events. Covariates were also extracted

based on previous studies on tiger-livestock depredation patterns (Miller et al., 2016, 2015; Rostro-García et al., 2016; Soh et al., 2014). The covariates for each grid-cell included: Slope, elevation; distance to villages, highway and water body; RAI of humans, livestock, wild prey and tiger; area of dense forest, open forest, scrubland and open land.

A correlation matrix among all the covariates was built and correlated variables with Pearson correlation coefficient ≥ 0.7 which were ecologically less important were removed from analyses. NDVI was correlated with types of vegetation cover and slope. Since NDVI can act as a single variable that can be used to define the intensity of vegetation at each site, all the other vegetation cover variables ($0.8 \geq r \leq -0.6$), as well as slope ($r \geq 0.7$), was excluded from analyses. Finally, 9 covariates were available for modelling (see Figure 18). Interactive as well as the quadratic relationship of different variables were also explored since variables such as distance to roads and villages are known to have a threshold relationship with livestock depredation incidents (Miller et al., 2016). The best model was selected based on the lowest AICc value (AIC corrected for sample size). Covariates with the significant beta-coefficients were considered as the strongest predictors for livestock depredation.

Conflict risk prediction map

The probability of livestock depredation at each grid-cell was calculated using the transformed estimates of beta-coefficients of the predictor variables. The transformation of a logistic link is given by the formula: $\mathbf{y = e^x / (1 + e^x).}$

To test the accuracy of the model, the area under the curve (AUC) of the best model's receiver operating characteristic (ROC) was calculated and ROC was plotted.

AUC in other words can be defined as the integral of the accuracy of the logistic model at every possible threshold values between 0 and 1. AUC values range from 0 to 1, in which an ideal model would have a value of 1. A model with a value of 0 would be reciprocating the results, i.e. it would predict true presence as absence and vice-versa. ROC curve is plotted with False Positive Rates (FPR), which is 1-specificity on the x-axis and True Positive Rates (TPR) or sensitivity on the y-axis. All models were run in R (Core Team, 2020) and RStudio (Team 2019). ROC curve was plotted and AUC was calculated using R package: Deducer (Fellows, 2012).

RESULTS

Photo-captures synthesis

A total of 191 camera traps were deployed across the 200 km^2 study area. The camera trap survey was performed from late December 2020 to early April 2021. A total effort of 15,607 trap nights resulted in 53,484 independent captures, which included carnivores, domestic prey, wild prey, human, among others (Table 15). In the context of the current study, wild prey is referred to as the combination of Sambar, Chital, Wild pig and Nilgai as they are known to be the preferred prey of tigers in the landscape (Chundawat, 2018); domestic prey/livestock includes goat, buffalo, cow and ox. At least 29 wild mammal species were photo-captured during the entire sampling period. The average number of sampling days of camera traps were 81.7 ± 12.7 (S.D).

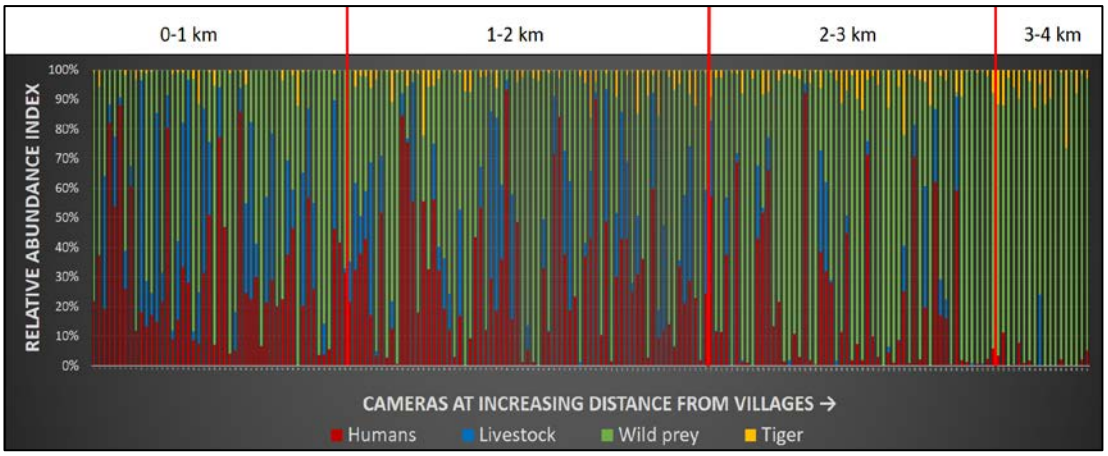

Figure 3. Summary of RAI at increasing distance from villages for different species. %RAI on y-axis and camera traps at increasing distance from villages on the x-axis

Q1. Proportion of human-dominated area used by tigers and frequency of occurrence

To build detection histories of tigers to run occupancy, camera trap data from the first 100 days of sampling was used. Each day was considered as one sampling occasion,

which thereby resulted in 100 occasions. In total, 15 site covariates were used in modelling the probability of space use by tigers. The naïve occupancy was estimated to be 0.73 (Table 2).

Table 1. Top models within Δ AIC 2, null and global models of tiger occupancy

Model	AIC	Δ AIC	AIC wt	Likelihood	# Param	–2LL
Ψ(sambar), ρ(.)	6078.86	0	0.3971	1	3	6072.86
Ψ(sambar + chital), ρ(.)	6080.15	1.29	0.2083	0.5247	4	6072.15
Ψ(sambar + chital + livestock), ρ(.)	6080.66	1.8	0.1614	0.4066	5	6070.66
Ψ(.), ρ(.)	6356.8	277.94	0	0	2	6352.8
Ψ(all covariates), ρ(.)	6386.8	307.94	0	0	17	6352.8

The best fit model for predicting the probability of space use by tigers was with the relative abundance index of sambar as site covariates (Table 1).

Table 2. Probability of space use by tigers, corrected for detection probability and influence of habitat covariates for the best fit model

naive Ψ	Ψ	S.E	95 % C.I		p-value	c-hat
			Lower	Upper		
0.733	0.738	0.044	0.64	0.811	<0.001	0.834

For model averaging, 3 models, along with the best fit model were considered within ΔAIC of 2 from the top model (Burnham and Anderson, 2002). However, since the effect of each covariate in the 3 models were non-significant, model averaging was finally avoided (Arnold, 2010). To represent the frequency of occurrence of tigers in the study area, the RAI of tigers recorded at each camera trap station were spatially interpolated using ordinary spherical kriging (Figure 4).

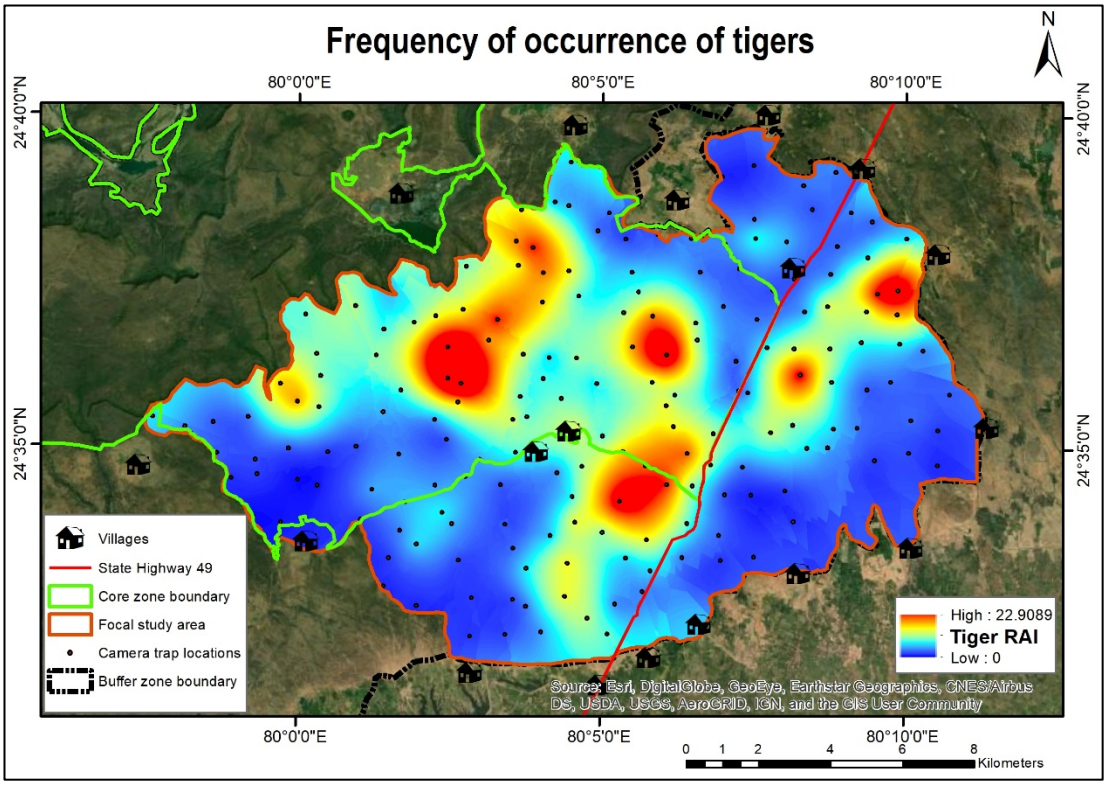

Figure 4. Frequency of occurrence of tigers

Q2. Activity centres of tigers in time & space and its variation with proximity to human settlements

A total of 878 independent captures of tigers were available for analysis from 191 camera traps at 4 distance classes (Table 3).

Table 3. Distribution of camera traps at each distance class

Distance class	No. of camera traps	No. of independent tiger captures
0-1 km	50	87
1-2 km	69	279
2-3 km	55	362
3-4 km	17	150
Total	191	878

Spatial activity

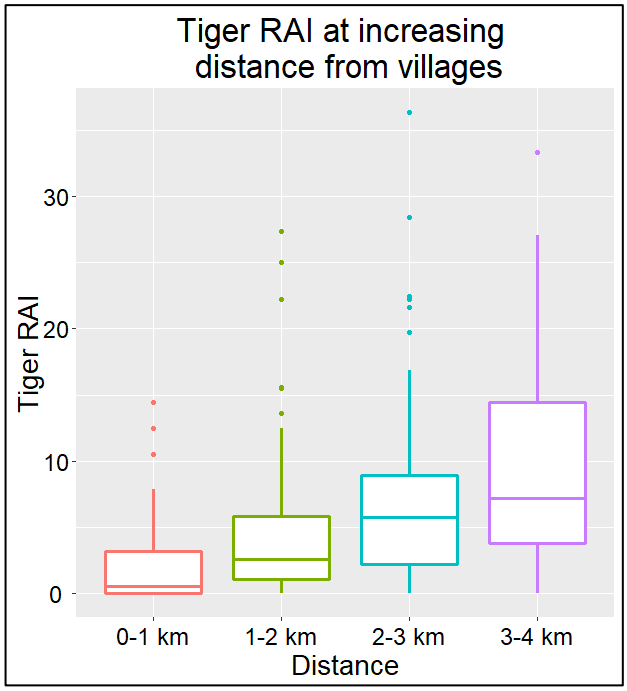

Figure 5. Box-whisker plot of tiger RAI at each distance class

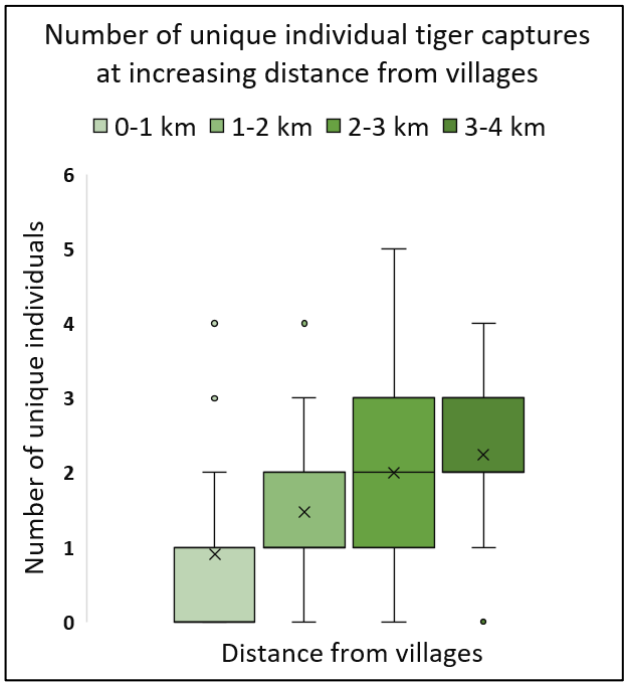

Figure 6. Box-whisker plot of unique individual tigers detected at each distance class

The boxplots showed a general positive trend in RAI (Figure 5) as well as the number of unique individuals captured with increasing distance from human settlements (Figure 6). Variation in each distance class was statistically significant as indicated by the results of Kruskal-Wallis test (Table 4).

Table 4. Krukal-Wallis test to check for differences within RAI at each distance class

Kruskal-Wallis test	
H (test statistic)	31.72
α	0.05
df	3
χ_c^2	7.815
p-value	<0.001

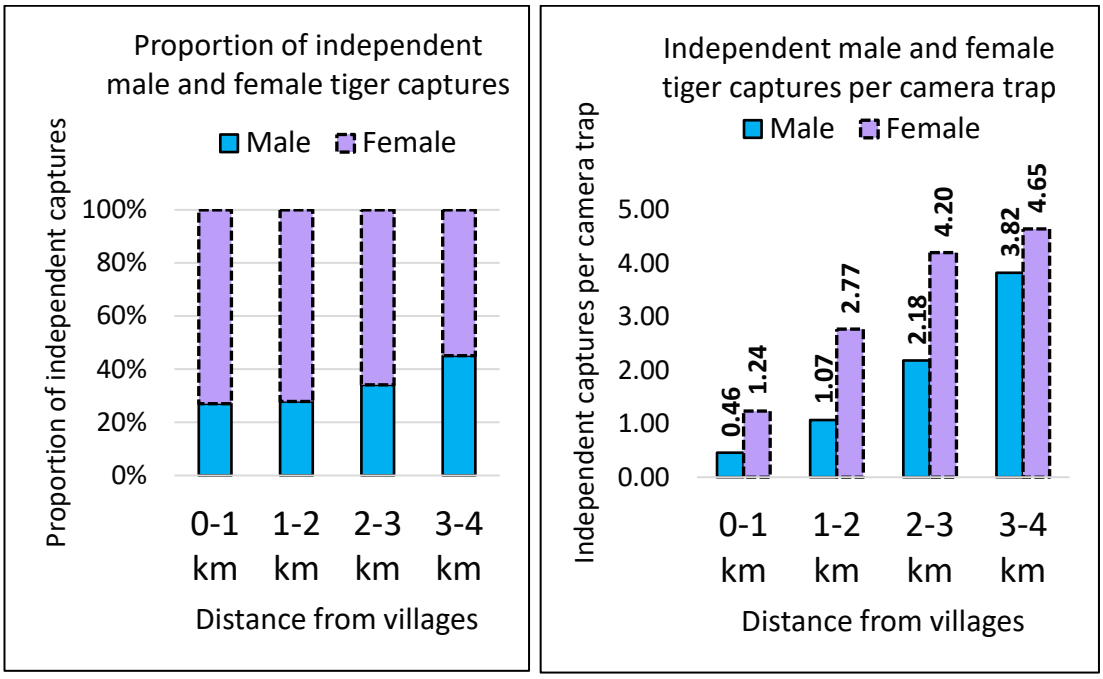

Figure 7. Proportion of independent capture rates of male and female tigers at increasing distance from villages

Both male and female tiger captures increased at increasing distance from villages but the proportion of female captures decreased (Figure 7).

Table 5. Top negative binomial GLM models within Δ AIC 2, null and global models for predicting tiger capture rate

Model	df	logLik	AICc	delta	weight
Tiger capture rate ~ Distance to villages + Distance to highway	4	-475.24	958.69	0	0.35
Tiger capture rate ~ Distance to villages + Distance to highway + RAI_Sambar + RAI_Spotted.Deer + RAI_Nilgai	7	-472.39	959.4	0.71	0.24
Tiger capture rate ~ Distance to villages + Distance to highway + RAI_Wildprey	5	-475.07	960.46	1.77	0.14
Tiger capture rate ~ Distance to villages + Distance to highway + RAI_Sambar + RAI_Spotted.Deer + RAI_Nilgai + RAI_Wild.Pig + RAI_Livestock + RAI_Humans	10	-471.48	964.19	5.5	0.02
Tiger capture rate ~ 1	2	-490.73	985.52	26.84	5.15E-07

Distance to villages was found to be the most significant predictor of tiger capture rate through the best fit model (Table 5), with a positive beta coefficient (Table 6).

Table 6. The untransformed estimates and significance levels of the variables in the top model for predicting tiger capture rate

	Estimate	Std. error	z-value	p-value	sig. level
(Intercept)	-3.75	0.203	-18.449	<0.001	***
Distance to villages	5.64E-04	9.64E-05	5.851	<0.001	***
Distance to highway	-5.39E-05	2.53E-05	-2.133	0.033	*

Capture rate of tigers = **exp (**-3.75 + 0.000564(**Distance to villages**) - 0.0000539(**Distance to highway**))

Temporal activity

To test for any seasonal variation in tiger activity during the study period, kernel density of tigers' activity from January-February and March-April were compared using Fisher's nonparametric test, which would check for a statistically significant shift in median activity time. With a p-value of 0.43, it was concluded that any shift in activity was non-significant (see Table 17 and Table 18). Therefore, all the captures used for activity and overlap analyses were treated without any seasonal influence. Photo-captures with discrepancies in recorded time of captures that couldn't be corrected with known times were discarded from the analysis.

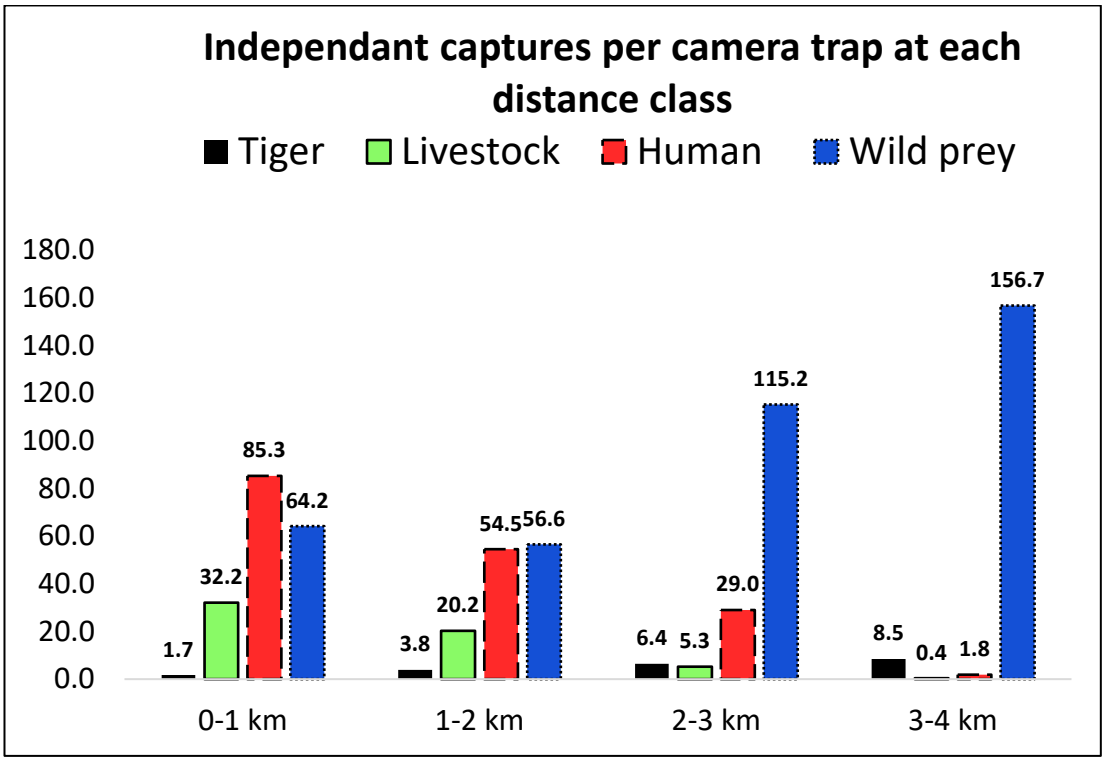

Figure 8. Bar chart of independent captures of species per camera trap at each distance class

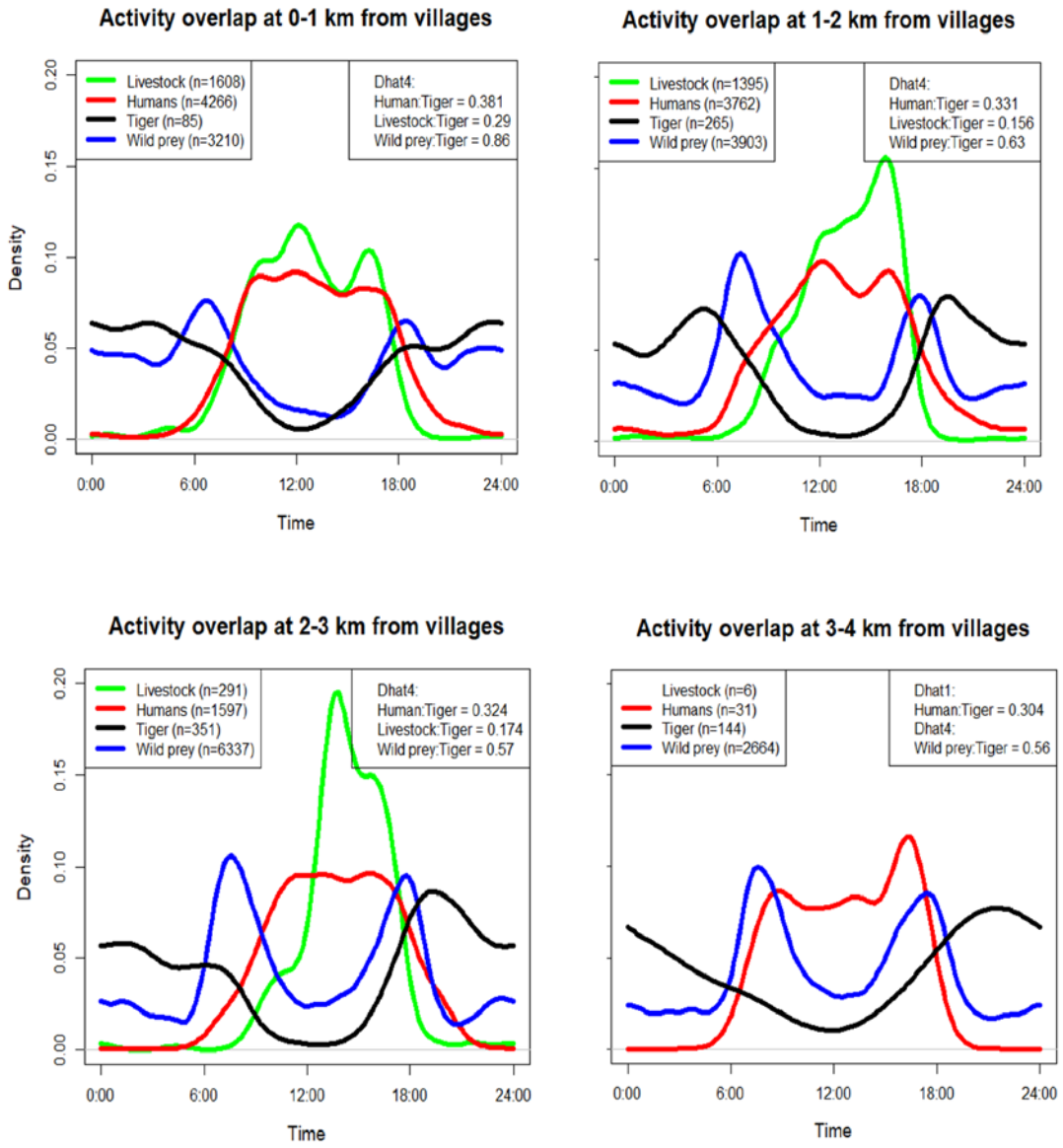

Figure 9. Activity overlap of species at each distance class

Plotting and analysis of temporal overlap between tiger & livestock were avoided for 3-4 km distance class since the number of captures for livestock was very low (n=6) and the coefficient of overlap over-represented the actual overlap in activity.

Table 7. Fisher's nonparametric test for Common Median Direction (to check for the shift in median activity time of tigers across each distance class)

Fisher's Nonparametric Test for Common Median Direction	
Pg (test statistic)	11.64127
α	0.05
df	3
χ_c^2	7.815
p-value	0.009

At 0-1 km distance class, the activity overlaps of tigers to both humans and livestock were highest (Figure 9). The activity peak of tigers is dampened and diverged away from the activity of humans and livestock. At 1-2 km, tiger activity peaks during crepuscular hours. At 2-3 km, the activity peaks more in the dusk-night hours. At the highest distance of 3-4 km, tiger activity is also detected during diurnal hours and peaks after dark. The activity overlaps with humans decreased consistently at increasing distances. The concentration of both human and livestock activity in the afternoon hours is also seen to increase with increasing distance.

Q3. Movement patterns of tigers and variation in movement rate to negotiate areas close to human settlements

Movement ranges of tigers from camera trap data within the study area

A total of 17 individual tigers were identified through photographic captures from the camera traps in the study area. 5 tigers, which were less than 2 years were excluded from the analysis of movement ranges since their ranges overlapped highly with that of their mother. There were also 3 sub-adult tigers: P142-21 (M), P213-62 (F), P213-

63 (F) (>2 years) but their ranges were more or less consistent throughout the study period which was exclusive to a certain degree and hence, was included in range mapping (Table 8).

Table 8. Individual tigers with number of camera traps with at least one capture and movement range area within study area estimated using 100% MCP

Tiger ID	Number of cameras with at least one capture	Area using 100% MCP (km^2)
P111 (M)	33	53
P142 (F)	31	37
P142-21 (M)	12	8
P213-62 (F)	12	7
P213-63 (F)	21	21
P234 (F)	24	27
P234-21 (F)	9	4
P234-22 (F)	18	19
P234-23 (F)	15	12
P241 (M)	33	58
T2 (F)	24	22
T7 (M)	28	44

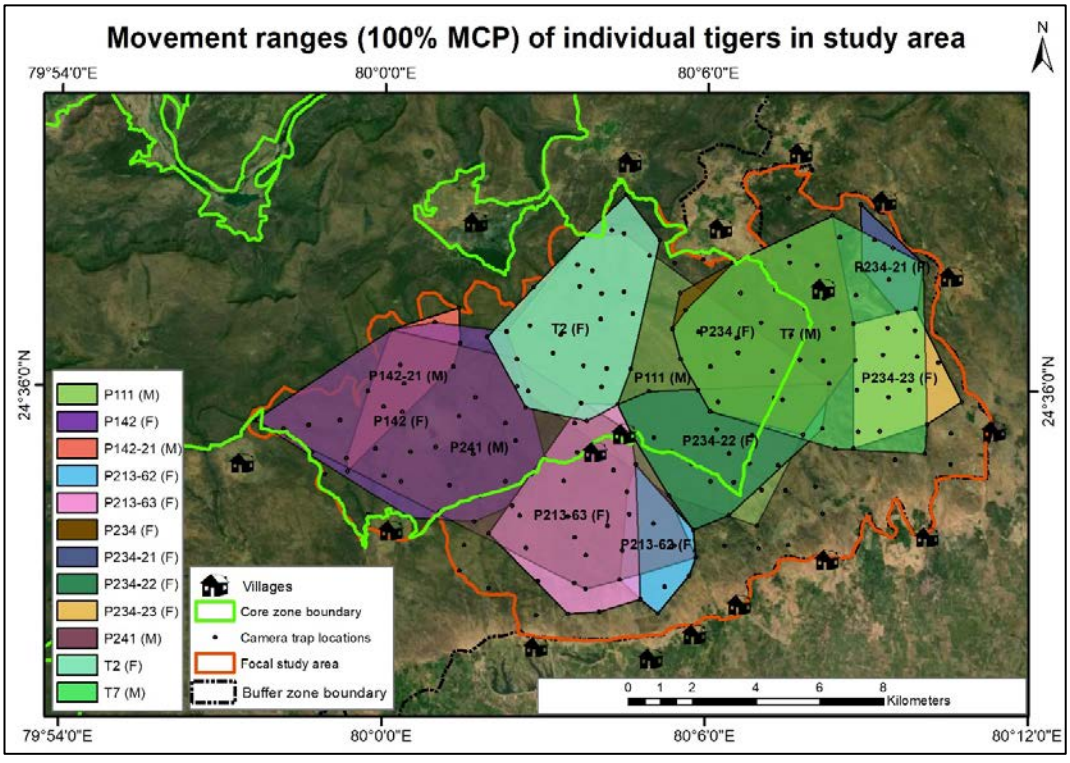

Figure 10. Movement ranges of individual tigers with 100% MCP within the study area

Movement patterns using data from GPS-collared tigers

A total of 8110 GPS locations from January – April 2021 of both tigers were available for analysis. 95% Fixed kernel density home range estimates of two collared tigers showed that for sub-adult, P213-63 (F) around 12% (4.5 km^2) of the total home range area (38 km^2) was within villages, whereas for the juvenile, P234-31 (M), 6% (1.1 km^2) of the total home range area (17 km^2) was within villages (Figure 11).

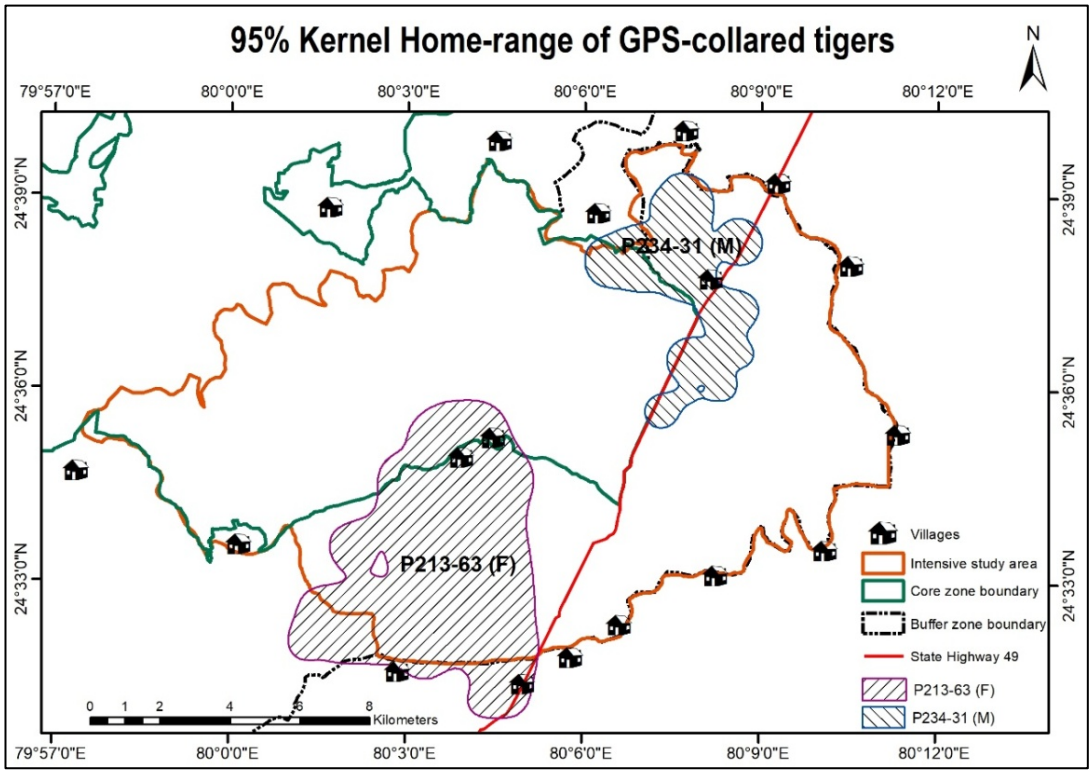

Figure 11. Fixed Kernel density home-range of GPS-collared tigers

To check for differences in distance to villages in day and night of the tigers, box-whisker plots were used. Mann-Whitney U test was performed to compare day and night differences in distance to villages to check for any significant difference (Table 10).

Table 9. Mean and median distance and their median absolute deviance and standard deviation of tigers' location to villages (overall, in the day and at night)

		Median distance (metres)	MAD	Mean distance (metres)	Std. Dev
P234-31 (M)	**Total**	715.4	546.727	892.9	677.25
	Day	707.2	571.68	885.5	675.222
	Night	720.7	530.266	900.3	679.335
P213-63 (F)	**Total**	1427.1	1072.81	1410.3	843.28
	Day	1573.3	1018.4	1486.1	838.93
	Night	1340	1098.08	1337	841.26

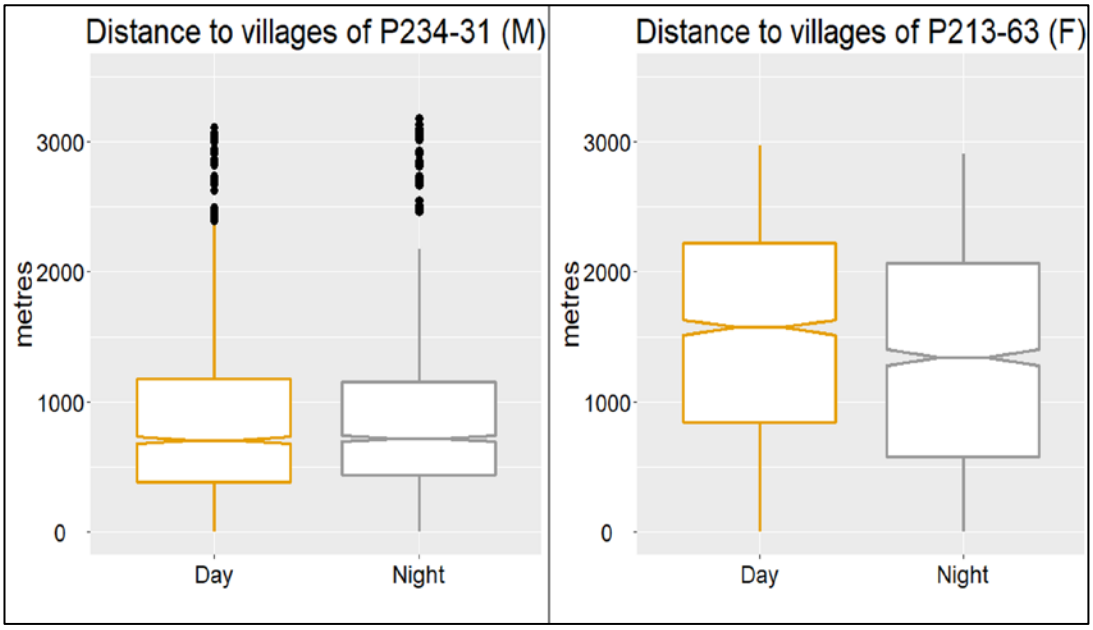

Figure 12. Box-whisker plots of tigers' distance to villages in day and night

Table 10. Mann-Whitney U test to compare day and night difference in distance to villages of GPS-collared tigers

	Mann-Whitney U test to compare day and night difference in distance to villages	
	P234-31 (M)	P213-63 (F)
U	3515472	980247
p-value	0.4408	<0.001

The plots (Figure 11) as well as the test for significance (Table 10) showed no variation in day and night distance to villages of P234-31 (M). However, it was significantly different for P213-63 (F), with 15% decrease in distance to villages at night compared to day (Table 9).

The difference in displacement was also similarly tested. Only measures of median and median absolute deviance (MAD) were calculated due to the highly skewed distribution of displacement (Table 11).

Table 11. Overall median displacement of tigers as well as displacement in day and night

		Median displacement (m/hr)	**MAD**
P234-31 (M)	**Total**	15.629	18.024
	Day	21.314	25.377
	Night	11.971	12.976
P213-63 (F)	**Total**	31.321	44.211
	Day	19.256	25.545
	Night	70.853	102.821

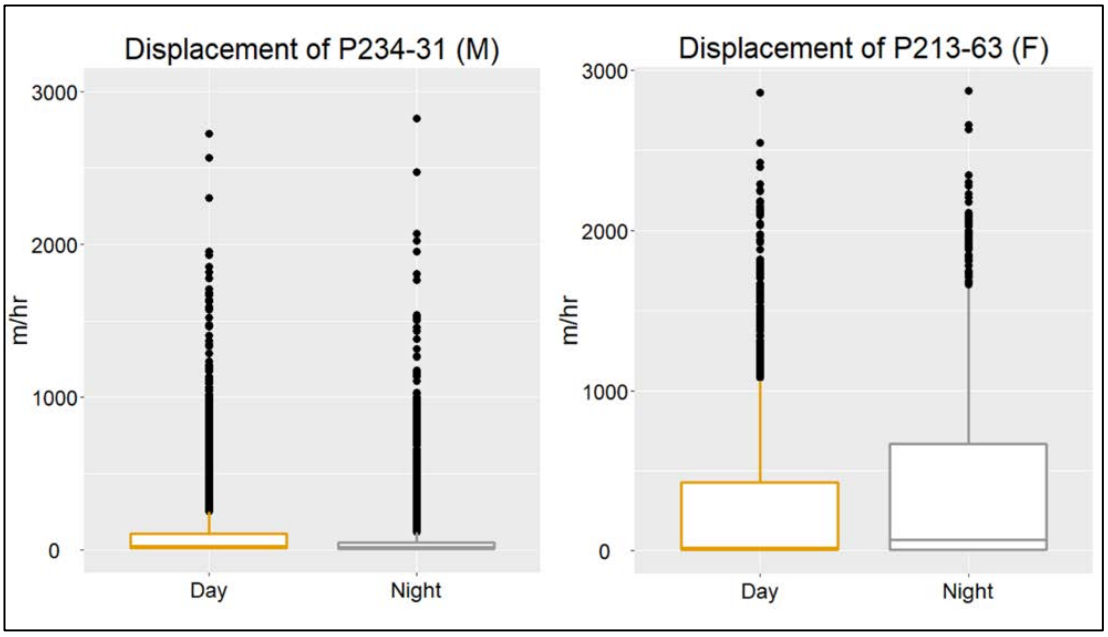

Figure 13. Box-whisker plots of tigers' displacement in day and night

Displacement of both animals in day and night differed significantly (Table 12). However, the displacement of P234-31 was higher in day while that for P213-63 was 73% higher at night compared to day (Table 11).

Table 12. Mann-Whitney U test to compare day and night differences in the displacement of tigers

	Mann-Whitney U test to compare day and night difference in displacement	
	P234-31 (M)	P213-63 (F)
U	1034945	789364
p-value	<0.001	<0.001

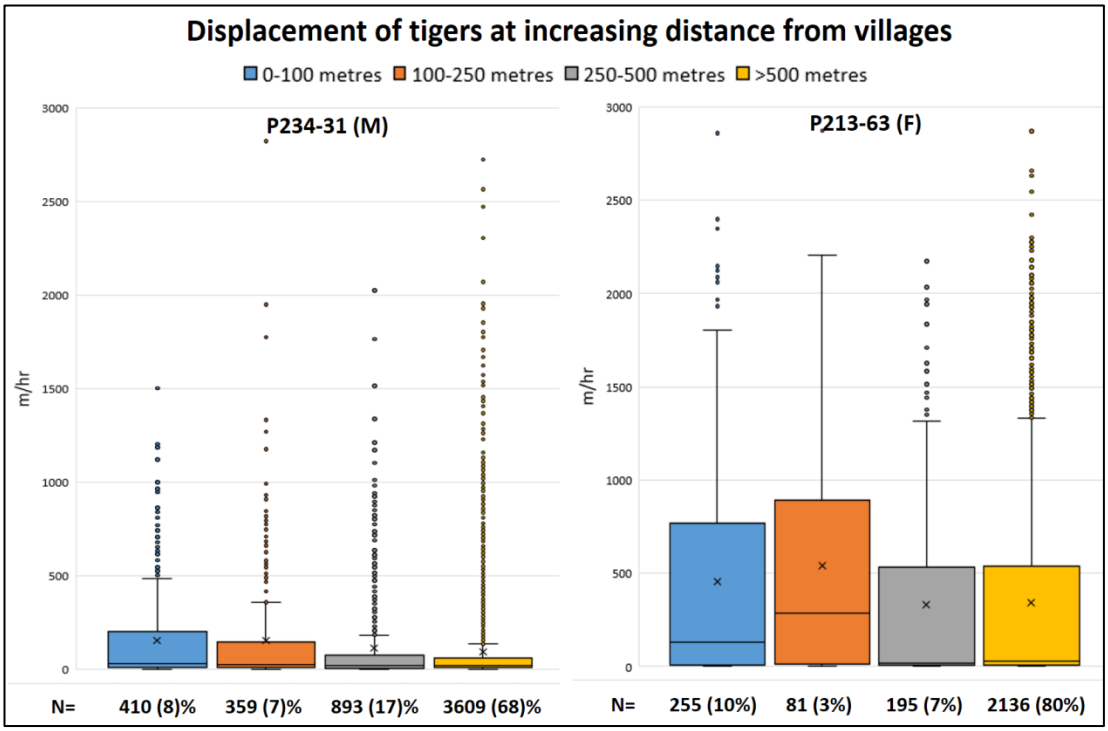

Figure 14. Box-whisker plots of tigers' displacement at increasing distance from villages. Categories (in metres): 0-100, 100-250, 250-500 and >500.

To check the proportion of GPS locations inside and in proximity to villages, the total number of locations within 0-100 metres and 100-250 metres were compared with the total (Figure 14). These distance classes were set in accordance with the comparison by Athreya et al., (2014). A considerable proportion of GPS locations of the tigers were inside or very near villages. (8 + 10) % of all the GPS fixes were within 0-100 metres and (7 + 3) % of the locations were within 100-250 metres of villages. The displacement of both tigers at very close (0-100 metres) and moderately close (100-250 metres) distances to villages were much higher compared to their overall displacement.

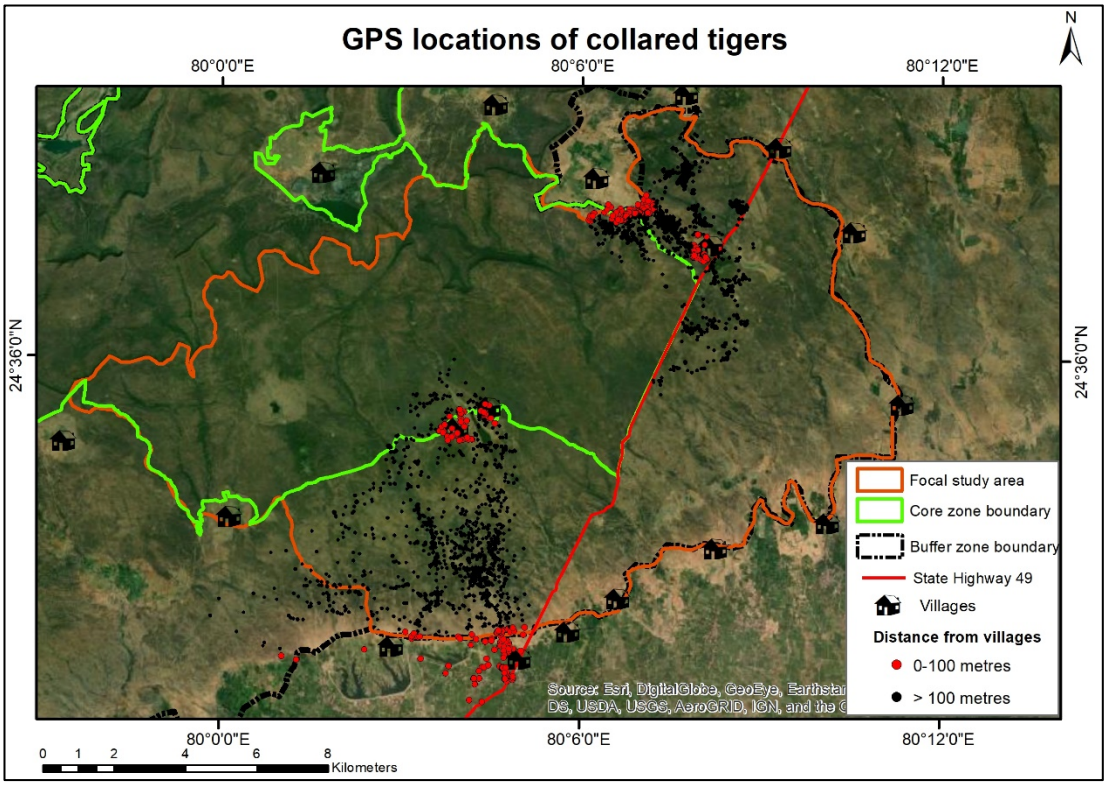

Figure 15. GPS location of collared tigers

Q4. Conflict probability prediction and risk mapping

Details of compensation for livestock killed by tigers were acquired from the forest department. Only the conflicts which occurred in and after 2018 were considered. Details of compensation were available till October 2020. A total of 252 recorded livestock depredation events occurred in Panna Tiger Reserve according to the compensation records. Of these, 106 were within the focal study area and the conflict prediction was done just for this area. Locations with missing location details or GPS coordinates were excluded from the analysis. A total of 45 kill locations were available from the compensation records.

Additionally, a site inspection was done in identified cluster locations from the GPS collar data of the two tigers. All locations where livestock kill remains were present was used for analysis. The kills which happened during the period of study, intimated informally by forest guards and villagers were also readily inspected. 8 sites were available from cluster inspection and direct depredation event site inspections.

The total data collected during fieldwork and compensation records were converted to binary form for each 1 km x 1 km grid cells, in which a value of 1 was assigned for each cell with at least one depredation event. A total of 33 such grids were present.

Distances to villages and highway were the most significant predictors for livestock depredation according to the best-fit models ranked by AICc (see Table 13 and Table 14). Model averaging for models within 2 ΔAIC was not performed due to non-significant coefficient values of variables (Arnold, 2010). Distance to villages and highway variables performed well overall and were consistently significant. Interactive and quadratic responses were also checked for but did not yield any significant results (see Table 20).

Depredation risk for each 1 km x 1 km grid cell was calculated by back transforming predictor variable estimates using the equation of the form $\mathbf{y = e^x / (1 + e^x)}$. AUC value for the best fit model was estimated at 0.77, indicating fairly high discriminatory power of the model (see Figure 19), i.e., the model correctly classifies a randomly drawn pair, each from a depredation-present and depredation-absent 1 km x 1 km grid cell groups 77% of the time.

Table 13. Top binomial GLM models within Δ AIC 2, global and null models for predicting spatial depredation probability of livestock

Model	df	logLik	AIC	AICc	delta	wgt	BIC
Kill ~ Distance to villages + Distance to highway	3	-74.40	154.80	154.93	0.00	0.26	164.55
Kill ~ Distance to villages + Distance to highway + RAI_Livestock	4	-73.74	155.47	155.69	0.76	0.18	168.48
Kill ~ Distance to villages + Distance to highway + RAI_Humans*RAI_Livestock	6	-71.99	155.99	156.44	1.52	0.12	175.50
Kill ~ Distance to villages + Distance to highway + RAI_Wildprey	4	-74.29	156.58	156.80	1.87	0.10	169.59
Kill ~ elevation + NDVI + Distance to villages*RAI_Livestock + Distance to highway + Dist_water*RAI_Livestock + RAI_Humans*RAI_Livestock + RAI_Wildprey*RAI_Tiger + I(Distance to villages^2) + I(Distance to highway^2)	16	-69.12	170.24	173.37	18.44	0.00	222.28
Kill ~ 1	1	-87.91	177.82	177.84	22.91	0.00	181.07

Table 14. Untransformed estimates of the best fit model for conflict risk-prediction

	Estimate	Std. Error	z-value	p-value	sig. level
(Intercept)	0.47	0.478	0.982	0.326	
Distance to villages	-6.04E-04	2.50E-04	-2.415	0.016	*
Distance to highway	-3.30E-04	9.44E-05	-3.498	<0.001	***

Probability of livestock kill

$$= \frac{\exp(0.47 - 0.000604(\text{Distance to villages}) - 0.0003302(\text{Distance to highway}))}{1 + \exp(0.47 - 0.000604(\text{Distance to villages}) - 0.0003302(\text{Distance to highway}))}$$

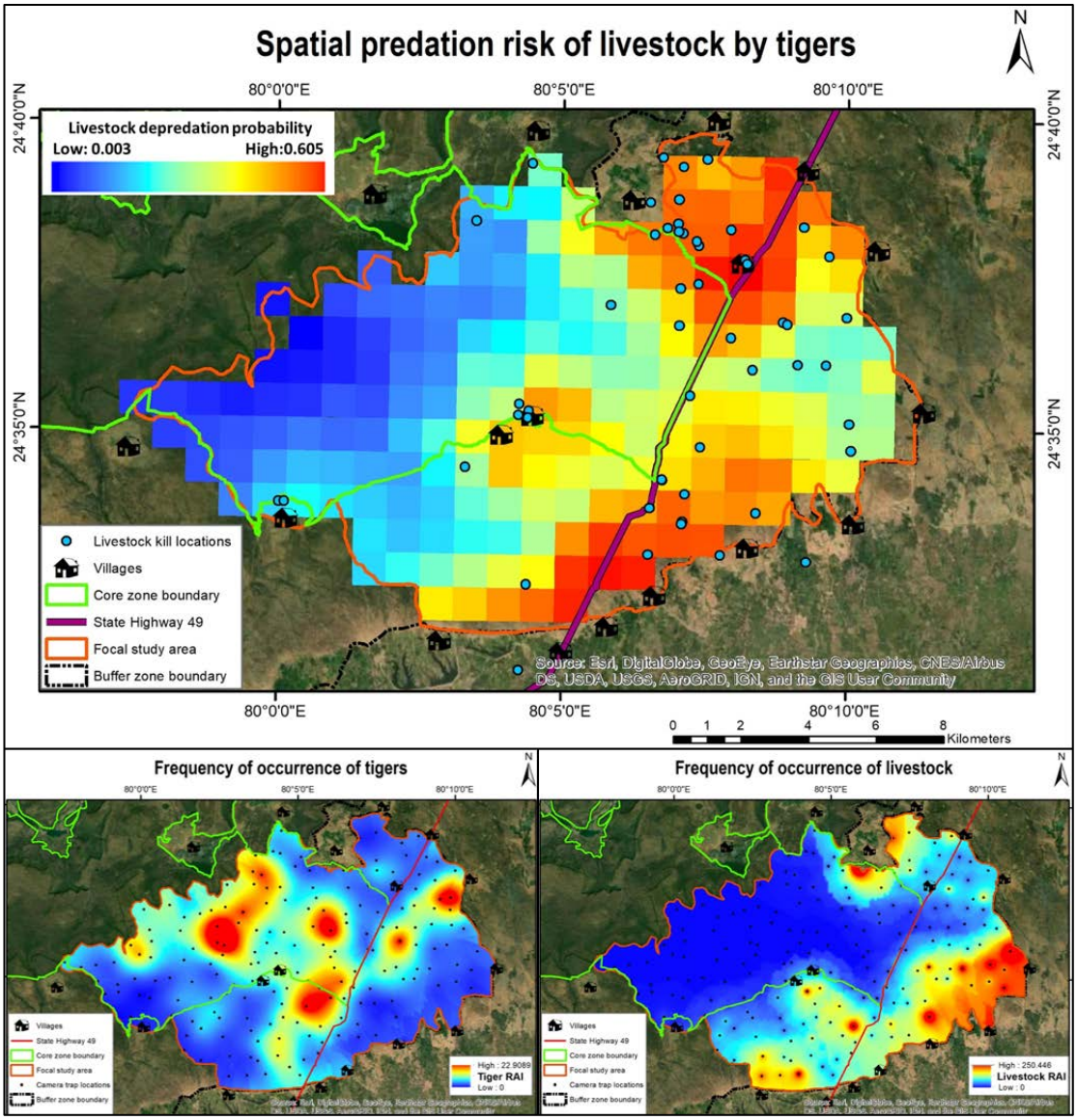

Figure 16. Spatial predation risk map of livestock by tigers and frequency of occurrence of tiger and livestock for comparison

DISCUSSION

Proportion, intensity and gradation in space use of the human-dominated area by tigers

Despite substantial anthropogenic disturbance, a relatively high proportion (74%) of the total 200 km^2 study area was used by tigers (Table 2). The naïve occupancy and modelled occupancy with covariates were only marginally different, indicating near-perfect detection of tigers in the area. This was also expected since all the known 17 tigers in the study area were captured, with a combined total of 878 independent tiger captures during the camera trap sampling (Table 3). The hotspots of occurrence of tigers were distributed mostly in the core zone of the Reserve (Figure 4). However, the buffer zone also showed few hotspots of tiger occurrence, likely since it was contiguous with the territorial forest division of North Panna and the area supported domestic prey availability, but at the cost of relatively lower wild prey availability (see Figure 20) and higher disturbance from nearby villages.

Studies have shown that the relative abundance index of tigers and their primary prey species to be significantly higher in low human-use areas (O'Brien et al., 2003) which was similar to the findings of the current study. Tiger abundances indicated by RAI showed a clear positive trend across increasing distance classes from villages (see Figure 5). It was also noted that the higher RAI at increasing distance from villages was not just an artefact of a limited number of individual tigers using less-disturbed areas more intensively but that there were more tigers using areas at higher distance from villages (Figure 6). The proportion of female capture rates at higher distances from villages were expected to be higher, but in the current study, an opposite trend was observed (Figure 7). Female tigers show higher site-fidelity and is largely

dependent on the resources available in an area (Chundawat, 2018) which is essential for raising the cubs. In a Tropical Dry Deciduous habitat like Panna, the resources such as water availability is scarce and seasonal. It is more so the case in the multi-use buffer zones of the Reserve and human settlements are also sustained by such availability of resources. The trend of lower proportion of female tiger capture rate at higher distances from villages can thereby be moderately substantiated. Modelling tiger captures as a response to wild prey abundance and elements of disturbance showed that the strongest predictor of tiger capture was distance to villages (Table 6). The current study, however, does not undermine the fact that habitat amelioration and effective management are more important for the conservation of tigers than the density of the surrounding human population (Carter et al., 2012b; Linnell et al., 2001). The relative abundance of sambar was the significant predictor of the occurrence of tigers. Cluster site inspection of P234-31 also showed kill remains of sambar at a site very close to a village (Plate 7), which might indicate the preference for a large-bodied wild prey, even in the presence of abundant free-ranging livestock in the human-dominated area. Scat analysis with DNA identification of predator species has to be performed to confirm such conjectures. Nevertheless, during the fieldwork, a total of 26 scat samples of tigers were collected, identified through field observations, including morphology of the scats, presence of scrape marks and movement information of radio-collared tigers available through continuous monitoring in the Reserve. Among this, 20 was from the buffer zone, close to villages and 6 were from the core zone (see Figure 17). Only about 25% of scats collected from the buffer zone contained hair samples of livestock. Without proper density estimates of wild and domestic prey in the region or identity confirmation of predator species through DNA samples extracted

from the scats, inference on prey preference of the tigers in the human-dominated region couldn't be drawn. Other studies in human-dominated landscapes have also indicated the affinity of the tigers to wild prey, despite high domestic prey availability (Athreya et al., 2014). However, bearing in mind the limitations and lack of systematic sampling design for scat collection, the estimate of 25% of collected scats containing livestock might indicate a lesser preference of livestock in tigers' diet. This is in comparison with estimates by Kolipaka et al., (2017) of 52% using kill site inspection of radio-collared tigers. This trend could also be related to the comparison of kill records by Panna tigers in the late 1990s and early 2000s where the livestock predation reportedly came down from a high 51% to 30% by 2000-2003 due to increased density of wild prey (Chundawat, 2018).

Temporal activity

The temporal patterns of the tiger also differed significantly across each distance class (see Table 7). In the 0-1 distance class, at the closest distance to settlements, the peak in tiger activity is much more dampened and diverged than in other distances, which could be explained by the high level of disturbance in the area, signified by the high number of human and livestock detection (Figure 9) or the average number of captures at each camera trap in a distance class (Figure 8), At this distance, tiger activity shows significant overlap with the activity of wild prey (86%). At 1-2 km, the crepuscular peaks in tiger activity are more discernible. This might be a more optimal distance than the 0-1 km distance class for tigers, as at this distance, they have access to both wild and domestic prey, but by being in relatively lower disturbed areas. As we move beyond 2 kilometres, a nocturnal peak in the tigers' activity is evident, conforming to

the animal's natural behaviour of nocturnality (Linkie and Ridout, 2011; Yang et al., 2019). At the highest distance of 3-4 km, the magnitude of difference in high and low of the tiger activity is least in comparison with all the other distance classes. This is expected as the areas at the highest distance from villages experiences the least disturbance from anthropogenic and livestock activity. The low overlap of activity of tigers and wild prey (56%) at the highest distance class maybe explained by the relatively higher abundance of wild prey in the area and tigers having the option to hunt at any time in their diel cycle, complemented by lower disturbance.

The predominant crepuscular and nocturnal activity of tigers is in agreement with other studies which has explored tiger activity patterns (Linkie and Ridout, 2011; Ramesh et al., 2012; Yang et al., 2019). The relatively low response of tiger activity to humans at increasing distance class could be because of the habituation of tigers to low-risk human exposures, since the buffer of the Reserve enjoys a certain degree of protection, despite being a multiple-use area.

Movement and livestock depredation patterns

The ranging patterns of tigers within the study area also showed the high intensity of regular use (Figure 10) by 17 tigers, with 5 being juveniles (<2 years), 3 sub-adults (>2 years) and 9 young adults/adults (>3 years) (classification according to Jhala and Sadhu, 2017), within a relatively small area of 200 km^2, almost the same home range area of an adult male tiger during the study by Chundawat et al., (2016) in Panna Tiger Reserve. The home ranges of tigers were proven to be 3-4 times larger than the estimates in other tropical habitats during the time (Chundawat et al., 2016; Karanth and Sunquist, 2000; Sharma et al., 2010). The tiger population of Panna Tiger Reserve

currently houses an estimated 55 tigers, which shows the success of reintroduction as a conservation tool supplemented by habitat amelioration and supports a higher density of tigers than ever before, according to the recent records obtained from the forest department.

At such high intensity of use, the tigers are faced with hard edges. Sub-adults and dispersing tigers of the Reserve often have to negotiate the human-dominated areas for exploratory behaviour or to look for potential easy prey. At the same time, they would also have to avoid confrontation with humans and the risk of persecution. The current study findings align with this idea. The sub-adult tigress, P213-63's displacement was significantly higher in the night than in the day. This is in agreement with other studies of large carnivore movement around human-dominated areas of the central Indian landscape (Athreya et al., 2014; Habib et al., 2021) and also of other large felids around the world (Kertson et al., 2011; Valeix et al., 2012). P213-63 also chose to explore the areas in proximity to human settlements under the cover of night. Overall, the highest displacement by the animal was exhibited when she was within 0-250 metres from the villages (see Figure 13). However, the results of the other tiger, P234-31 was different. The displacement of P234-31 was higher in the day than the night. This could be because, P234-31, being a juvenile male tiger, avoids confrontation with resident dominant males and explores the area during the day.

About 16% of the total GPS locations of tigers in the study area was within 0-100 metres of villages. This is in contrast to the findings of the study by Athreya et al., (2014) of a radio-collared tigress in a human-dominated landscape of Central India with just 0.2% of the locations within a distance of 100 metres from the village

boundary. This also confirms the patterns observed during the study by Kolipaka et al., (2018) in Panna that the likelihood of dispersing or sub-adult tigers using areas close to villages was high.

Despite 12% and 6% of the study tigers' home range areas being within the boundary of villages, there were relatively fewer negative interactions than expected. Nevertheless, livestock depredations did happen occasionally and were a cause of concern. Livestock depredation, especially that of buffaloes are a cause of serious economic impact to the local communities (Chundawat, 2018; Kolipaka et al., 2017). Historically, in Panna, it has been observed that the tigers whose diet had relatively higher livestock component revealed from scat analysis, had lower survival (Chundawat, 2018) owing to their persecution caused by persistence in human-dominated areas. However, in recent years, negative perceptions of people towards tigers in the park have apparently improved.

Informal interactions with the villagers during livestock depredation site inspection revealed observational confirmation of some of the results, that P213-63 came close to villages in the night and returned to the Reserve before daybreak. Depredation happened within this period of dark hours and the tigress preyed on cattle that were freely ranging inside the village. A large number of cattle in the periphery of the Reserve remains unguarded in the night (Kolipaka et al., 2015; Srivastava, 2014) and hastens the frequency of livestock depredation events around the Reserve (Kolipaka et al., 2017). Corralling of livestock is not widely practised in the villages surrounding the Reserve, but it would prove as an essential step in mitigating the conflicts with tigers.

The spatial risk prediction of livestock depredation indicated a significant negative relationship of distance to villages and highways to depredation probability (Table 14). The State Highway 49 cuts through the focal study area for 15 kilometres from the north-eastern to the south-western boundary. In addition to being deadly to the local wildlife, specifically tigers (TOI, 2020), the linear intrusion also allow ease of access to the multi-use buffer zone of the Reserve by livestock and their herders. Along with direct intrusions through expanding forest trails from villages by both humans and livestock, anthropogenic pressures acts as the drivers in expediting the occurrence of conflicts in the area. This is also substantiated by the modelling done for spatial livestock depredation probability, with distance to villages and highways as the strongest and only significant predictors among all the models (see Table 13 and Table 20). It also indicates the non-significance of abundances of tiger, wild prey or livestock as the predictor variables. Low overlap of areas with high livestock abundance and high tiger abundance is also evident from Figure 15. The results also show relatively low importance of vegetation cover in predicting conflict, similar to findings from another study in the central Indian landscape (Neelakantan et al., 2019). It is also substantiated by findings from Krishnamurthy et al., (2016) and Sarkar et al., (2017), that behavioural changes which the tigers adapt during phases of dispersal, especially through sub-optimal dispersal corridors affects the dynamics of conflicts around human-dominated areas nestling the source population of protected areas.

CONCLUSIONS AND RECOMMENDATIONS

Large carnivores all over the world are affected by the growing population of humans, which exacerbates processes of habitat loss and fragmentation. However, in recent years, technological advancements have given us opportunities to understand the space-time use of large carnivores in human-dominated landscapes and how it is affected by anthropogenic disturbances. With the population of large carnivores increasing within the protected areas, spill-over of young dispersing individuals are imminent. For the carnivores, human-dominated areas hinder their dispersal. But for the people residing around the protected areas, the movement of a large carnivore would not be preferable, as it could result in serious economic impacts due to events such as livestock depredation and impedes conservation efforts of the species. Such has been the case in the human-dominated region of Panna Tiger Reserve, with the high-intensity area used by tigers, livestock and humans along with instances of livestock depredation.

Post-hoc methods of conflict mitigation such as providing monetary compensation for depredated livestock only provides a temporary solution. But from the perspective of tigers, as long as the conditions permits, depredation events would continue to happen. Tigers may not differentiate between wild or domestic prey and would make a choice based on catchability. It has been well-established that large carnivores consider the catchability of prey as a more important factor than the abundance of the prey itself (Hopcraft et al., 2005; Laundré et al., 2010, 2009). Livestock, in that respect, is a much easier prey due to the lower risk awareness as a consequence of domestication in comparison to wild prey. By controlling the grazing and movement of livestock in the identified conflict hotspots and tiger activity centres, as well as effective herding and corralling practices of livestock in the night would be

an impactful measure in decreasing the interfaces leading to conflict. Another recommendation relevant to the movement of tigers is the restriction of vehicular movement as part of night safari currently practised around the buffer zone of the Reserve. This would be essential for successful movement, with regard to the dispersal of the tigers which evidently explore the human-dominated areas at the night. Similar recommendations were also done for the tigers around Nepal's Chitwan National Park by Carter et al., (2012b).

Studies within the central Indian landscape has shown a general pattern of low reliance of households on forest resources, with members in the house having a salaried job (Neelakantan et al., 2019). Promoting alternate sources of livelihood through initiatives and strengthening the institutions such as Eco-Development Committees (EDCs) could go a long way in establishing a positive relationship with the people, park and the animals (Carter et al., 2012a; Seidensticker et al., 1999). With respect to the current study area, strengthening of EDCs established near the villages of Akola and Jardhoba should be taken up in priority through which sustainable grazing practices can be adopted. Along with it, promoting tourism activities in the day and employing local villagers as forest guards and tourist guides would give them an alternate source of livelihood than depending on cattle grazing or forest resource. Increasing the frequency of monitoring of radio-collared tigers in this area would also be useful in warning the villagers. Timely intervention and adoption of effective mitigation measures could significantly improve both the quality of life of people around protected areas as well as the species that the area is being protected for.

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APPENDICES

Plate 1. GPS-collaring of P234-31 (M)

Plate 2. Direct sighting of P234-31 (M) near Jardhoba village

Plate 3. The collared tigress P213-63 captured in one of the camera traps

Plate 4. Camera trap deployment and checking in the buffer zone

Plate 5. Presence of livestock for grazing and villagers for firewood collection in the buffer zone.

Plate 6. Variability of livestock kill site attributes

Plate 7. Remains of sambar kill made by P234-31 near Jardhoba village

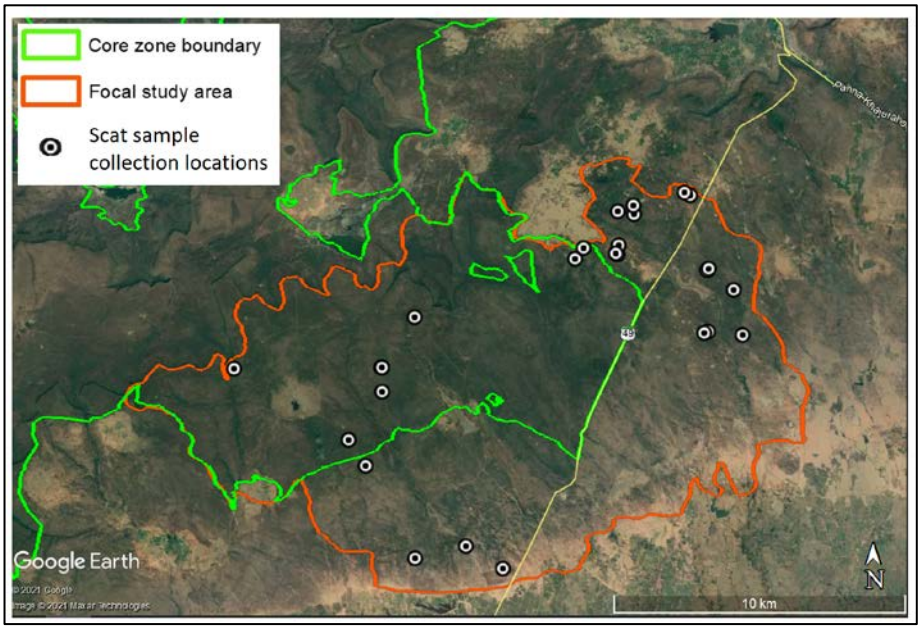

Figure 17. Scat sample collection locations

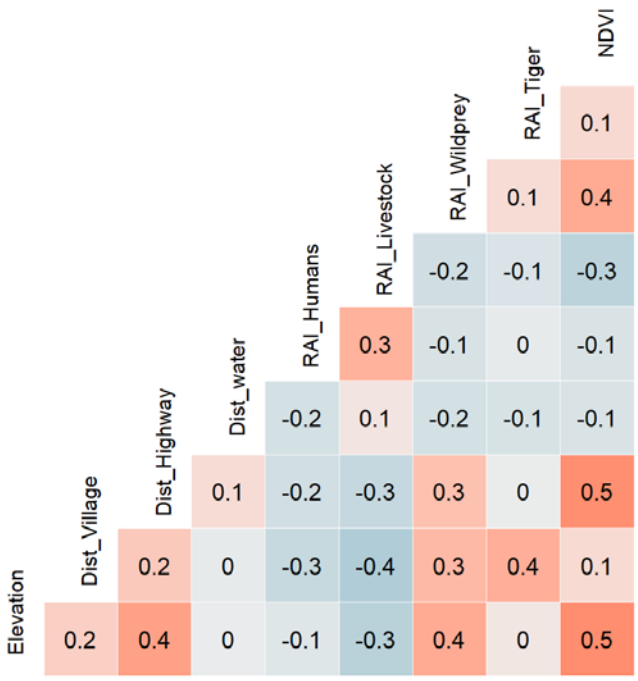

Figure 18. Correlation matrix of selected covariates used for modelling spatial risk prediction for livestock.

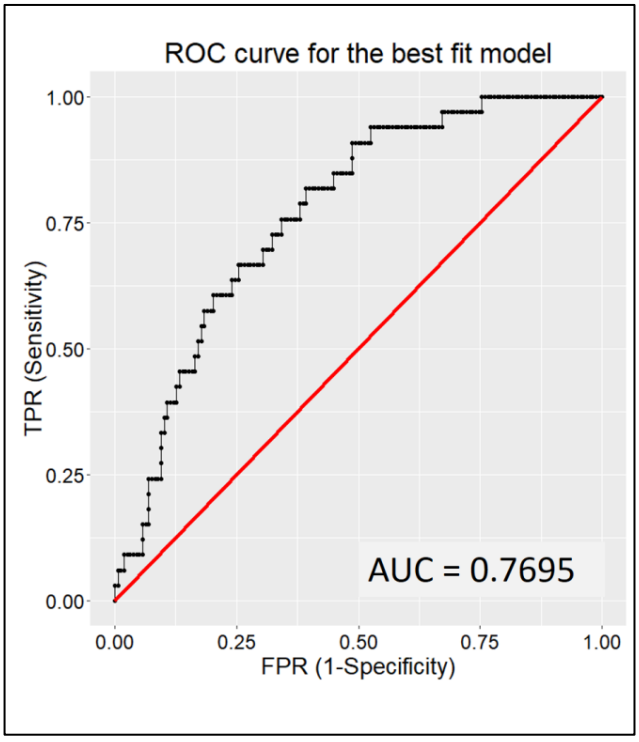

Figure 19. ROC curve for the best fit model to predict livestock depredation in the study area

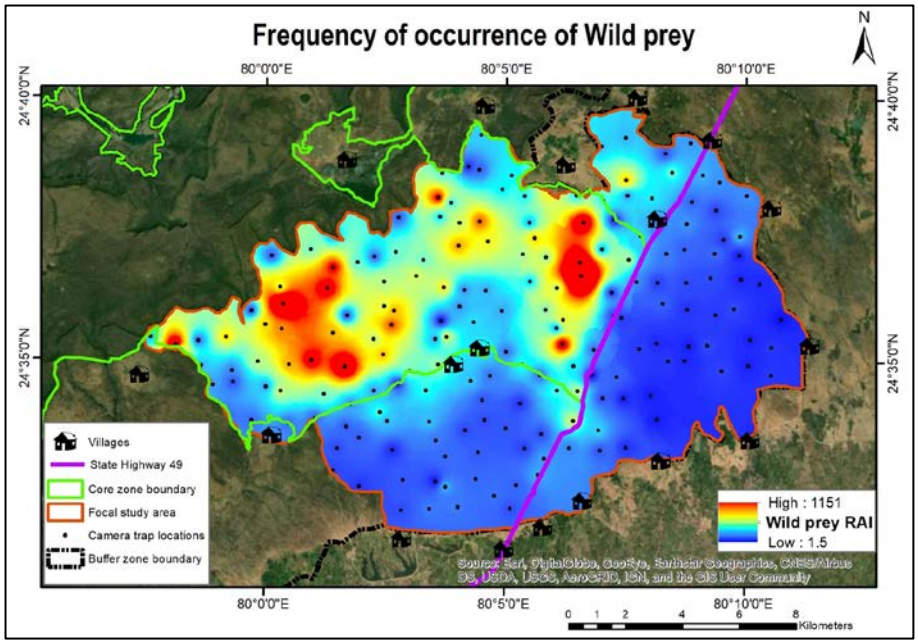

Figure 20. Frequency of occurrence of Wild prey

Table 15. Summary of camera trap captures

S. no.	Species/Group	No. of captures
1	Asiatic Wildcat	327
2	Birds	2865
3	Common Palm Civet	415
4	Dog	661
5	Four-Horned Antelope	750
6	Golden Jackal	1903
7	Gray Langur	1089
8	Grey Wolf	73
9	Honey Badger	28
10	Humans	10436
11	Indian Crested Porcupine	1100
12	Indian Fox	291
13	Indian Gazelle	151
14	Indian Hare	4052
15	Indian Pangolin	12
16	Jungle Cat	541
17	Leopard	761
18	Livestock	3690
19	Madras Treeshrew	5
20	Mongoose	517
21	Nilgai	2768

22	Rodents	74
23	Rhesus Macaque	2
24	Rusty-spotted Cat	37
25	Sambar	5725
26	Sloth Bear	266
27	Small Indian Civet	967
28	Spotted Deer	9855
29	Squirrel	40
30	Striped Hyaena	835
31	Tiger	878
32	Wild Pig	2370
	Total	**53484**

Table 16. Watson's goodness of fit test of von Mises distribution and isotropy for tiger activity at each distance class

	Watson's goodness of fit test							
	von Mises distribution				**Circular uniform distribution**			
Distance class of activity	0-1 km	1-2 km	2-3 km	3-4 km	0-1 km	1-2 km	2-3 km	3-4 km
α	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Test Statistic	0.0581	0.42	0.3889	0.0468	0.5343	1.862	2.5789	1.2065
Critical value	0.066	0.079	0.079	0.079	0.187	0.187	0.187	0.187
Null hypothesis	Not rejected	Rejected	Rejected	Not rejected	Rejected	Rejected	Rejected	Rejected
Bias corrected concentration parameter, K	0.6928	-	-	0.873	-	-	-	-

Table 17. Watson's goodness of fit test of von Mises distribution and isotropy for tiger activity from Dec-Feb and March-April

	Watson's goodness of fit test			
	von Mises distribution		**Circular uniform distribution**	
Time-period of tiger activity	Tiger activity (Dec-Feb)	Tiger activity (March-April)	Tiger activity (Dec-Feb)	Tiger activity (March-April)
α	0.05	0.05	0.05	0.05
Test Statistic	0.7615	0.2341	3.527	3.6843
Critical value	0.066	0.079	0.187	0.187
Null hypothesis	Rejected	Rejected	Rejected	Rejected

Table 18. Fisher's nonparametric test result for Common Median Direction to check for the shift in median activity time of tigers in Dec-Feb and March-April

Fisher's Nonparametric Test for Common Median Direction	
Pg (test statistic)	0.626
α	0.05
df	1
χ_c^2	3.84
p-value	0.428

Table 19. Models run for tiger capture rate using negative binomial GLM and covariate estimates

Models rank	1	2	3	4	5	6
(Intercept)	-3.74657	-3.69967	-3.75881	-3.78963	-3.72129	-3.86512
Dist_SH	-5.4E-05	-6.7E-05	-5.9E-05	-6.5E-05	-6.2E-05	-6.2E-05
Dist_Vill	0.000564	0.00056	0.00055	0.000583	0.000555	0.000599
offset(log(sampling_days))	+	+	+	+	+	+
RAI_Nilgai	-	-0.00931	-	-0.01037	-	-0.01029
RAI_Sambar	-	0.002563	-	0.002553	-	0.002645
RAI_Spotted.Deer	-	0.001166	-	0.000786	-	0.000906
RAI_Wild.Pig	-	-	-	0.005269	-	0.004445
RAI_Humans	-	-	-	-	0.000707	0.000464
RAI_Livestock	-	-	-	-	-0.00308	-
RAI_Wildprey	-	-	0.0004427	-	0.0003397	-
init.theta	0.882	0.919	0.883	0.921	0.893	0.925
df	4	7	5	8	7	9
logLik	-475.235	-472.393	-475.067	-472.195	-473.988	-471.833
AICc	958.6857	959.3978	960.4593	961.1807	962.5882	962.6606
delta	0	0.712118	1.773613	2.495049	3.90252	3.974936
weight	0.346451	0.242665	0.142727	0.099506	0.049229	0.047478

0.046891	0.022132	0.002919	5.15E-07
3.999819	5.501417	9.552662	26.83819
962.6855	964.1871	968.2384	985.5239
-477.235	-471.482	-475.724	-490.73
4	10	8	2
0.853	0.927	0.869	0.696
-	-	-	-
-	-0.00209	-0.00213	-
-	0.000644	0.000758	-
-	0.004772	0.00508	-
-	0.000708	-	-
-	0.002422	0.003851	-
-	-0.0098	-	-
+	+	+	+
0.000517	0.000591	0.000577	-
-	-6.6E-05	-	-
-3.89621	-3.79119	-4.06982	-2.9055
7	8	9	10

Table 20. Models run for livestock depredation risk using binomial GLM and covariate estimates

weight	0.25812186	0.17654916	0.12094459	0.10117226	0.09154608
delta	0	0.75966482	1.51619856	1.87321438	2.07317863
AICc	154.925535	155.685200	156.441734	156.798750	156.998714
logLik	-	-	-	-	-
df	3	4	6	4	4
Dist_water:RAI_Livestock	-	-	-	-	-
I(Dist_Vill^2)	-	-	-	-	-
I(Dist_SH^2)	-	-	-	-	-
Dist_water:RAI_Tiger	-	-	-	-	-
Dist_Vill:RAI_Livestock	-	-	-	-	-
RAI_Tiger:RAI_Wildprey	-	-	-	-	-
elevation	-	-	-	-	-
Dist_water	-	-	-	-	-
NDVI	-	-	-	-	-
RAI_Tiger	-	-	-	-	-
RAI_Wildprey	-	-	-	-0.00087	-
RAI_Humans:RAI_Livestock	-	-	-9.2E-05	-	-
RAI_Humans	-	-	0.004055	-	-0.00011
RAI_Livestock	-	-0.00547	0.004541	-	-
Dist_Vill	-0.0006	-0.00071	-0.00065	-0.00059	-0.00061
Dist_SH	-0.00033	-0.00033	-0.00032	-0.00033	-0.00033
(Intercept)	0.469576	0.807327	0.427063	0.520674	0.491375
Model rank	1	2	3	4	5

0.08558008	0.06526119	0.02878271	0.02248496	0.01840869	0.01416857	0.00465893	0.00364138	0.00226966	0.00163332	0.00089292
2.20795848	2.75006847	4.38731391	4.88116958	5.28121739	5.80481118	8.02929188	8.52213655	9.46759602	10.1256255	11.3333746
157.133494	157.675604	159.312849	159.806705	160.206753	160.730347	162.954827	163.447672	164.393131	165.051161	166.258910
-	-	-	-	-	-	-	-	-	-	-
5	7	8	8	7	9	10	10	11	11	12
-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-9.2E-06
-	-	-	-	-	-	-	-	0.000275	-	-
-	-	-	-	-	-	-	0.00511	-	0.002569	0.001941
-	-	-	-	-	-	-3.8E-05	-6.3E-05	1.06E-05	-2.9E-05	0.000117
-	4.235729	5.50714	-	4.366155	5.417936	5.394268	-	5.283504	4.433212	4.338259
0.027145	-	-	0.031576	0.027168	0.030452	0.03027	0.030081	-0.00217	0.030093	0.035172
-	-	-0.00159	-0.00071	-0.00203	-0.0017	-0.00172	-0.00136	-0.00321	-0.00184	-0.00209
-	-0.00011	-0.00011	-9.3E-05	-	-0.00011	-0.00011	-0.00011	-0.00011	-0.00011	-0.00013
-	0.004561	0.004417	0.004035	-	0.004479	0.00446	0.00438	0.004586	0.00459	0.005317
-0.00551	0.007341	0.007037	0.004503	-0.00485	0.007323	0.007358	0.007261	0.007612	0.008218	0.015218
-0.00079	-0.0006	-0.00056	-0.00073	-0.00071	-0.00065	-0.00065	-0.00069	-0.00068	-0.00064	-0.00053
-0.00034	-0.00035	-0.00036	-0.00032	-0.00036	-0.00036	-0.00036	-0.00033	-0.00037	-0.00035	-0.00037
0.77615	-0.8915	-1.14002	0.442855	-0.38714	-1.142	-1.1262	-1.44125	-0.88492	-1.80641	-1.66023
6	7	8	9	10	11	12	13	14	15	16

0.00089292	0.00084986	0.00068629	0.00067227	0.00038464	0.00022325	0.00014878	2.55442E-
11.3333746	11.4322294	11.8597699	11.9010544	13.0177467	14.1057572	14.9174069	18.4415537
166.258910	166.357765	166.785305	166.826590	167.943282	169.031293	169.842942	173.367089
-	-	-	-	-	-	-	-
12	12	10	13	13	11	12	16
-	-	-	-	-	-	-	1.53E-05
-	-	-	-	-	-	3.54E-07	3.03E-07
-	-	-	-	-	2.31E-09	-4.7E-09	1.14E-09
-	-	-	0.000141	-	-	-	-
-9.2E-06	-	-	-1E-05	-7.8E-06	-	-	-6.4E-06
-	0.000301	-	-	0.000249	-	-	0.000184
0.001941	0.003673	0.001019	0.001491	0.002971	0.001016	0.000817	0.003635
0.000117	2.7E-05	-1.2E-05	-0.00063	0.000147	-3.1E-06	-0.00015	-0.00053
4.338259	3.898924	3.939359	4.463153	3.896891	3.95308	3.014803	3.42995
0.035172	-0.00587	0.026802	0.003455	0.00392	0.027186	0.023993	0.006991
-0.00209	-0.00349	-0.00208	-0.00209	-0.00342	-0.00208	-0.00254	-0.00348
-0.00013	-0.00012	-	-0.00012	-0.00013	-	-	-0.00014
0.005317	0.004788	5.01E-05	0.005026	0.00532	6.04E-05	-0.00014	0.005685
0.015218	0.008891	-0.00477	0.014915	0.014697	-0.00472	-0.00526	0.008943
-0.00053	-0.00067	-0.00071	-0.00057	-0.00057	-0.00071	-0.00182	-0.00155
-0.00037	-0.00037	-0.00036	-0.00035	-0.00038	-0.00038	-0.00032	-0.00038
-1.66023	-1.83556	-0.64195	-1.30823	-1.71251	-0.62579	0.391365	-1.07112
17	18	19	20	21	22	23	24