MOVEMENT AND SPACE USE PATTERN OF TIGERS IN THE EASTERN VIDARBHA LANDSCAPE, MAHARASHTRA, INDIA

THESIS

SUBMITTED TO THE

FOREST RESEARCH INSTITUTE DEEMED to be UNIVERSITY

DEHRADUN, UTTARAKHAND

For

THE AWARD OF THE DEGREE OF

DOCTOR OF PHILOSOPHY IN FORESTRY

(Wildife Science)

By
Zehidul Hussain

Research Centre

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

2023

DECLARATION

I hereby declare that the thesis titled **"Movement and space use pattern of tigers in the Eastern Vidarbha Landscape, Maharashtra, India"**, submitted by myself Mr. Zehidul Hussain (Enrolment No. 17PHD464) to Forest Research Institute (FRI), Deemed to be University, Dehradun for the award of the degree of Doctor of Philosophy in Forestry (Wildlife Science) is a record of original research work carried out by me under the supervision of Dr. Bilal Habib and co-supervision of Dr. Parag Nigam, Wildlife Institute of India, Dehradun., The doctoral research has not formed the basis for an award of any other degree or diploma in other university or organization. I also declare that the thesis embodies my own work, observations, and analysis, and in that respect, the investigation appears to advance knowledge in the subject. The thesis has been duly checked through URKUND, a plagiarism detection tool approved by FRI and has plagiarism to acceptable limits.

Dehradun, the August 24, 2023

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I would like to inform you that the following decisions have been taken for your enrolment as Research Scholar for the Degree of Doctor of Philosophy in Forestry in this Institute:-

1. You have been registered for Doctor of Philosophy i.e **01.09.2018 to 31.08.2023** as PhD Research Scholar.
2. Your Enrolment number is: - **17PHD464**
   (For all further correspondence please quote your enrolment number.)
3. Name of Research Centre: - **Wildlife Institute of India, Dehradun**
4. The Topic of research approved by the FRI University: **"Movement and Space Use Pattern of Tigers in the Eastern Vidarbha Landscape, Maharashtra, India."**
5. Name of Discipline: **- Wildlife Science**
   (As per clause 3.3 of the Ph.D. Ordinance)
6. (i) Name of Supervisor : - **Dr. Bilal Habib**
   (ii) Name of Co-Supervisor: - **Dr. Parag Nigam**
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15. **The Research Scholar may not later than three months from the date of issue of registration letter, modify the scheme of the research work or nature or scope of the subject, on the recommendation of the Supervisor and RAC, with the approval of Director.**

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    The recommendations of the R.A.Cs for extension of term of registration must reach this office before expiry of the term of registration.

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17. Prior to the submission of the thesis but at least 3 months before the expiry of term of registration, the scholar shall make a presentation in the Department before the Research Advisory Committee of the Institution concerned in Pre-thesis Submission Seminar. The minutes of RAC meeting for pre-thesis submission seminarts to be send to the Registrar, FRI Deemed University with full comments alongwith a panel of examiners duly signed by R.A.C.

18. Ph.D. scholars must publish at least one (1) research paper in refereed journal and make two paper presentations in conferences/seminars before the submission of the thesis for adjudication, and produce evidence for the same in the form of presentation certificates and/or reprints.While submitting for evaluation, the thesis shall have an undertaking from the research scholar and a certificate from the Research Supervisor attesting to the originality of the work, vouching that there is no plagiarism and that the work has not been submitted for the award of any other degree/diploma of the same Institution where the work was carried out, or to any other Institution..

19. **Please ensure that the clause 13 of the Ph.D. Ordinance is fully complied with before submission of the thesis to University.**

20. **Please note that your Registration as Research Scholar is to be governed as per rules, regulation, and ordinances of FRI Deemed to be University, with applicable amendments made by the University from time to time. For all further correspondence, please quote your enrolment number.**

(A.K. Tripathi)
Registrar
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Encl: 1. **Fee receipt No. 3981 dated 08.10.2018 for Rs. 28,500/-**
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Acknowledgement

I stand at the height of an incredible journey, the completion of my doctoral thesis, and I am overwhelmed with gratitude to all those who have supported and contributed to this demanding, yet rewarding journey. Without unwavering support, encouragement, and assistance, this achievement would not have been possible. Therefore, I extend my heartfelt thanks to the following individuals and groups who have been instrumental in making this endeavour a reality. First, I express my deepest gratitude to my family for their unending love, understanding, and encouragement throughout this journey. Their constant belief in me and their sacrifices to ensure that I could pursue my passion have been the foundation upon which I built my academic pursuits.

To my wife, whose patience, understanding, and unwavering support have been my guiding light throughout the challenging years of fieldwork, I owe a debt of gratitude that words cannot be fully expressed. Your presence by my side has been a source of strength and inspiration, and I am immensely grateful for your enduring love and encouragement. I extend my appreciation to my circle of friends, whose unwavering support, camaraderie, and moments of levity provided much-needed relief during intense fieldwork. Your friendships have been a constant source of motivation, and I am thankful for the cherished memories we have created together. The success of my research in the Eastern Vidarbha Landscape of Maharashtra would not have been possible without the cooperation and assistance of the forest officials and workers. Their expertise, guidance, and tireless efforts to facilitate research in this region have been invaluable. I extend my sincere gratitude to each of them for their assistance, patience, and willingness to share knowledge.

Additionally, I extend my thanks to all other workers, local communities, and stakeholders who were part of the fieldwork. Their cooperation and willingness to share their insights and experiences enriched my research and made this journey truly enlightening. I would also like to express my appreciation to my academic advisors and mentors, whose guidance, expertise, and valuable feedback were indispensable throughout this research. Their dedication to my growth as a researcher has been commendable, and I am grateful for the imparted knowledge and skills.

Finally, I acknowledge the institutions and organisations that provided financial support and resources for my research. Their investment in my academic pursuits has been vital in bringing my vision to fruition. In conclusion, the completion of my doctoral thesis is a testament to the collective efforts and support of those who have been part of my journey. To each one of you, I offer my heartfelt gratitude. Your contributions have not only enriched my academic pursuits, but also enriched my life. Thank you for being an integral part of this unforgettable chapter of my academic and personal growth.

Executive Summary

1. Movement is a crucial ecological process that influences the survival, population dynamics, and evolution of animals. Animal movement patterns are diverse and are influenced by life stages, sex, age, and habitat requirements. The relationship between animal movement and conservation is complex, particularly due to human-induced environmental changes. Human activities have led to habitat destruction, fragmentation, and alterations in resource availability, affecting the movement of species and disrupting ecosystem functions. Recent studies have shown that human activities can reduce animal displacement and affect wildlife behaviour, leading to conflicts with human settlements. Adapting to changing environments may require wide-ranging terrestrial mammals, such as tigers, to modify their movement patterns for long-term survival.

2. Conservation strategies for highly mobile species must consider movement in decision-making processes. Large-ranging carnivores, such as tigers, face challenges in human-dominated landscapes owing to habitat fragmentation and competition with humans for space. Maintaining connectivity between the subpopulations and isolated populations is crucial for long-term survival. Large carnivore populations face numerous challenges in a fragmented world owing to habitat loss, degradation, and increased human land use. These factors affect the movement and behaviour of carnivores, which in turn affects their survival and persistence. Human activities have accelerated habitat fragmentation, separating high-quality habitats into small patches surrounded by unsuitable habitats and anthropogenic features. Linear features, such as roads, negatively impact carnivores, including increased wildlife mortality, reduced ecological connectivity, and altered behaviour. Understanding the response of large carnivores to environmental and anthropogenic factors is essential for their conservation. The Central Indian Landscape is a stronghold for tiger populations, but critical areas lie outside protected areas under high human pressure. Anthropogenic factors vary with different land uses, influencing tiger movement and behaviour. This study aimed to understand the spatial and seasonal variability of tigers space use, movement patterns and identify the factors influencing their dispersal movement.

3. This study emphasises that various factors influence animal movement, including individual characteristics and external factors such as resource availability, distribution, competition, and predation. Animals adjust their space use based on seasonal changes in resource

availability. Additionally, movement patterns and space use can be influenced by habitat disruption, forcing individuals to displace and establish new home ranges. Landscape features play a significant role in animal home ranges, with resource distribution determining the extent of the required area. Fragmentation of habitats and human activities can affect landscape connectivity, leading to isolation, reduced gene flow, and potential genetic bottlenecks or local extinctions. Thus, maintaining habitat connectivity is crucial for long-term survival of highly mobile species.

4. The study highlights the need for comprehensive datasets and technological advancements, such as GPS tracking, to study animal movement and behaviour. It also emphasises the importance of studying dispersal patterns, as dispersed individuals often encounter human-dominated landscapes and face increased vulnerability to anthropogenic effects. This study focused on quantifying movement patterns and space use across three life stages: pre-dispersal, dispersal, and post-dispersal phases. The results revealed differences in space use within and outside protected areas, with individuals outside protected areas requiring larger territories. The study also identified seasonal variations in space use and movement patterns, with dispersed tigers exhibiting the highest space use. Land-use composition, landscape configuration, and anthropogenic disturbances influence the use of tiger space. These findings provide insights into the factors influencing tiger movement and space use in a human-dominated landscape. They highlighted the importance of maintaining habitat connectivity, reducing anthropogenic disturbances, and restoring suitable habitats outside protected areas to facilitate dispersal and ensure the long-term survival of tigers.

5. This study also focused on the movement behaviour of sub-adult tigers during different dispersal phases. Recent advancements in fine-scale movement data analysis, such as Hidden Markov Models (HMMs), have enabled the interpretation and classification of behavioural states from animal movement data. Moreover, HMMs consider factors, such as age, sex, and environmental variables, to understand the stationary and transition probabilities of movement behaviours. This approach provides valuable insights into the movement behaviour of large carnivores, especially in complex and dynamic environments. The findings revealed three distinct behavioural states of tigers: resting, area-restricted movement (ARM), and travelling. During dispersal, tigers showed increased movement in ARM and travelling states, especially in fragmented landscapes with a high human presence. They displayed faster and more directed movements, potentially minimising risks and

reaching suitable habitats. Tigers in the post-dispersal phase allocated most of their time to territorial movement and resting, with a minimal distinction between ARM and travelling states. Territory maintenance and defense play crucial roles during this phase.

6. The study also investigated the influence of environmental and anthropogenic factors, such as time of day, temperature, habitat, and roads, on tiger behaviour. Stationary state probabilities varied based on diel time, temperature, and habitat across dispersal phases. Tigers exhibit adaptive behaviour by altering their stationary probabilities, being more active during dawn and dusk, and shifting their behaviour according to temperature variations. Time of day and habitat significantly affected state stationary probabilities and movement during the dispersal and post-dispersal phases. Tigers displayed higher probabilities of travelling during dusk and late evening, with faster movements at night to reduce encounters with humans. They also showed variations in behaviour when moving through forested and non-forested habitats. Transition probability provides insights into the temporal dynamics of state-switching behaviour. Tigers exhibited distinct state transitions during different dispersal phases and in response to time of day and ambient temperature fluctuations. The transition from resting to travelling was higher in the early morning and late evening, indicating increased activity levels. Ambient temperature influenced the transition from foraging to fast movements, with higher temperatures promoting continued travelling behaviour.

7. Habitat selection and animal movement are crucial ecological processes that determine species distribution, abundance, and interactions within the environment. Animals choose habitats that provide resources, refuge from predators, or facilitate movement, while avoiding habitats that pose risks. Competition between and within species also influences the habitat selection. Studying habitat selection helps us to understand how animals respond to foraging resources, environmental risks, and landscape features. However, most studies have overlooked the influence of behaviour on habitat selection, which can lead to incorrect conclusions. Recent advancements in GPS and telemetry have enabled the study of animal behaviour coupled with habitat selection. Behavioural studies have demonstrated the importance of behaviour-specific habitat selection across various species. This study focused on multiscale and behaviour-specific habitat selection during the pre-dispersal, dispersal, and post-dispersal phases.

8. On a larger spatial scale, tigers prefer forested areas with dense cover for their daily activities and movements. They avoided areas with agriculture and human settlement. Forests and vegetation cover facilitate tiger movement, whereas highways act as barriers. Tigers prefer smaller roads with less human activity for movement. High population density and proximity to human settlements also influence tiger habitat selection at a landscape scale. Forest fragmentation poses challenges to tiger movement, as they select smaller forest patches and avoid forest edges at a finer scale.

9. Tigers modify their movement patterns based on the time of the day, showing faster movement at night on a fine scale. They demonstrate different habitat selections during the pre-dispersal, dispersal, and post-dispersal phases. Pre-dispersal tigers prefer forest and grassland areas, while dispersing individuals rest in various habitats and prefer areas near drainages/streams. Post-dispersal tigers prefer forests, grasslands, and areas with dense vegetation. This study emphasises the importance of behaviour-specific habitat selection in understanding species-habitat relationships and informing conservation strategies. By considering specific behaviours and their associated habitat preferences, researchers can identify behaviours with the greatest impact on fitness or conservation. The adaptability of tigers to human-dominated landscapes is reflected in their movement and habitat selection patterns. The findings highlight the need to account for behavioural states when studying habitat selection and selecting appropriate spatiotemporal scales for analysis.

10. In conclusion, this study enhances our understanding of tiger behaviour and the factors influencing tiger movement patterns. These findings will contribute to the conservation and management of tigers, particularly in human-dominated landscapes. By considering the behavioural adaptations of tigers during different life stages, conservation efforts can be better adapted to ensure their long-term survival and coexistence with human activities. Moreover, these findings provide valuable insights into tiger habitat selection and movement patterns, particularly during different dispersal phases. It is also important to include behaviour-specific habitat selection and appropriate spatiotemporal scales. This enhances our understanding of large carnivore ecology and aids in formulating more robust conservation and management strategies.

Organisation of the Thesis

The thesis is structured into eight chapters, each consisting of an introduction to the topic, elaboration of the methods and analysis used, results, and discussion. In this thesis, I investigated the movement pattern, space use, resource selection, and behaviour of tigers. I also quantified the environmental and anthropogenic factors that influence movement and behaviour within and outside the protected areas of the Eastern Vidarbha Landscape, Maharashtra.

Chapter 1: Introduction

The study of animal movement, space use, resource selection, and behaviour is crucial for understanding the ecology and conservation of wildlife populations. Advances in telemetry technology have enabled researchers to track animal movement and gather data on habitat use at unprecedented scales. This information can be used to assess the effects of anthropogenic disturbances on animal behaviour and inform conservation management strategies. Furthermore, analyses of animal behaviour and resource selection can provide insight into species interactions, predator-prey dynamics, and the impacts of climate change on wildlife populations. Studying animal movement and behaviour is vital for understanding and protecting biodiversity in a rapidly changing world.

Chapter 2: Movement Ecology and Conservation: A Review

Movement ecology is a relatively new field that explores fundamental questions about why, how, when, and where organisms move, and how external factors influence this process. Movement is a critical component of life and is diverse across different forms of life. Animal movement patterns are crucial in determining species abundance and diversity, and significantly impact population dynamics and genetic connectivity. Extrinsic factors such as habitat quality, resource availability, and anthropogenic features also significantly influence animal movement. Understanding the environmental drivers of movement is essential for effective management and conservation.

Chapter 3: Hypothesis and Objectives

This chapter focuses on the hypotheses and objectives of the study of the Eastern Vidarbha Landscape. The primary hypothesis of this study is that the movement patterns of tigers in a human-dominated landscape are influenced by a combination of ecological and human-caused factors, which vary across multiple scales. The research's comprehensive understanding of the interplay between ecological and human-induced factors contributes to broader knowledge on how large carnivores, such as tigers, cope with habitat fragmentation and increased human activities.

Chapter 4: Study Area and Methods

This chapter focuses on the Eastern Vidarbha Landscape (EVL) in Maharashtra, India, a part of the larger Central Indian Landscape. The region is a mosaic of agricultural land, human settlements, and wildlife areas, with forest cover accounting for 27.5% of the total area. Large carnivores such as tiger, leopard, sloth bear, and gaur coexist with several ungulate species in the region. EVL is crucial for connecting the central and southern Indian tiger populations and facilitating gene flow between them. The landscape encompasses six tiger reserves within the forested area and several habitat patches outside the protected area network. This study provides important insights into the conservation of tiger populations in India, and highlights the need for conservation efforts in this region.

Chapter 5: Space Use and Movement Patterns

Space use and home ranges are essential components of animal movement ecology. Animals must navigate complex and heterogeneous landscapes to locate resources, find mates, and avoid predators. Landscape heterogeneity, such as changes in land use or habitat quality, can significantly affect animal movement patterns and space use. I explored the current knowledge regarding movement patterns, space use, and their relationship with landscape heterogeneity. Different methods have been used to quantify space use and home range, and to examine the role of environmental factors in shaping animal movement patterns. Ultimately, this chapter highlights the importance of understanding the relationship between animal space use and landscape heterogeneity for effective wildlife management and conservation.

Chapter 6: Movement Behaviour

Large carnivores face challenges in an increasingly fragmented world where habitat loss and human land use alter their movement and behaviour. Understanding the movement behaviour of large carnivores is crucial for their conservation in human-dominated landscapes. This study investigated the movement behaviour of sub-adult tigers during the pre-dispersal, dispersal, and post-dispersal phases in the central Indian landscape. The behaviour was quantified using conventional and generalised Hidden Markov Models. The study identified 3-state behaviour displayed by dispersing and non-dispersing sub-adult tigers. I also show how intrinsic and extrinsic factors shape the movement patterns. The study found that factors such as the time of day, temperature, and habitat significantly influenced behavioural states.

Chapter 7: Behaviour-dependent habitat selection

In this chapter, I evaluated behaviour-dependent habitat selection using the resource selection function (RSF) and step selection function (SSF) at multiple scales. The minimum convex polygon of the observed GPS locations for tigers, buffered by a circular mean male home range size, defined space availability. We randomly sampled GPS locations with a 20:1 ratio of available to use and generated the RSF with standardised variables. The GPS locations were coded as 'TRUE' for used and 'FALSE' for availability. These methods help us to understand how animals decide on habitat use and aid conservation efforts.

Chapter 8: Synthesis and Conservation Implications

I synthesised the findings of the three objectives to bring them into a general context and explain how they contribute to scientific progress in movement ecology. I also provide recommendations for conservation measures for the long-term survival of the population. I also focused on explaining the importance of animal movements for ecosystem functions and, therefore, explain the integration of movement ecology and biodiversity research, which would help ensure ecosystem functioning.

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CHAPTER 1

MOVEMENT ECOLOGY: PATTERNS AND PROCESSES

Chapter 1

Movement Ecology: Patterns and Processes

1.1 General Introduction

Movement is a fundamental ecological process, defined as a change in the spatial location of an organism over time (Nathan et al., 2008). This phenomenon is prevalent, varies across different life forms, and plays a central role in numerous ecological and evolutionary processes. Movement plays a significant role in the survival of most animals and helps shape the structure and dynamics of populations and communities, ecology, and evolution (Swingland and Greenwood, 1983; Turchin, 1998; Clobert et al., 2001; Nathan et al., 2008). For example, movement is essential for obtaining resources, escaping threats, dispersing, and finding mates (Swingland & Greenwood, 1983; Clobert et al., 2001; Levey et al., 2002). Consequently, population dynamics are affected by genetic connectivity and individual fitness (Nathan et al., 2008; Morales et al., 2010). Moreover, animal movement is driven by resources, which can vary depending on the individual's needs and accessibility of suitable resources (Hansson & Akesson, 2014).

Animal movement and its environmental interactions give rise to diverse movement patterns (Johnson et al., 1992; Schick et al., 2008). These patterns play a crucial role in shaping species abundance and diversity, offering valuable insights into space utilisation and habitat preferences (Allen and Singh, 2016). Animals can exhibit different types of movement depending on their life stages, which can vary across spatial and temporal scales. Individuals within a species may exhibit different movement patterns depending on their sex, age, life history stage, and reproductive status (Nathan et al., 2008; Martin et al., 2013). For example, some individuals migrate seasonally over long distances to avoid seasonal variations in food availability (Dingle, 2014; van Moorter et al., 2013), whereas others disperse over great distances from their natal area to new habitats in the early stages of life (Bowler & Benton 2005; Vasudev et al., 2015). Animals may also limit their movement to specific areas known as home ranges that meet their food, shelter, and mate needs (Burt, 1943; Borger et al., 2008; Van Moorter et al., 2016).

Movement ecology offers a clear framework for understanding the movement patterns and factors influencing the process. This paradigm considers the abiotic environment, internal physiology of animals, ability to process information, navigation, and biomechanical capacity to move (Nathan et al., 2008). The relationship between animal movement and conservation is complex and requires a comprehensive understanding of challenges and potential solutions. For example, human-driven environmental shifts have increased temperature and altered precipitation patterns. Global anthropogenic activities have created external pressures that have affected animal movement and altered natural processes that influence the availability of habitats and resources (Tucker et al., 2018). Furthermore, land-use changes result in habitat destruction and fragmentation (Daye & Healey, 2015) and may restrict animal movements, thus disrupting ecosystem functions such as dispersal, food networks, metapopulations, and disease dynamics (Kremen et al., 2007; Bauer and Hoye, 2014; Tucker et al., 2018).

Recent studies have shown that mammals inhabiting areas with a high human footprint exhibit a 50% reduction in their median displacement compared with those in areas with a lower human footprint (Tucker et al., 2018). Similar studies on large carnivores, such as tigers, suggest that they move faster and more at night outside protected areas (Habib et al., 2021). Moreover, in human-dominated landscapes, wildlife conflicts are a significant concern because the proximity of wildlife to human settlements increases the likelihood of negative interactions. In response to human-induced modifications, species may adapt to a shifting environment, change their distribution ranges, or become extinct (Holt 1990; Wiens et al. 2009). It may also shift resource distribution and availability, impacting species habitats and ecological processes (Parmesan, 2006; Chen et al., 2011; Schewe & Levermann, 2012; Jayasankar et al., 2015).

The rapid rate at which landscape changes compel wide-ranging terrestrial mammals to adapt and change their movement patterns for long-term survival. Thus, the conservation of highly mobile species presents complex challenges, requiring approaches that consider movement in decision-making processes, because traditional spatially focused methods are likely to be insufficient (Runge et al., 2014; Allen and Singh, 2016). Large-ranging carnivores, such as tigers, account for 70% of the population in India and 7% of their historic global range. Most tiger populations are in Protected Areas (PA), covering 2.21% of the geographical region, and 35% reside outside these PAs (Habib et al., 2021). Tiger populations are mostly confined to small protected areas because their habitats are highly fragmented, affecting their movement within and outside protected areas (Habib et al., 2021; Thatte et al., 2018). Furthermore, the fragmented landscape outside PAs creates competition for space (Habib et al., 2021). Thus, the long-term survival of the tiger population in a fragmented landscape depends on the successful movement from one area to another, thus maintaining connectivity between subpopulations and isolated populations (Ash et al., 2020).

The adaptability of large carnivores is essential for the survival and maintenance of their population dynamics. However, to maintain a stable population, tigers must negotiate human-modified landscapes under various land use types. Landscape connectivity plays a significant role in enhancing a species' ability to adapt to environmental change. It influences various aspects, such as demography (Clobert et al., 2001), dispersal and colonisation (Hanski, 1998), maintenance of genetic diversity through gene flow (Hendrick, 2005), and long-term population persistence (Swingland & Greenwood, 1983). Enhancing connectivity through wildlife corridors is a crucial conservation tool for safeguarding animal movements and fostering landscape connectivity (Gilbert-Norton et al., 2010). These corridors have been proven to facilitate movement between habitat patches (Haddad et al., 2003; Gilbert-Norton et al., 2010) and decrease individual mortality during dispersal (Kenneth Dodd et al., 2004; Glista et al., 2009).

The conservation of large carnivores such as tigers in human-dominated landscapes is a pressing challenge in conservation biology. For the long-term survival of the tiger population, suitable habitat distribution and connectivity between the carnivore populations are required to mitigate the extinction risk of tigers. Therefore, understanding why and how tiger populations respond differently to environmental and anthropogenic factors is fundamental to understanding the movement and behaviour of the species. Moreover, prioritising vulnerable habitats is critical for allocating conservation efforts and reducing biodiversity losses (Strassburg et al., 2020; Watson et al., 2020). With the recent advancements in GPS technology, it is possible to gain new insights into animal movement, behaviour, and response to environmental and anthropogenic features (Kays et al. 2015). Current advances have also opened new opportunities to relate animal movements to remotely sensed data on environmental conditions.

The Central Indian Landscape is one of the strongholds of the tiger population where the habitat remains intact and suitable. However, some of the critical tiger-bearing areas in the landscape lie outside PAs, with high human pressure. Anthropogenic pressure varies according to human presence in such a human-wildlife matrix and may influence the movement and behaviour of tigers in different land uses. One key challenge for ecologists is to improve our understanding of how anthropogenic global change affects movement processes, their underlying mechanisms, and what these changes mean at the ecosystem level. Thus, studying movement parameters is imperative to understand fundamental biological processes, such as dispersal strategies, foraging, social interactions, and general space use patterns that determine community and population structures (Nathan et al., 2008). To effectively conserve species and ecosystem function, it is essential to identify species movement attributes and biotic and abiotic factors that compel them to move across spatial and temporal scales. Moreover, it is also important to understand the impacts of species movements on ecosystem function, external pressures created by human activities, and ecological factors that influence movement behaviour.

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CHAPTER 2

INSIGHTS FROM MOVEMENT ECOLOGY AND WILDLIFE CONSERVATION: A REVIEW

Chapter 2

Insights from Movement Ecology and Wildlife Conservation: A Review

2.1 Introduction

The term "movement ecology" was coined in the early 2000s, when this emerging discipline aimed to derive testable hypotheses and empirically link work with theoretical models (Holden 2006). Movement ecology investigates fundamental questions about organism movement, including why, how, when, and where the organisms move, and how this process is linked to external factors. The conceptual framework of movement ecology allows us to understand or explore the causes, mechanisms, and patterns of movement and helps us understand the consequences of movement on the ecology and evolution of individuals, populations, and communities.

Movement is a fundamental characteristic of life, and is diverse among life forms. Movement is defined by Turchin (1998) as *'the process by which individual organisms are displaced in space over time'*. The movement of living organisms is widespread and plays a central role in ecological and evolutionary processes (Nathan & Giuggioli, 2013). Movement mechanisms vary among life forms including microorganisms, plants, and animals. These organisms move in various ways, either actively or passively, locally, or in transit, to new areas. Moreover, various processes across multiple spatial and temporal scales drive the movement mechanisms. Movement patterns can differ in animal and plant dispersal, which involves one- or two-way migration, irruption, nomadism, or accidental displacement. Although different types of movement exist, the most common are foraging, dispersal, and migration (Nathan et al., 2008).

An animal's movement and interaction with the environment result in various movement patterns (Johnson et al., 1992; Schick et al., 2008). Such movement patterns determine the abundance and diversity of species. Understanding animal movement patterns also aids in the informed planning of potential wildlife corridors, future range expansion predictions, and individual or population habitat requirements. (Colchero et al., 2011; Buchmann et al., 2012; Avgar et al*.,* 2013; Clark et al., 2015; Allen, 2016). Movement affects population dynamics and genetic connectivity among populations, and affects an individual's fitness (Nathan et al., 2008;

Morales et al., 2010). Moreover, identifying the factors responsible for animal movement will allow us to understand individual or population behavioural responses, space use, and resource selection patterns.

Depending on their sex, age, life-history stage, and reproductive status, individuals within a species may display various movement patterns. (Nathan et al., 2008; Martin et al., 2013). Extrinsic factors such as habitat quality, resource availability, and anthropogenic features (settlement, roads, and land-use changes) in a landscape also influence animal movement. These external factors are also linked to the spatial and temporal variability in environmental conditions. Our understanding of the effects of landscape heterogeneity on animal movement is still relatively limited as it requires studying the movement of multiple individuals across various environmental conditions. Therefore, it is essential to identify these environmental features and their roles in animal movement. Gaining a deeper understanding of the environmental drivers of movement is crucial and may help inform management and conservation.

There are four ecological themes for movement data visualisation: (a) spatiotemporal dynamics of home ranges and utilisation, (b) identification of spatiotemporal patterns in movement, (c) classification or identification of behaviour, and (d) linking movement data with environmental context. The home range, conventionally defined as "the area traversed by the individual in its normal activities of food gathering, mating, and caring for young, is one of the most fundamental concepts for understanding individual movement in an area of its utilisation. Ecologists can now quantitatively characterise home range and space use patterns over time. Applying such quantification methods to movement paths often compares space use among individuals or species to examine processes, such as niche partitioning, optimal foraging, social aggregation, or even decision-making (Dougherty et al., 2017). Therefore, movement forms the primary link between home range size and resource selection.

Movement ecology research has rapidly expanded over the past decade, offering new opportunities for wildlife research and practical applications. It now provides crucial insights into integrating species movement into management planning. There is growing recognition of the need to understand and predict movement processes driving biological invasions, the spread of pests and diseases, persistence of local populations, and entire species considering global environmental changes. Understanding this mechanism should facilitate our knowledge of the consequences of movement on the ecology and evolution of individuals, populations, and communities. The development of management strategies that are flexible in time and space, using movement data, may increase the efficacy of management actions. Therefore, wildlife management and conservation may benefit from strengthening the connection with the movement ecology. The potential for wildlife management is highlighted by the movement management framework, which establishes a crucial link between movement ecology and wildlife conservation.

2.2 The Movement Ecology Framework

Nathan et al. (2008) provided four general frameworks for movement-ecology research. These four basic components are needed to describe the mechanism of an organism's movement: its internal state, motion and navigation capacities, and external factors affecting movement (Figure 2.1). This framework investigates fundamental questions about organisms, including why, how, when, and where movement occurs and how this process is linked to external factors. The conceptual framework also allows us to understand or explore causes, mechanisms, and movement patterns. The five mechanistic approaches to understanding movement are: (*a) motivation for movement, (b) how movement is performed, (c) navigation capacity, (d) external factors (biotic and abiotic factors), and (e) interaction of all the above four components*. By answering these five questions, we can identify the key life history traits, behaviour, and external factors that determine movement.

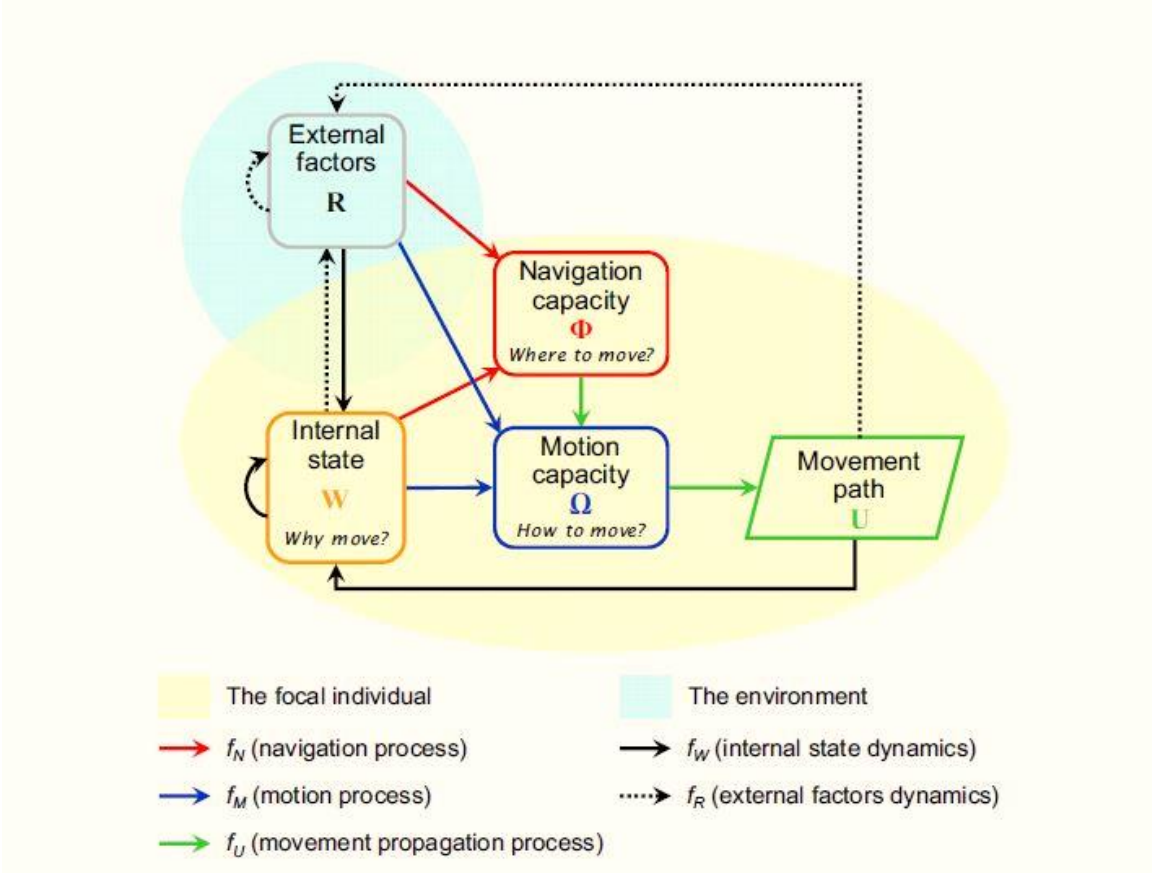


Figure 2.1: General framework for the movement ecology paradigm composed of four components: Internal state, motion capacity, navigation capacity and external factors (Nathan et al., 2008)

2.3 Advancement in Movement Ecology

The understanding of animal movement became more convenient with the revolution of radio-telemetry that began in the early 1960 (Cochran and Lord, 1963). Since then, radio-telemetry has been widely used to understand animal ecology, animal movement, home range, habitat use, survival, and productivity for population estimation. The telemetry method also provides information on how animals use their environment, migration, dispersal, and activity patterns. Initially, very high-frequency (VHF) radio devices were used for wildlife tracking. With the advancement of technology, traditionally used VHF radio transmitters have been replaced by more advanced GPS transmitters, revolutionising animal tracking studies (Cagnacci et al., 2010; Kays et al., 2015). The field of movement ecology has started gaining popularity owing to technological and analytical advancements that have been made in tracking animal movements (Tomkiewicz et al., 2010). A significant advantage of GPS telemetry is that the animal's location can be collected with different time intervals or fixes with high temporal resolution and accuracy to meet the demands of the study.

Traditional wildlife conservation methods, such as protected areas, have limitations such as extended space use and crossing human-dominated areas. With the help of movement data, flexible management strategies can be developed that are time and space and may improve the effectiveness of management actions. Therefore, wildlife management and conservation may benefit from strengthening this link with movement ecology. The movement management framework provides an essential link between movement ecology, wildlife management, and conservation, thereby highlighting the potential for managing wildlife.

2.4 What is the need for Movement Ecology?

Traditionally, wildlife management plans have been implemented in distinct and demarcated areas. The traditional methods of wildlife management involve establishing protected areas, such as national parks or wildlife centres. However, wildlife conservation is required when a population or species becomes threatened or endangered owing to poor management, over-exploitation, habitat loss/degradation, or stochastic events. Conservation steps include restoration or prevention of further declines in a population, species, or ecosystem. Ideally, conservation planning provides a structured and systematic framework that helps identify conservation needs and goals (Margules & Pressey 2000).

Recent research has shown that even the largest PAs fail to protect a species fully (Thirgood et al., 2004). Animals do not understand the physical boundaries of their habitats or move beyond the margin of their needs. Once animals move outside protected areas, they are often exposed to exploitation (Holdo et al., 2010) or considered pests (Woodroffe and Ginsburg, 1998). Protected landscapes are also frequently used for the extraction of natural resources (Sanderson et al., 2002), leading to habitat degradation (Ewers and Rodrigues, 2008) and, in some cases, isolation through fragmentation (Haddad et al., 2015). The ability of PAs to hold wildlife is also questioned, as climate change alters the characteristics of such landscapes, and additional assistance is necessary to track species' changing distributions and adaptation (Araújo et al., 2011; Singh & Milner-Gulland, 2011).

Movement ecology comes into play to eliminate the limitations of protected areas alone. Movement ecology recognises the challenges of managing animal movements outside demarcated areas and provides management plans. Present-day management plans include creating wildlife corridors within non-protected areas to promote the easy movement of species. Creating such corridors requires knowledge of ideal habitats that can serve as corridors and how a species moves in a fragmented landscape. Until recently, this knowledge was not accessible, but with advancements in movement ecology, such knowledge could be acquired and used to improve the effectiveness of management actions.

2.4.1 Movement Ecology and Wildlife Management

Discoveries in movement ecology have created a paradigm shift when thinking about conservation and management. Conservation of long-ranging species has led to the emergence of the concept of migratory connectivity (Webster et al., 2002). Furthermore, it has become evident that management actions must consider migratory individuals' winter and summer ranges and stopover sites along the migratory route (Martin et al. 2007). Landscape connectivity is another key concept in which movement is vital for providing ecosystem services, such as pollination (Kremen et al., 2007), or maintaining processes such as dispersal and subsequent genetic diversity (Baguette & Van Dyck, 2007). Species movements are either more, or there are too many conflicting land uses, such as housing, farming, and forestry, for PAs to be effective (Sanderson et al., 2002, Thirgood et al., 2004). Movement ecology can provide the knowledge needed to identify novel management actions that can improve the scale of management. Modern research has realised the importance of understanding animal movement as there are aspects in many fields of science which inherently rely upon an understanding of movement ecology, including ecosystem management (Berkes et al., 2008), animal behaviour (King et al., 2018), evolutionary science (Peck, 2001), population dynamics (Patterson et al., 2008; Holyoak et al., 2008), and conservation science (McLane et al., 2011).

2.5 The study species: Tiger (*Panthera tigris*)

The Tiger (*Panthera tigris tigris*), Asia's largest obligatory terrestrial carnivore, is endangered by the IUCN Red List of Threatened Species. It is currently found in 13 Asian countries, including Bangladesh, Bhutan, Cambodia, China, India, Indonesia, Lao PDR, Malaysia, Myanmar, Nepal, Russia, Thailand, and Vietnam. This species is found in diverse habitat types and at different altitudes, temperatures, and rainfall regimes (Sunquist et al., 1999). Tigers are wide-ranging, territorial felids, and the Tropical Dry Forest is the largest habitat that supports tiger populations on the Indian subcontinent (Wikramanayake, 1998; Smith et al., 2011). The current and historical ranges of tigers are shown in Figure 2.2. Tigers are behaviourally flexible and can adapt to various alterations in their landscapes (O'Brien et al., 2003). Their resilience, a product of adaptability and high fecundity, has allowed tigers to survive massive onslaughter and habitat loss in the past century (Kawanishi, 2002). Recent conservation strategies for tigers prescribe an enlarged focus of conservation efforts on multiple metapopulations (Wikramanayake et al., 2004; Sanderson et al., 2006), leading to the identification of Tiger Conservation Landscapes (TCLs), which include several Protected Areas and interconnecting habitat patches or corridors (Sanderson et al., 2006).

India accounts for 57% of the world's tiger population and only 7% of its historical global range. Due to government policies and conservation efforts, tiger numbers have increased, and they are listed in Schedule I of the Indian Wildlife (Protection) Act, 1972, providing them with the highest level of protection. However, most of the tiger population resides in Protected Areas (PA) designated as tiger reserves, which cover only 2.21% of the geographical region, and 35% live outside these PAs (Habib et al., 2021). Tiger populations are mostly confined to small PAs, and the habitat outside these PA is highly fragmented, limiting the movement of tigers within and outside the PAs (Habib et al., 2021; Thatte et al., 2018). Furthermore, increased human activity and infrastructure development pose significant anthropogenic pressure on tiger populations. To ensure long-term survival of tigers, it is crucial to maintain connectivity between subpopulations and isolated populations by allowing successful dispersal from one area to another.

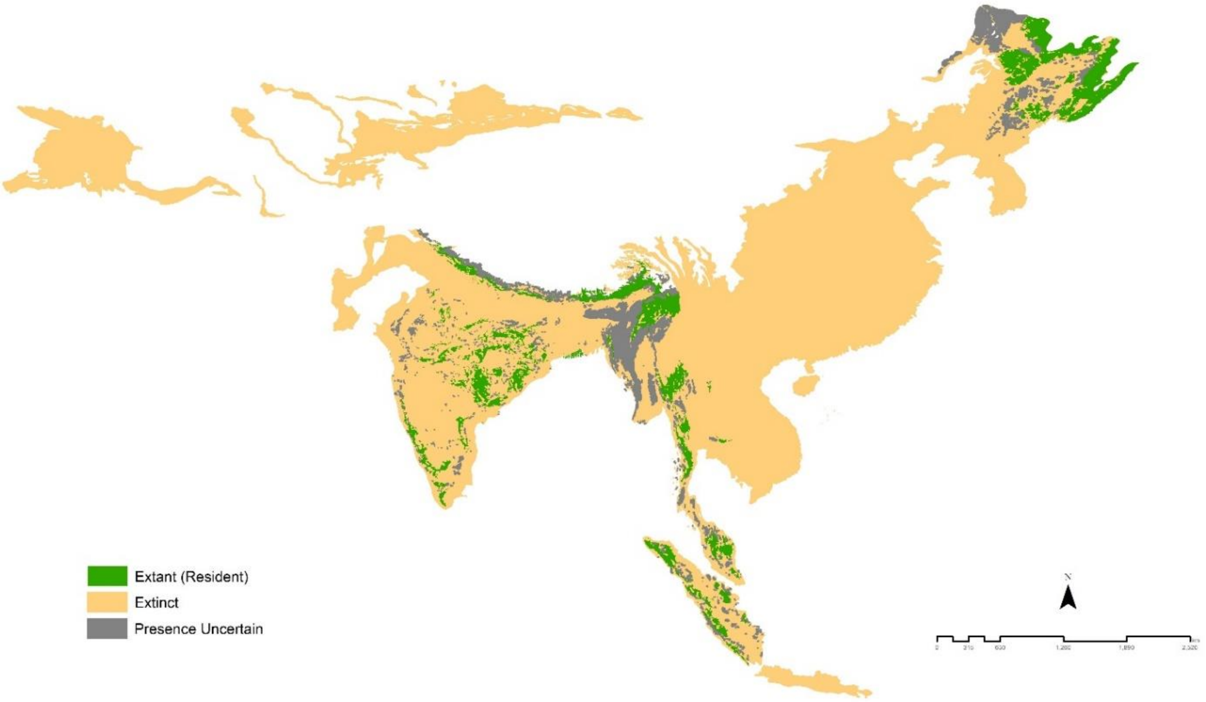


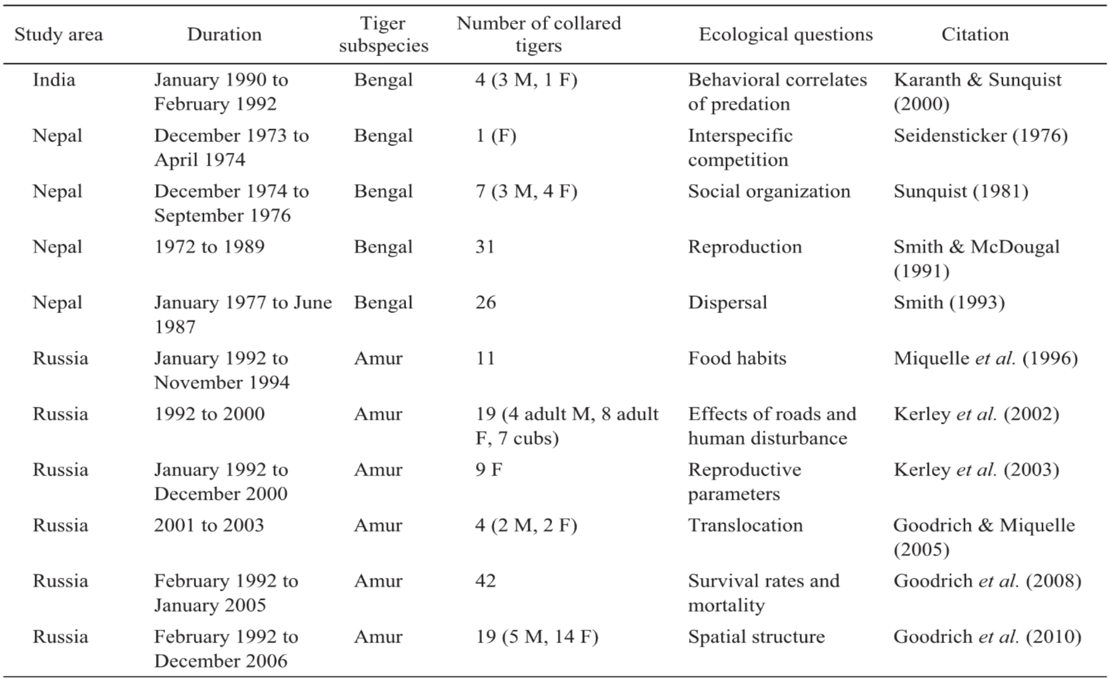
Figure 2.2. Global distribution of tiger (*Panthera tigris*) showing extant (resident), extinct and uncertain presence (Source: IUCN Red List)

2.5.1 A review of tiger studies

Research from the Russian Far East to the Indian subcontinent has focused on natural history, social organisation, communication, movement, and feeding behaviour. Several studies have covered distribution, ecology, home range, habitat use, prey selection, conflict, and conservation efforts. For example, in the Indian subcontinent, various aspects of tiger conservation have been studied, such as general ecology (Schaller, 1967; Johnsingh, 1983; Seidensticker & McDougal, 1993), social organisation (Sunquist, 1981), population estimation (Karanth, 1995; Karanth & Nichols, 1998; Karanth et al., 2004; Kawanishi & Sunquist, 2004; Hariha, 2005; Jhala et al., 2008; Wegge et al., 2009; Wang & Macdonald, 2009), the land tenure system (Panwar, 1979; Smith et al., 1987; Gogate & Chundawat, 1997), dispersal (Smith, 1984; Hussain et al., 2022), and the impact of tiger reintroduction (Sankar et al., 2010). Additionally, researchers have explored tiger prey selection and food habitats (Schaller, 1967; Johnsingh, 1983; Johnsingh, 1992; Karanth & Sunquist, 1995; Stoen & Wegge, 1996; Wegge et al., 2009; Sankar & Johnsingh, 2002; Biswas & Sankar, 2002; Bagchi et al., 2003; Andheria et al., 2007; Avinandan et al., 2008; Ramesh et al., 2009; Wang, 2008; Khan & Monirul, 2008) as well as their interactions with other co-predators, such as leopards (Seidensticker, 1976; Wang, 2008; Odden et al., 2010). More recently, studies on tigers were carried out to understand the home range patterns and size of home ranges can be highly variable across their habitat and landscape (Goodrich et al., 2010; Jhala et al., 2010; Naha et al., 2016; Sarkar et al., 2016).

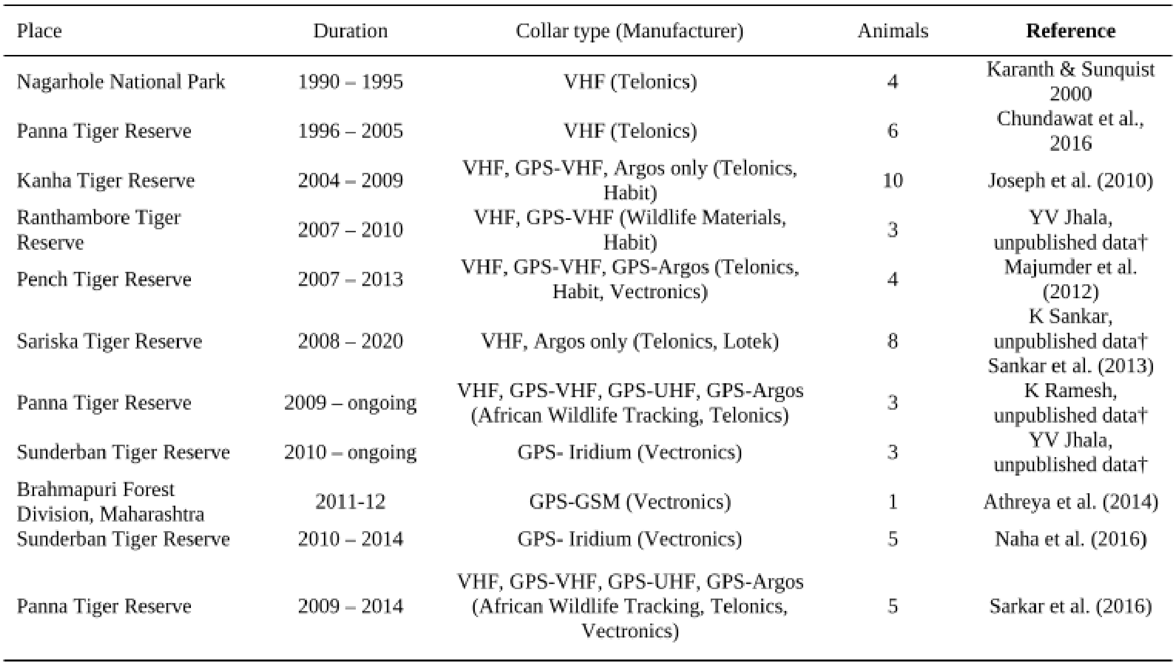
Advancements in movement ecology have enabled the tracking of animals and the linking of their movements to environmental data (Table 2.1). Radio telemetry research on tigers began in 1973 by the Smithsonian-Nepal Tiger Ecology Project in Royal Chitwan National Park, Nepal (Seidensticker et al., 1974). Researchers at the Royal Chitwan studied tiger movements and social-spatial behaviour (Sunquist, 1981), the dispersal of tigers (Smith, 1993), and the effects of poaching (Kenney et al., 1995). Radio-tagging of tigers and other large mammals provided valuable insight into their life history, movements, and activities that traditional methods could not capture (Schaller 1967; Table 1). Radio-telemetry-based studies on the ecology of Amur tigers began in 1992 as part of the Siberian Tiger Project (Miquelle et al., 1996). In India, radio telemetry has been used to study tiger ecology and interspecific competition in the tropical dry forests of the Panna Tiger Reserve (Chundawat et al., 1999) and the tropical forests of the Nagarhole National Park (Karanth & Sunquist, 2000). These studies investigated predator competition and its effects on movement patterns, activity, hunting strategies, and social organisation (Table 2.2).

Table 2.1: Studies on radio-collared tigers using very high frequency (VHF) radio transmitters (source: Miller et al., 2010)



Study area	Duration	Tiger subspecies	Number of collared tigers	Ecological questions	Citation
India	January 1990 to February 1992	Bengal	4 (3 M, 1 F)	Behavioral correlates of predation	Karanth & Sunquist (2000)
Nepal	December 1973 to April 1974	Bengal	1 (F)	Interspecific competition	Seidensticker (1976)
Nepal	December 1974 to September 1976	Bengal	7 (3 M, 4 F)	Social organization	Sunquist (1981)
Nepal	1972 to 1989	Bengal	31	Reproduction	Smith & McDougal (1991)
Nepal	January 1977 to June 1987	Bengal	26	Dispersal	Smith (1993)
Russia	January 1992 to November 1994	Amur	11	Food habits	Miquelle *et al.* (1996)
Russia	1992 to 2000	Amur	19 (4 adult M, 8 adult F, 7 cubs)	Effects of roads and human disturbance	Kerley *et al.* (2002)
Russia	January 1992 to December 2000	Amur	9 F	Reproductive parameters	Kerley *et al.* (2003)
Russia	2001 to 2003	Amur	4 (2 M, 2 F)	Translocation	Goodrich & Miquelle (2005)
Russia	February 1992 to January 2005	Amur	42	Survival rates and mortality	Goodrich *et al.* (2008)
Russia	February 1992 to December 2006	Amur	19 (5 M, 14 F)	Spatial structure	Goodrich *et al.* (2010)

Table 2.2: Summary of radio-collaring (VHF/GPS) studies of tigers in India



Place	Duration	Collar type (Manufacturer)	Animals	**Reference**
Nagarhole National Park	1990 – 1995	VHF (Telonics)	4	Karanth & Sunquist 2000
Panna Tiger Reserve	1996 – 2005	VHF (Telonics)	6	Chundawat et al., 2016
Kanha Tiger Reserve	2004 – 2009	VHF, GPS-VHF, Argos only (Telonics, Habit)	10	Joseph et al. (2010)
Ranthambore Tiger Reserve	2007 – 2010	VHF, GPS-VHF (Wildlife Materials, Habit)	3	YV Jhala, unpublished data†
Pench Tiger Reserve	2007 – 2013	VHF, GPS-VHF, GPS-Argos (Telonics, Habit, Vectronics)	4	Majumder et al. (2012)
Sariska Tiger Reserve	2008 – 2020	VHF, Argos only (Telonics, Lotek)	8	K Sankar, unpublished data† Sankar et al. (2013)
Panna Tiger Reserve	2009 – ongoing	VHF, GPS-VHF, GPS-UHF, GPS-Argos (African Wildlife Tracking, Telonics)	3	K Ramesh, unpublished data†
Sunderban Tiger Reserve	2010 – ongoing	GPS- Iridium (Vectronics)	3	YV Jhala, unpublished data†
Brahmapuri Forest Division, Maharashtra	2011-12	GPS-GSM (Vectronics)	1	Athreya et al. (2014)
Sunderban Tiger Reserve	2010 – 2014	GPS- Iridium (Vectronics)	5	Naha et al. (2016)
Panna Tiger Reserve	2009 – 2014	VHF, GPS-VHF, GPS-UHF, GPS-Argos (African Wildlife Tracking, Telonics, Vectronics)	5	Sarkar et al. (2016)

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CHAPTER 3

HYPOTHESIS AND OBJECTIVE

Chapter 3

Hypothesis and Objectives

3.1 Hypothesis

Animal movement, including resource acquisition, evading threats, dispersal, and finding mates, is crucial for survival (Nathan et al., 2008). The ability of animals to navigate through their habitats directly affects their population dynamics and genetic diversity. However, the increased human footprint has led to habitat fragmentation and increased anthropogenic activity (Haddad et al., 2015). This situation poses a significant threat to large carnivores, such as tigers, with long-range movements that often bring them into contact with humans, endangering their population's viability. Hence, maintaining habitat connectivity is imperative for the long-term survival of tiger populations in landscapes dominated by human activity.

In India, tiger populations are widely distributed and are found in protected and non-protected areas (Habib et al., 2021). Protected areas play a crucial role in biodiversity conservation and the maintenance of ecological balance. These areas receive higher levels of legal protection and management aimed at preserving biodiversity, ecosystem services, cultural significance, and a limited human presence (Macura et al., 2011; Naniwadekar et al., 2015). Conversely, areas outside protected areas lack formal legal protection and may be subject to various land uses, including agriculture, urbanisation, and industrial activities. Areas outside protected areas, such as Reserved Forests or Protected Forests, are vital for sustaining tropical biodiversity (Velho et al., 2016). However, these areas are susceptible to human pressure, land use changes, and road networks, which have implications for the overall health and sustainability of ecosystems in human-dominated landscapes (DeFries et al., 2010).

In the Anthropocene, with increasing human populations and consequent habitat loss and fragmentation, protected areas serves as crucial refuges for many threatened wildlife species (Laurance et al., 2012; World Database on Protected Areas, 2016). Currently, these conservation islands are often surrounded by expanding human-dominated landscapes, leading to increased human-wildlife interactions, especially with wide-ranging mammals (Manral et al., 2016). Consequently, understanding how human-dominated landscapes affect tiger movement is important for conservation and management of this species. In this context, I hypothesised that *" the movement patterns of tigers in the Eastern Vidarbha Landscape are* *influenced by a combination of ecological and human-caused factors that vary across multiple scales within the landscape".* These factors include habitat characteristics, vegetation cover, habitat fragmentation, and anthropogenic factors such as human settlements, population, and road density. I expect that the impact of these factors on tiger movement will vary across multiple scales in the landscape. By examining these influences, insights into the complexities of tiger movements in a human-dominated landscape can be identified as potential strategies for conservation. By investigating the interplay between ecological and human-caused factors, this study aims to contribute to the understanding of how tiger movement is affected within and outside protected areas in the Eastern Vidarbha Landscape of Maharashtra. The objectives of this study were as follows:

3.2.1 To study the space use and movement of tigers in the Eastern Vidarbha Landscape

a. *How home range and movement patterns of tigers differ in protected and non-protected areas?*

b. *Is there a difference in home-range use and movement patterns between sex and age class?*

c. *How movement patterns and space use differ in sub-adult tigers during the pre-dispersal, dispersal, and post-dispersal phase?*

3.2.2 To identify the behavioural pattern of dispersing tigers in the Eastern Vidarbha Landscape

a. *To study the movement modes in sub-adult tigers during pre-dispersal, dispersal, and post-dispersal phase*

b. *To study the movement modes among sexes across the landscape*

3.2.3 To evaluate resource selection patterns using radio-telemetry across the landscape

a. *How resource selection patterns vary between protected and non-protected areas*

b. *How environmental and anthropogenic factors influence resource selection*

CHAPTER 4

STUDY AREA AND METHODS

Chapter 4

Study Area and Methods

4.1 The Eastern Vidarbha Landscape

This study was conducted within and outside the protected areas of the Eastern Vidarbha Landscape (EVL), Maharashtra, India. This region forms a major part of the larger Central Indian Landscape. The Vidarbha region comprises Nagpur and Amravati divisions, including 11 districts of Akola, Amravati, Bhandara, Buldana, Chandrapur, Gadchiroli, Gondia, Nagpur, Wardha, Washim, and Yavatmal. It is located between 18° 40' 21.42" N to 21° 38' 58.23" N and 75° 59' 24.90" E to 80° 53' 49.03" E. The region is bounded to its north and northeast by Betul, Chhindwara, Seoni, and Balaghat districts of Madhya Pradesh, and to the east and southeast by the Durg and Bastar districts of Chhattisgarh state. To the south, it is bounded by Andhra Pradesh and the southern boundary of the Vidarbha region is delimited by Painganga and Pranhita Rivers and to the west, Jalgaon and Aurangabad districts of Maharashtra state. The largest river in Vidarbha is the Wainganga, which flows into the Godavari River in the south with its principal tributaries, the Wardha, Kanhan, and Painganga. In the north, five small rivers—Khapra, Sipna, Gadga, Dolar, and Purna—are tributaries of the river Tapti. The region encompasses an area of approximately 97,320 km^2, with forest cover accounting for 27.5% of the total area (Habib, Nigam, et al., 2021). The landscape is a mosaic of agricultural land, human settlements, and wildlife areas (Habib et al., 2017). Large carnivores in the region include the tiger (*Panthera tigris*), which co-occurs with other species, such as the leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), gaur (*Bos gaurus*), and several other ungulate species.

The region has a tropical monsoon climate with dry and hot summers and hot, rainy, and cold winters (Nandankar et al. 2011). In the EVL, the annual precipitation varies from 400 to 2,000 mm. The major forest types are southern-moist mixed deciduous, dry deciduous, and teak forests (Champion & Seth, 1968). Regarding the total forest area, 2.83% was classified as Very Dense Forest, 6.69% as Moderately Dense Forest, 6.98% as Open Forest, and 1.38% as scrub forest. The forest patch of the Vidarbha region has a sizable tiger population and forms a connecting link between the central and southern Indian tiger populations. It plays a pivotal role in the exchange of individuals and facilitates gene flow between these two populations, thereby increasing the viability of tiger populations in India. The tiger-occupied landscape of Maharashtra consists of six tiger reserves within patchily distributed forested areas. Five of these tiger reserves are situated in eastern Maharashtra, and their forested interconnectivity is recognised as the Vidarbha Tiger Conservation Landscape. In addition, several other habitat patches in the state constitute part of the identified TCLs in contiguity with the TCLs in adjoining states. Most corridors connecting the protected areas lie outside the protected area (PA) network and under different land ownership tenures. The intensive field encompassed protected and outside protected areas. The protected areas include Tadoba-Andhari Tiger Reserve, Umred-Karhandla Wildlife Sanctuary and Tipeshwar Wildlife Sanctuary. On the other hand, the Brahmapuri forest division represents the landscape outside the protected area (Figure 4.1)

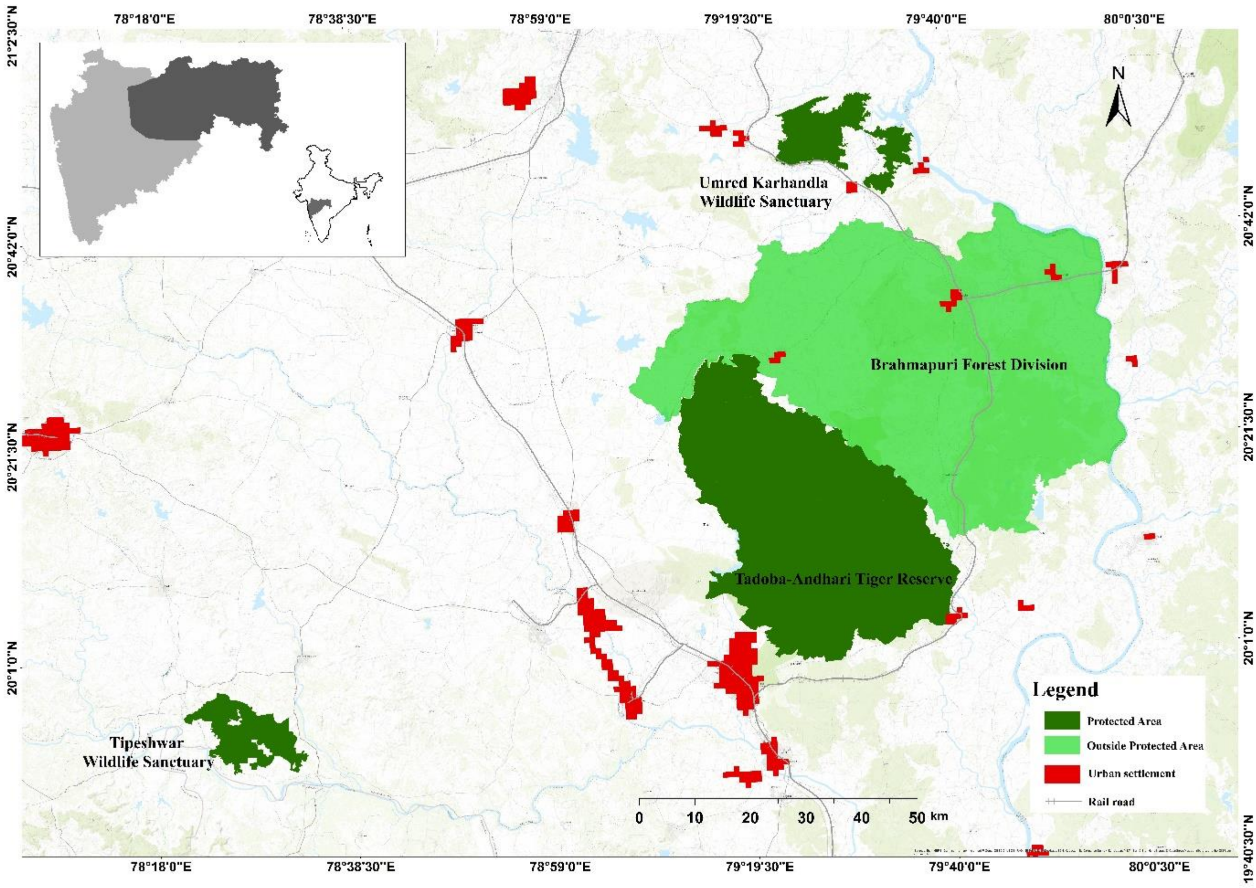

Figure 4.1: Study area showing protected and outside protected areas of the Eastern Vidarbha Landscape where tigers (n=15) were captured and fitted with GPS collars

4.2 Protected Areas

4.2.1 Tadoba-Andhari Tiger Reserve

Tadoba-Andhari Tiger Reserve (TATR) is situated in the Chandrapur district (20º04′53″ to 20º25′51″N and 79º13′13″ to 79º33′34″E) and serves as one of the major source populations of large carnivores, especially tigers in the Central Indian Tiger Landscape. The tiger reserve is the largest in Maharashtra, with a total area of 1,727 km^2. The tiger population in TATR is vital for the metapopulation dynamics connecting the adjoining tiger populations in the north, such as Pench and Navegaon-Nagzira Tiger Reserve through Umred Karhandla Wildlife Sanctuary, Bor Tiger Reserve and Indravati and Kawal Tiger Reserves through the forests of Chandrapur - Gadchiroli districts in the south. This connectivity extends until Kanha National Park is in the northwest of the landscape.

The vegetation of TATR can be classified as southern tropical dry deciduous (Champion and Seth, 1968). The area is dominated by dry flora species like Teak (*Tectona grandis*), Bhera (*Chloroxylon swietenia*), Dhawada (*Anogeissus latifolia*), Mahua (*Madhuca indica*), Rohan (*Soymida febrifuga*), Salai (*Boswellia serrata*) and Tendu (*Diospyros melanoxylon*). The ecosystem also has highly contrasting tracts of riparian vegetation in numerous perennial and non-perennial streams that are interspersed throughout the forest. Species like Jamun (*Syzygium cumini*), Arjun (*Terminalia arjuna*) and Mango (*Mangifera indica*) can be found in these riparian tracts, which serve as a refuge to the fauna during the harsh and dry summers that the forest experiences. TATR also harbours bamboo forests, mainly *Dendrocalamus strictus*, which play an important role in the life cycle of Tadoba.

The terrain in TATR is predominantly flat, with a mildly hilly region in the west and Chimur hills in the north reaching elevations up to 315 msl. Several streams drain rainwater into the Irai and Andhari Rivers that run through the reserve. Large reservoirs such as the Irai and Nalleshwar are located at the western and eastern boundaries. These water sources and the several lakes inside the reserve support the landscape ecosystem during the dry season.

4.2.2 Umred-Karhandla Wildlife Sanctuary

The Umred-Karhandla Wildlife Sanctuary (UKWLS) is located in the Bhandara and Nagpur districts of eastern Maharashtra. Located on the bank of the Wainganga River, the sanctuary comprises dry savannahs and dry deciduous forests. It was declared a sanctuary in 2012, with an area of 180 km^2. Owing to its proximity to tiger reserves such as Tadoba-Andhari, Pench, Bor, Navegaon-Nagzira, and other tiger-inhabited regions such as Bramhapuri, this area has served as a significant habitat for tiger populations in recent years. Moreover, the sanctuary is a stepping-stone corridor that is essential for the region's long-term persistence of the tiger meta-population.

The vegetation type of UKWLS is mainly dry deciduous, with *Tectona grandis* as the predominant species, along with *Terminalia tomentosa, Terminalia alata, Dyospyrus melanoxylon, Largestroemia perviflora, Zizyphus sp.,* and *Madhuca longifolia*. Grassland patches are seen in areas with species such as *Heteropogon contortus* and *Chysopogon fulvus*. Though small in size, the sanctuary is home to varied mammals which include carnivores like tiger (*Panthera tigris*), dhole (*Cuon alpinus*), leopard (*Panthera pardus*), sloth bear (*Melurusus urcinus*), ratel (*Mellivora capensis*). It is also home to herbivores such as chital (*Axis axis*), sambar (*Rusa unicolor*), nilgai (*Boselaphus tragocamelous)*, and wild boar (*Sus scrofa*).

4.2.3 Tipeshwar Wildlife Sanctuary

The Tipeshwar Wildlife Sanctuary (TWLS) is a small protected area nestled in the rugged hillocks of southern Vidarbha. The sanctuary covers a geographic area of 148.63 km^2 (Figure 2). The sanctuary lies in the Yavatmal district of Maharashtra between 78°20'22″ to 78°47'56" E and 19°50'59" to 19°55'44" N. The sanctuary lies very close to the state border, dividing Telangana from Maharashtra. The sanctuary got its name from 'Goddess Tipai', who is worshipped in the region and has a temple dedicated to her inside the sanctuary. Rivers such as Purna, Krishna, Bhima, and Tapti feed into the sanctuary. The sanctuary is mainly isolated and has limited connectivity with the Kawal Tiger Reserve in Telangana to the South and Melghat Tiger Reserve to the north. Tipeshwar forests can be classified as tropical dry and moist deciduous forests. The forest is dominated by Teak (*Tectona grandis*) along with other species like Dhawada (*Anogeissus latifolia*), Ain (*Terminalia alata*), Tendu (*Diospyros melanoxylon*), Sehna (*Lagerstroemia parviflora*), Bherra (*Chloroxylon switenia*), Kallam

(*Mitragyna parviflora*), Beheda (*Terminalia bellirica*), Salai (*Boswellia serrata*), Bija (*Pterocarpus marsupium*), etc. The forest is a mosaic of woodlands along with lush meadows.

Tipeshwar is also home to a host of faunal species like Tiger (*Panthera tigris*), Leopard (*Panthera pardus*), Dhole (*Cuon alpinus*), Wolf (*Canis lupus*), Golden Jackal (*Canis aureus*), Sloth Bear (*Melursus ursinus*), Striped Hyaena (*Hyaena hyaena*), Jungle Cat (*Felis chaus*), Wild Pig (*Sus scrofa*), Rhesus Macaque (*Macaca mulatta*), Langur (*Semnopithecus spp.),* Sambar (*Rusa unicolor*), Barking Deer (*Muntiacus muntjak*), Nilgai (*Boselaphus tragocamelus*), Four Horned Antelope (*Tetracerus quadricornis*), Chinkara (*Gazella bannettii*), Blackbuck (*Antilope cervicapra*), Ratel (*Mellivora capensis*), and Pangolin (*Manis crassicaudata*).

4.3 Outside Protected Areas

4.3.1 Brahmapuri Forest Division

Brahmapuri Forest Division is in the Eastern Vidarbha Landscape of Maharashtra's Chandrapur district. The division comprises 1192.87 km^2 of forest area, out of which 201.72 km^2 is under the administrative control of the Forest Development Corporation of Maharashtra (FDCM), with Ghodazari Wildlife Sanctuary having an area of 153 km^2. This division is surrounded by Chadchiroli in the north, TATR in the north, Pauni in the west, and Rajouri in the east. The Brahmapuri forest area is a corridor connecting TATR in the south and Umred Karhandla Wildlife Sanctuary, Nawegaon-Nagzira Tiger Reserve and Pench Tiger Reserve in the north, which further connects to Kanha Tiger Reserve in Madhya Pradesh. This landscape is rich in biodiversity, and although it is not part of any Protected Area (PA), it supports a decent tiger population.

The area is mostly flat, with undulating and hilly terrain in the Ghodazari sanctuary and the adjacent areas. Wainganga is the main river & is situated on the western boundary of the division and is the recipient of the tributaries viz. Sati, Khobragadi, Garvi, Kathani. The area has more than 600 villages, of which more than 300 are close to forests, making tiger conservation a serious challenge in such human-dominated landscapes.

The vegetation type of Brahmapuri is mainly dry deciduous, with *Tectona grandis* being the predominant species, along with *Terminalia tomentosa, Terminalia alata, Dyospyrus melanoxylon, Largestroemia perviflora, Cleistanthus collinus, Zizyphus* sp., and *Madhuca longifolia*. Grassland patches are present in areas with species such as *Heteropogon contortus* and *Chysopogon fulvus*. Apart from holding a sizeable population of tigers, the place also holds a healthy population of leopards (*Panthera pardus*), wolf (*Canis lupus*), dhole (*Cuon alpinus*) and striped hyena (*Hyaena hyaena*). Noteworthy small carnivores that are found in the area are rusty spotted cat (*Prionailurus rubiginosus*), jungle cat (*Felis chaus*) and small Indian civet (*Viverricula indica*). Herbivores like chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*), nilgai (*Boselaphus tragocamelus*), chousingha (*Tetracerus quadicornis*) are also found here in good number.

4.4 Capture and radio-collaring of tigers

In the Eastern Vidarbha Landscape of Maharashtra, 15 tigers were captured and fitted with GPS radio collars between 2016 and 2020 (Table 4.1). Across various age and sex classes, 10 tigers were captured from PAs (eight males and two females) and five from outside PAs (one male and four females). Collaring was conducted within PAs in the Tadoba-Andhari Tiger Reserve (TATR) and two Wildlife Sanctuaries (Umred-Karhandla and Tipeshwar Wildlife Sanctuary). In TATR, sub-adult tigers were captured from both core and buffer areas. Core areas are critical tiger habitats without human activities, whereas buffer areas lie on the periphery of the core zones and include a matrix of human-wildlife habitats. Sub-adult tigers were captured from the same litter in combinations of male-male, male-female, and female-female from different mothers (Table 4.2). All subadults were >1 year old and were captured while still in their natal area.

Tigers were immobilised with Medetomine hydrochloride, Ketamine hydrochloride, and Xylazine combination. The administered doses were determined based on age and visual observations of body weight. The drugs were injected remotely using an air-pressurised Dan-Inject projector (Model IM) from an open vehicle. After immobilisation, Iridium GPS radio collars (Vectronics, Germany) were fitted, which had a high location accuracy (± 5 m). The collars were padded with foam layers to accommodate the neck growth until adulthood. The GPS data were downloaded via satellite links (Iridium) and closely monitored on the ground using VHF tracking. Each individual was tracked until it established its territory, and the collars were removed using a drop-off mechanism (Table 4.3).

Table 4.1: Details of the age of tigers radio-collared between 2016 and 2021 in the protected and outside-protected areas of Maharashtra, India

Individual ID	**Sex**	**Date of Collaring**	**Place of Collaring**	**Age at collaring (months)**
T09	Male	17.03.2016	Umred Wildlife Sanctuary	18
T10	Male	17.03.2016	Umred Wildlife Sanctuary	18
Brahmapuri female	Female	03.06.2016	Halda (Brahmapuri)	19
Brahmapuri male	Male	04.06.2016	Halda (Brahmapuri)	19
Shivanjhari female	Female	06.03.2017	Kolsa (TATR)	18
Shivanjhari male	Male	09.03.2017	Kolsa (TATR)	18
Faazlu	Male	09.06.2018	Rampuri Nallah (TATR)	24
Kaalu	Male	10.06.2018	Rampuri Nallah (TATR)	24
Tipu Male	Male	25.02.2019	Tipeshwar Wildlife Sanctuary	30
Walker Male	Male	27.02.2019	Tipeshwar Wildlife Sanctuary	30
E1 female	Female	28.02.2019	South Brahmapuri (Brahmapuri Division)	18
E4 female	Female	28.02.2019	South Brahmapuri (Brahmapuri Division)	18
E3 female	Female	01.03.2019	South Brahmapuri (Brahmapuri Division)	18
Bran Male	Male	26.04.2019	Mahalgaon (TATR)	17
Arya Female	Female	24.04.2019	Mahalgaon (TATR)	17

Table 4.2: Details of sub-adult tigers radio-collared in protected and outside-protected areas of Maharashtra, India, during 2016-2021

Category	**Name**	**System**	**Litter combination**	**Tiger name**
Protected Area	Tadoba-Andhari Tiger Reserve	Core, Tiger Reserve	Male-Male (n=2)	T7-C1 T7-C2
		Core, Tiger Reserve	Male (n=1) Female (n=1)	Shivanjhari male Shivanjhari male
		Buffer, Tiger Reserve	Male (n=1) Female (n=1)	Bran Arya
	Umred-Karhandla Wildlife Sanctuary	Wildlife Sanctuary	Male-Male (n=2)	T09 T10
	Tipeshwar Wildlife Sanctuary	Wildlife Sanctuary	Male-Male (n=2)	T1-C1 T1-C3
Outside Protected Area	Brahmapuri Forest Division	Forested area	Male-Female (n=2)	Brh male Brh female
			Female-Female (n=3)	E1 E3 E4

Table 4.3: Details of tigers monitored during 2016 and 2022 in the Easter Vidarbha Landscape of Maharashtra, India

Individual name	Collar ID	Collar date	Collar drop date	No. of locations	Collar functional days
Tadoba-Andhari Tiger Reserve					
Arya	21599	24.04.2019	19.02.2020	425	46
	14616	19.02.2020	05.10.2020	2616	230
Bran	21601	26.04.2019	15.03.2022	131	85
Fazlu	21599	09.06.2018	08.12.2018	1532	183
Kaalu	21600	10.06.2018	02.06.2019	3324	358
	36049	02.06.2019	13.12.2019	1441	195
Shivanjhari female	21597	06.03.2017	14.01.2019	5156	680
Shivanjhari male	21601	09.03.2017	18.03.2018	2135	375
Umred-Karhandla Wildlife Sanctuary					
T09	19864	17.03.2016	13.01.2017	2887	303
	21596	13.01.2017	03.03.2018	3882	393
T10	19865	17.03.2016	29.10.2016	1812	227
	21595	05.12.2016	19.04.2017	1385	135
Tipeshwar Wildlife Sanctuary					
T1-C3	21594	25.02.2019	08.12.2019	4036	287
T1-C1	21602	27.02.2019	28.03.2020	6250	397
Brahmapuri Forest Division					
Brh Female	21593	03.06.2016	04.11.2016	833	155
Brh Male	21594	04.06.2016	09.08.2016	292	66
E1	21593	28.02.2019	31.05.2019	3546	92
E3	21260	01.03.2019	27.01.2020	4286	333
E4	21598	28.02.2019	18.01.2020	189	140

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CHAPTER 5

TO STUDY THE SPACE USE AND MOVEMENT OF TIGERS IN THE EASTERN VIDARBHA LANDSCAPE

Chapter 5

To study the space use and movement of tigers in the Eastern Vidarbha Landscape

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5.1 Introduction

Animal movement is influenced by a suite of processes that act at different scales in space and time (Nathan, 2008). These movements are essential for animals to find and occupy areas within their habitats that meet their ecological needs. Thus, understanding space use, home range dynamics, and movement patterns are fundamental aspects of animal ecology and crucial for effective conservation and management strategies. Space use refers to how animals utilise and occupy areas within their habitats, while home range, as defined by Burt (1943), represents "the area traversed by the individual in its normal activities of food gathering, mating, and caring for the young". An animal's space use is influenced by various factors, including individual characteristics, such as sex, age, and body size, as well as external factors that depend on population density, such as resource availability, distribution, competition, and predation (McNab, 1963; Frair et al., 2007; Börger et al., 2008; Tamburello et al., 2015). However, the availability of resources such as food, mates, and nesting habitats can change seasonally; thus, animals often adjust the extent and intensity of their space use on a temporal basis (McLoughlen & Ferguson, 2000; Cline & Haig, 2011). In contrast, individuals in a more productive or stable ecosystem make relatively few migrations and have minimal seasonal distributional alterations in space use (Sekercioglu, 2010; Chapman et al., 2011).

The dynamics of habitat use, influenced by spatial and temporal variations, play a significant role in numerous ecological interactions occurring both within and between species (Chappell 1978; Werner et al. 1981; Boon et al. 2008; Fischer and Schröder 2014; Owen-Smith 2015). For example, disturbances in their habitat might force individuals to displace and establish new territories, whereas migration can lead individuals to establish territories in multiple locations (e.g. wintering and breeding sites). Similarly, not all areas within an animal's home range are equally utilised. Areas intensively used by animals are referred to as core areas (Cederlund & Sand, 1994; Samuel et al., 1985). The core areas often include valuable resources, such as foraging patches, shelter, or mates, and are revisited more frequently compared to areas outside the core area (Benhamou, 2004). As a measure of space use, home ranges and core areas serve as metrics for understanding how animals interact with their environment. They also provide insights into the causes and effects of ecological processes, such as habitat selection (Rhodes et al., 2005), predator-prey dynamics (Lewis & Murray, 1993), community structure (Fagan et al., 2013), and disease spread (Kenkre et al., 2007).

Landscape characteristics influence animal home range through two primary mechanisms. First, the spatial distribution of resources determines the size of the area required to obtain sufficient resources (Carr & Macdonald, 1986; Johnson et al., 2002; Mitchell & Powell, 2004). Home ranges tend to be smaller in areas where resources are concentrated or of high quality, as animals require less space to obtain critical resources (Anderson et al., 2005; Pejchar et al., 2005). Second, anthropogenic pressures can alter landscapes, leading to increased dispersion of resources by fragmenting habitat patches. In a highly impermeable landscape matrix, where habitat patches are isolated, animals may exhibit smaller home ranges, or vice versa. Additionally, population growth and linear infrastructure development contribute to the increased fragmentation of natural landscape connectivity. For example, fragmentation of suitable habitats can impede movement corridors, resulting in isolation, reduced gene flow, and potential genetic bottlenecks or local extinctions. Conversely, well-connected landscapes with continuous habitats facilitate wider movement, promote gene flow, and enhance population resilience.

Understanding the factors contributing to variations in space use in human-dominated landscapes is crucial for identifying species persistence in such landscapes. Conservation efforts face significant challenges when dealing with species with extensive ranges and spatiotemporal variability in space use. In landscapes with high human population density and fragmented habitats, the movement of carnivores is more vulnerable to the effects of anthropogenic landscapes (Ripple et al., 2014), given their large home ranges and long-distance dispersal (Crooks et al., 2011; Dobson et al., 2006). However, understanding of spatiotemporal variability and its implications for conservation management is still limited, primarily because of a lack of comprehensive datasets (Kays et al., 2015). Landscape heterogeneity can influence the interactions and competition in carnivore species. Therefore, studying the movement of species in a human-dominated landscape is crucial for understanding their responses to environmental heterogeneity and anthropogenic influences. Thus, understanding the space use and movement of tigers will aid in identifying threats and barriers to movement and prioritising critical areas and corridors for dispersal. Moreover, linking movement ecology to conservation efforts has significant implications for future landscape conservation and wildlife management.

5.1.1 Carnivore space use in a human-dominated landscape

Globally, human activities have altered habitat structure and connectivity, shifting ecosystem processes and resource availability (Rebele, 1994; Kareiva et al., 2007; Alberti et al., 2017). Consequently, large carnivores are experiencing rapid decline due to anthropogenic activities and illicit commercial trade in body parts (Weber & Rabinowitz, 1996). In landscapes with high human density and fragmented wildlife areas, the movement of long-range carnivores becomes more vulnerable, as it requires large home ranges and consequently long dispersal distances (Ripple et al., 2014; Crooks et al., 2011; A. Dobson et al., 2006). Thus, large carnivores coexisting with humans may attempt a trade-off, balancing activities that enhance their fitness, such as foraging near humans, against the risk of human-caused mortality. This trade-off results in a variety of heterogeneously distributed behavioural responses of large carnivores to threats posed by humans (Oriol-Cotterill et al., 2015).

India harbours 57% of the world's tiger population, within 7% of its historical global range. Most of these tiger populations are found in protected areas, with 35% residing outside of these PAs (Habib et al., 2021). However, the tiger population is primarily restricted to small protected areas owing to habitat fragmentation, and few corridors permit movement between habitats (Habib et al., 2021; Thatte et al., 2018; Yumnam et al., 2014). Additionally, 70% of these PAs are smaller than 200 sq. km and highly dependent on the surrounding areas outside the protected zones, which serve as buffers and corridors for wildlife movement (Velho et al., 2016; Ghosh-Harihar et al., 2019). Surviving outside PAs presents greater challenges owing to habitat heterogeneity, resource availability, and human pressure (DeFries et al., 2010; Milda et al., 2020).

Therefore, a crucial aspect of tiger conservation is understanding tiger movement within protected areas and the surrounding landscapes in human-dominated regions. It is imperative to understand tiger space use across different life stages (pre-dispersal, dispersal, and post-dispersal phases) considering the challenges posed by habitat heterogeneity, resource availability, and human activities, within and outside protected areas. Understanding the role of landscape features in animal movement is important for understanding ecological processes (Collins & Barrett, 1997; Jetz et al., 2004; Fuller & Harrison, 2010) and developing effective conservation strategies (Chetkiewicz & Boyce, 2009; Zeller et al., 2017).

However, our understanding of the effects of landscape heterogeneity on animal movement is still relatively limited as it requires studying the movement of multiple individuals across various environmental conditions. Therefore, it is crucial to identify these environmental features and their roles in animal movement. Gaining a deeper understanding of the environmental drivers of movement is crucial and may help inform management and conservation. Understanding and identifying the factors responsible for animal movement will allow us to understand the behavioural response and space use and identify the underlying mechanisms determining species richness and resource selection. Therefore, movement forms the primary link between home range size and habitat/resource selection.

The spatial resource variability hypothesis states that as the patchiness of resource availability increases, individuals will use large areas of resources necessary to meet their energy requirements, provided that the resource quality remains the same across the landscape (Hiller et al., 2015; Johnson et al., 2002). Long-ranging carnivores, such as tigers in a human-dominated landscape, occupy a continuum of forested landscapes from fragmented to homogenous forested areas. Habitat loss, fragmentation, and anthropogenic development have had adverse effects on the space use of tigers in the current Anthropocene. It is crucial to understand how landscape heterogeneity and configuration influence the space of tigers in a varied landscape of human disturbance. Therefore, I hypothesised that with the increase in habitat fragmentation and anthropogenic disturbances, the space use of tigers would differ within and outside the protected areas of the Eastern Vidarbha Landscape, Maharashtra. Furthermore, the temporal resource variability hypothesis suggests that seasonal changes in resource availability can reduce animal movement while providing various nutritional requirements, leading to smaller home ranges (Hiller et al., 2015; McClintic et al., 2014). I assume that when seasonally available resources are concentrated (protected areas), individuals may use smaller areas for their daily requirements, whereas fragmented and highly anthropogenic areas (outside protected areas) may have larger areas across all seasons.

I used multiple-year GPS data of sub-adult tigers during three dispersal phases within and outside protected areas to understand the spatiotemporal variability in space use in a varied landscape. The objective of this study was to quantify the movement and space of sub-adult tigers across different life stages, that is, the pre-dispersal, dispersal, and post-dispersal phases. In addition, I determined how movement patterns and space use were influenced by landscape heterogeneity across the landscape.

5.2 Study Area

The Eastern Vidarbha Landscape (EVL), a part of the Central Indian Tiger Landscape, is a highly biodiverse region. It lies between N18°11'20.69" to N21°43'15.79" and E78°03'37.09" to E80°54'09.42" and encompasses a forested area of approximately 22,500 km^2 covering six districts: Bhandara, Chandrapur, Gadchiroli, Gondia, Nagpur, and Wardha. The region supports over 350 tigers in six tiger reserves, three wildlife sanctuaries, and an outside protected area. The intensive study area includes protected areas such as Tadoba-Andhari Tiger Reserve, Umred-Karhandla Wildlife Sanctuary, and Tipeshwar Wildlife Sanctuary (Figure 5.1). On the other hand, the Brahmapuri forest division represents the landscape outside the protected area. The functional connectivity between these tiger-bearing habitats is fragmented due to the presence of high human pressure and the presence of linear infrastructure.

The landscape is home to diverse faunal species like tiger (*Panthera tigris*), leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), gaur (*Bos gaurus*) and several other ungulate species. The forest type is mainly moist deciduous forests, and the major tree species are teak (*Tectona grandis)*, palash (*Butea monosperma)*, dhoura (*Anogeissus latifolia),* jamun *(Syzygium cumini),* Indian laurel (*Terminalia elliptica).* The intensive field area includes protected areas such as Tadoba-Andhari Tiger Reserve, Umred-Karhandla Wildlife Sanctuary and Tipeshwar Wildlife Sanctuary (figure 3). It also includes the Brahmapuri Forest Division, which is a non-protected area in the Chandrapur district.

The region has three main seasons: the monsoon from June to September; the cool, dry winter from October to March; and the hot, dry season from April until the onset of rain at the beginning of June (Nandankar et al., 2011). The temperature of Vidarbha ranges from a minimum of 12-25°C to a maximum of 30-48°C, with the relative humidity varying from 10-15 to% to 60-95%. The annual precipitation is 1700 mm, and approximately 90% occurs between June and September. The region has unique topographical characteristics, with its fertile black cotton soil, exotic forest, and mineral resources. More than 65% of the population depends on rain-fed agriculture, with cotton and soybean being the major crops.

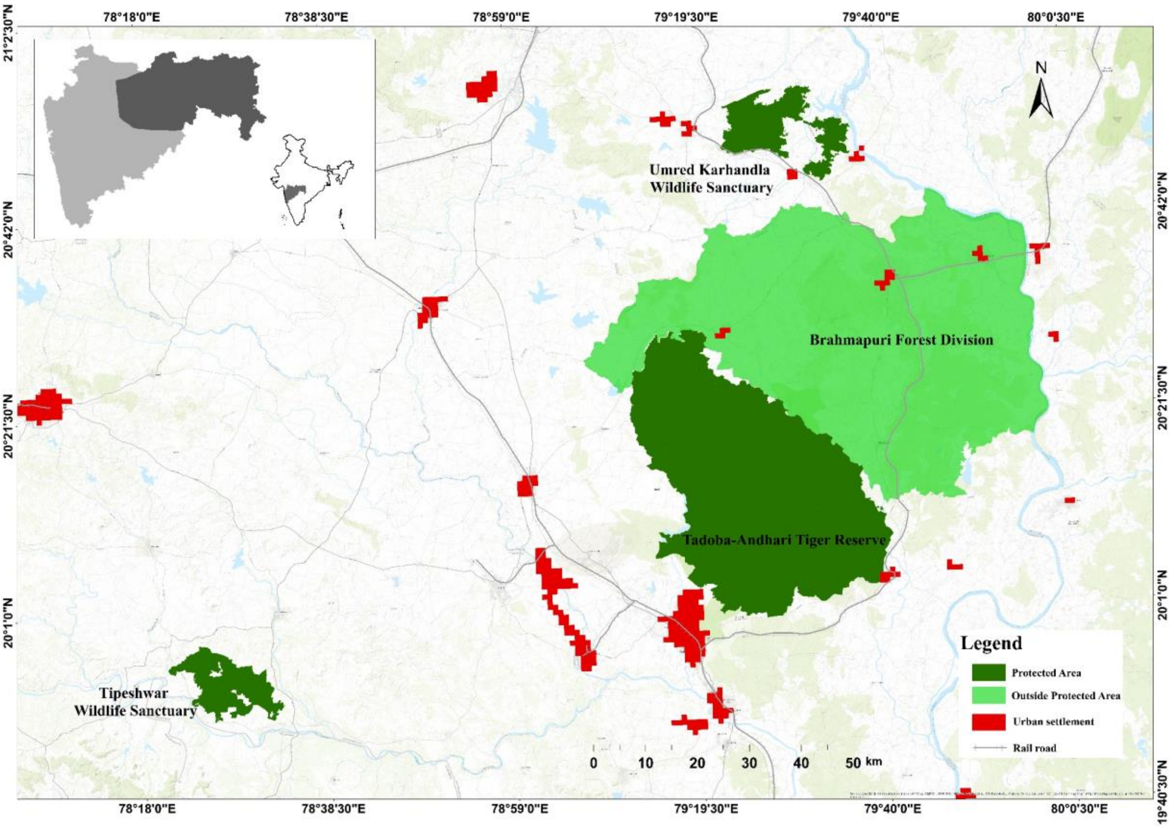


Figure 5.1: The Eastern Vidarbha Landscape showing the intensive study areas within and outside protected areas of Maharashtra, India

5.3 Methods

5.3.1 Identifying movement into different life stages: pre-dispersal, dispersal, and post-dispersal phase

Dispersal is a three-stage process that involves emigration, transience, and settlement (Clobert et al. 2012; Van Dyck & Baguette, 2005). The transient phase occurs during the sub-adult life stage, including natal dispersal and exploratory forays. Tiger movements during this phase are characterised by one-way directional bouts broken up by a period of localising behaviour and transient home ranges (Smith, 1993). Thus, tiger behavioural or life stages were classified into pre-dispersal, dispersal, and post-dispersal phases. The pre-dispersal phase was identified by the movement of individuals within their natal area. The dispersal phase involves movement from the area of birth to another habitat, where it reproduces and establishes a new territory (Howard, 2015; Waser & Jones, 1983). The post-dispersal phase was identified by movement in an area with a stable and well-defined home range over time.

Semi-variogram plots were used to characterise movement modes and to identify whether an individual tiger is a resident (territorial) or non-resident (dispersing). Consequently, an individual's life stage was determined based on the criteria of range residency behaviour. This was determined by examining the plots of semi-variance in positions as a function of the time lag between observations (variograms). A distinct asymptote at a significant lag (time interval) assigns residents to collared individuals or vice versa (Calabrese et al., 2016; Fleming & Calabrese, 2017). Using the R package *"ctmm"*, the visual verification of range residency through variogram analysis was carried out following the process outlined by Calabrese et al. (2016).

Non-resident tigers were further classified into three distinct life stages: pre-dispersal, dispersal, and post-dispersal phases. The dispersal age was also quantified using net squared displacement (NSD). The NSD is a useful metric for analysing changes in an animal's movement patterns over time. Generally, for any organism moving within a specific interval, the straight-line distance from the start to the endpoint is called the net displacement. The square of this value is called the NSD (Turchin, 1998). NSD is the fundamental quantity for studying the movement of organisms or particles (Turchin, 1998; Nouvellet et al., 2009) and is defined as:

$$\mathrm{NSD(t)} = (\mathrm{xt} - \mathrm{x0})^2 + (\mathrm{yt} - \mathrm{y0})^2$$

where (x0, y0) is the location of the first observation, and (xt, yt) is the animal's location at time *t.* Different patterns of NSD can be predicted a priori for individuals exhibiting different movement behaviours (Borger & Fryxwell, 2012). By plotting NSD over time, one can identify animal movement, whether it is moving nomadically, dispersing between two habitats, migrating between seasonal ranges, or stationary in a local area (Figure 1).

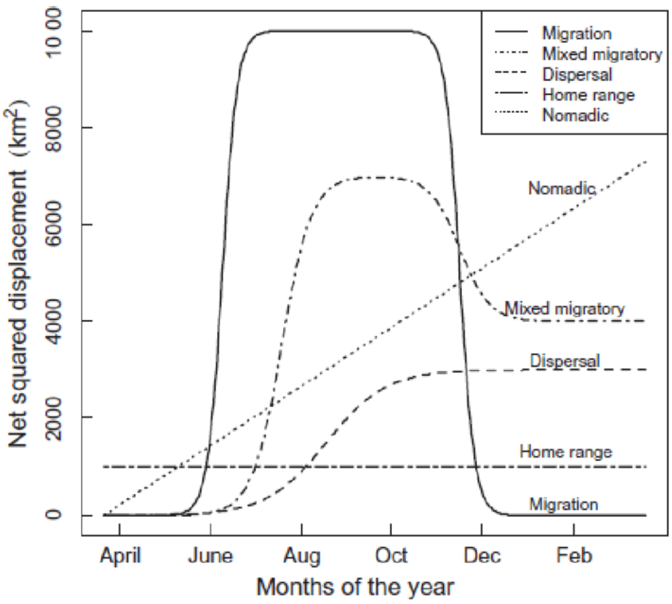


Figure 5.2: Net Square Displacement (km^2) showing migration, mixed migratory, dispersal, home range and nomadic movement of movement modes

5.3.2 Telemetry data and movement metrics

The collar was set up to record locations every 1–3-h depending on the individual's dispersal phases (i.e. pre-dispersal, dispersal, and post-dispersal). During the pre-dispersal phase, the GPS location was received every 3-h when sub-adult tigers were in their natal area. During dispersal, locations were received every 1-h when tigers moved out of their natal areas. In the post-dispersal phase, locations were received every 3–5-h, where the individual movement was consistent with an established tiger within a defined home range.

The movement metrics, i.e., movement rate, daily distance travelled, and daily displacement, were calculated for three distinct phases or life stages: pre-dispersal, dispersal, and post-dispersal. The daily distance travelled was calculated by summing the step length (Euclidean distance between successive locations) in 24-h, and daily displacement as the linear distance between the start and end locations for each 24-h period. To define 24-h, the time between the first location at midnight and the first location following midnight was considered. The movement rate (m/h) was estimated across the three dispersal phases by scaling the step length divided by the time the individual took to complete the distance because of varying interfix intervals (Hussain et al., 2022; Leblond et al., 2016). Movement parameters were calculated using adehabitatLT (Calenge, 2015) and the animal movement tool (Signer et al., 2019) in R programming software (R Core Team, 2022).

5.3.3 Space use estimation

To estimate space use at different spatial scales, utilisation distribution (UD) was calculated across life stages (pre-dispersal, dispersal, and post-dispersal phases) within protected and outside protected areas. I also analysed the spatial utilisation of tigers across different seasons: summer (1st April to 30th June), monsoon (1st July to 30th September), and winter (1st October to 30th March). UD is a probability density that reflects an animal's relative frequency of occurrence over time and space. I did not estimate the entire home range but was interested in tigers' occurrence distribution during the three dispersal phases. Therefore, the dynamic Brownian Bridge Movement Model (dBBMM; Kranstauber et al., 2012), an advanced BBMM method, was used to calculate UD. Similar to conventional BBMMs, dBBMMs require the sequential collection of animal locations and the telemetry error associated with each location. Both methods calculate the Brownian motion variance ($\sigma 2m$); however, conventional BBMMs assume that $\sigma 2m$ is constant throughout the path. While dBBMMs allow $\sigma 2m$ to vary along the movement trajectory for user-defined subsets of n locations (windows). According to the recommendations of Kranstauber et al. (2012), I specified the moving window size (i.e. the size of the sliding window along an animal's trajectory) and margin (i.e. margins at the start and end within each window in which no changes in behavioural state can occur) to account for potential differences in movement patterns or behavioural changes. The range of moving window sizes and margins was based on individual sampling rates, as there were individual differences during the dispersal phases and in the temporal resolution of the GPS fixes. A biologically appropriate window size of 7 – 27 GPS locations (equivalent to 21–84 h) and a margin of 3 – 9 (equivalent to 6 – 18 h) were chosen based on the temporal resolution of each trajectory of individual tigers. Window sizes and margins were also chosen considering the dispersal phase of individual tigers. The average telemetry error for each location was ±5 m when fitting the dBBMM. These parameters were included in the BBMM to estimate the utilisation distributions (UDs) at 20 m resolution. The dBBMM implemented in the package 'move' (Kranstauber et al., 2012b) was used in R 4.2.2 (R Core Team, 2022) to estimate the utilisation distribution across the dispersal phases. The non-parametric Kruskal-Wallis test was used to compare the medium space use (50% and 95% dBBMM) during the pre-dispersal, dispersal, and post-dispersal phases.

5.3.4 Land use reclassification

Land use data for Maharashtra and Telangana were characterised into 13 classes with a resolution of 60 m. The land use layer of 1:25,000 scale was acquired from the open-source Bhuvan website (NRSA, 2016; http://bhuvan.nrsc.gov.in/). For further analysis, the 13 original classes were reclassified into five major categories: built-up, agricultural, forest, grassland, and water. The land cover was reclassified in ERDAS Imagine 2016 and ArcMap 10.6.1.

5.3.5 Landscape metrics

I used class-level metrics to analyse the connectivity and landscape configuration effects on the space use of tigers during the three dispersal phases (Table 5.1). The land cover class metrics were calculated separately for three spatial scales (50%, 95%, and 99% isopleth) for the forest and agriculture classes, treating other classes as background layers. I used the software *'Fragstat'* (McGarigal, Cushman, & Ene, 2012) to analyse eight class metrics (defined as the analyses of habitat type) across the three spatial scales of each individual. The proportion of land cover availability (PLAND) was evaluated to quantify each land cover type within different isopleths of space use. Aggregation is a key aspect of landscape ecology which refers to the degree to which patches are spatially aggregated (Neel, McGarigal & Cushman, 2004; Wang, Blanchet & Koper, 2014). I used the CLUMPY index, an aggregation index that provides a measurement ranging between -1 and 1 (i.e. completely disaggregated to completely aggregated).

Additional metrics calculated were Patch Density (PD) and Euclidean nearest neighbour index (ENN) to measure the aggregation of any given habitat. The percentage of like adjacencies (PLADJ) for landscape configuration was selected as an index. This index measures the patchiness of a landscape by determining the proportion of patches adjacent to another patch of the same land-cover class. Its values range from 0 (every cell of a given land cover is a different, discrete patch) to 1 (all cells of the same land cover consist of a single patch; McGarigal et al., 2002). These configuration metrics were chosen a priori because they reflect landscape fragmentation and patch diversity (Dewan et al., 2012; McGarigal et al., 2002). Moreover, covariates were chosen because of their connections to the definitions of connectivity, landscape configuration, and spatial heterogeneity.

Table 5.1: The landscape metrics were computed to see the effect on the space use of tigers during the pre-dispersal, dispersal, and post-dispersal phase

Landscape metrics	***Metric description***	***Unit***
Percentage of landscape (PLAND)	The percentage of land use class is a fundamental measure of landscape composition, specifically, how much of the landscape is comprised of a particular patch type.	Percent
Patch density (PD)	PD equals the number of patches of the corresponding patch type divided by the total landscape area (m2), multiplied by 10,000 and 100 (to convert to 100 hectares).	Number per 100 hectares
Edge density (ED)	ED equals the sum of the lengths (m) of all edge segments in the landscape, divided by the total landscape area (m2), multiplied by 10,000 (to convert to hectares).	Meters per hectare
Mean patch area (AREA_MN)	The mean area of patches of a particular LULC class.	Hectares
Mean Euclidian nearest neighbour distance (ENN_MN)	Euclidean nearest neighbour distance (ENN) is perhaps the simplest measure of patch isolation.	
Clumpiness Index (CLUMPY)	CLUMPY equals the proportional deviation of the proportion of like adjacencies involving the corresponding class from that expected under a spatially random distribution (aggregation index)	Percent
The proportion of like adjacencies (PLADJ)	The percentage of cell adjacencies involving the corresponding patch type is like adjacencies.	Percent
Patch cohesion index (COHESION)	COHESION approaches 0 as the proportion of the landscape comprised of the focal class decreases and becomes increasingly subdivided and less physically connected.	None

5.3.6 Forest Fragmentation Analysis

Forest fragmentation results in a decrease in the overall size of forested areas, an expansion of forest edges, and the division of large, contiguous forest regions into smaller, disconnected fragments (Laurence, 2000). Forest fragmentation was mapped using *Landscape Metrics* and created with land use data using a tool named "Landscape fragmentation tool V.2.0", a plugin of ArcMap software developed by Vogt et al. (2007). This method is a pixel-level classification and mapping of land cover patterns. The tool requires a raster file as the input, with only two classes representing forest and non-forest. The other input required by the tool was the edge-width parameter. This is the distance over which the fragmented land use type of interest (forest) can be degraded by fragmented land cover types (non-forest). It determines the width of the edge and perforated forest zones as well as the thickness of the patches. Edge effects are abrupt changes in vegetative populations or community structures found at the boundaries of two or more habitats. Depending on the issue of interest, the edge width reported in the ecology literature ranges from 50 m to several hundred meters. I used a 100-metre edge width as it was commonly used for general-purpose analysis (Vogt et al., 2007)

In terms of output, the tool generates a raster file classifying the forest into four categories based on the forest pattern: *core, patch, perforated, and edge*. 'Core forest' is relatively far from the forest–non-forest boundary, and 'patch forest' comprises coherent forest regions too small to contain core forest. Furthermore, it was subdivided into small, medium, and large cores. 'Perforated forest' defines the boundaries between core forest and relatively small perforations, while 'edge forest' includes interior boundaries with relatively large perforations and the exterior boundaries of core forest regions. Non-forest includes agricultural and water areas in the study area (Table 5.2). Notably, the patch, edge, and perforated categories are highly susceptible to edge-effect degradation. Although the resolution of land use data differs for the three years due to different satellite sensors, the output generated from the *'Landscape fragmentation tool V.2.0'* is constant at a 10 m resolution making it possible to compare the results across spatial and temporal scales (Vogt et al., 2007).

Table 5.2: Description of the terms used to quantify forest fragmentation (Ram et al., 2021)

Forest categories	**Description**
Patch forest	Forest pixels along the edge of an interior gap in a forest that is degraded by 'edge effects'
Edge forest	Forest pixels along the exterior perimeter of a forest that is degraded by 'edge effects'
Perforated forest	Small, isolated fragments of forest that are surrounded by non-forest features and completely degraded by 'edge effects'
Small core	Forest patches with an area smaller than 250 acres (< 1 km^2)
Medium core	Forest patches with area between 250 and 500 acres (1 - 2 km^2)
Large core	Forest patches with an area larger than 500 acres (> 2 km^2)
Non-forest	Non-forest patches with agriculture or water

5.3.7 Anthropogenic variables

To account for anthropogenic disturbances, I considered the Euclidean distance between the edge of the utilisation distribution polygon and the nearest railway line and human settlement. The distance to these features was calculated from the edge of the polygon across the three spatial scales of space use (50%, 95%, and 99% isopleth). I also calculated roads (highways and primary roads; source: www. openstreetmap.org) and population density within the spatial scales of space use. All the variables, sources, and resolutions are listed in Table 5.3. All analyses were performed using ArcMap 10.6.1.

Table 5.3: Description of the anthropogenic variables within the three spatial scales (50%, 95%, and 99% isopleth) of tiger space use

Anthropogenic variables	*Description*	*Unit*
Distance to the railway line	The average nearest distance from the edge of the 99%, 95%, and 50% dBBMM utilisation distribution.	Metres
Distance to human settlement	The average nearest distance from the edge of the 99%, 95%, and 50% dBBMM utilisation distribution.	Metres
Road density	The road density is within the 99%, 95%, and 50% dBBMM utilisation distribution.	Km/sq.km
Population density	The road density is within the 99%, 95%, and 50% dBBMM utilisation distribution. (https://www.worldpop.org/; 100m x 100m)	No. of people per sq.km

5.4 Statistical Analyses

For statistical analysis, I conducted a correlation test involving 22 variables of landscape configuration and anthropogenic disturbances. Variables with a correlation coefficient (> 0.70) were removed from the analysis. The remaining variables were retained for the subsequent regression analysis. The landscape metrics included the percentage of forest (forest_PLAND), patch density (forest_PD), edge density (agriculture_ED), mean patch area (forest_AREA_MN), mean Euclidean nearest neighbour distance for forests (forest_ENN_MN), mean Euclidean nearest neighbour distance for agriculture (agriculture_ENN_MN), and clumpiness index (forest_CLUMPY). Anthropogenic disturbances included road density, population density, mean distance to the railway line, and distance to human settlements.

5.4.1 Effect of landscape metrics and anthropogenic disturbances on the space use of tigers during the pre-dispersal, dispersal, and post-dispersal

To assess the influence of environmental and landscape variables on space use at different spatial scales (50%, 95%, and 99% dBBMM), I included utilisation distribution (UD) as the response variable and dispersal phase, area (protected and outside protected area), landscape metrics, and anthropogenic disturbances as fixed factors. Similarly, for the temporal model, fixed factors consisted of dispersal phase, area, season, and sex. The individuals' space use was found to be dependent on sex, dispersal phase, and seasonal variations. Therefore, interaction terms, such as season by sex and season by dispersal phase, were included in the model. Alternative a priori hypotheses were developed for spatial and temporal models to test different combinations of variables associated with space use, dispersal phase, landscape configuration, and anthropogenic disturbances (Table 5.4). Additionally, I tested whether changing the scale of UD from 50% to 99% isopleth would affect the model selection results.

Table 5.4: A *priori* hypotheses and corresponding candidate models exploring the effect of dispersal phase, landscape characteristics and anthropogenic disturbances within and outside protected areas on the space use of tigers at three spatial scales of 99%, 95%, and 50% dBBMM

Hypothesis	**Model structure**
Spatial	
Null	Space use ~ 1
Model 1(Core)	Space use ~ dispersal phase + area
Model 2 (Landscape metrics)	Space use ~ dispersal phase + area + landscape metrics
Model 3 (Human disturbance)	Space use ~ dispersal phase + area + anthropogenic disturbances
Full	Space use ~ dispersal phase + area + landscape metrics + anthropogenic disturbances
Temporal	
Null	Space use ~ 1
Model 1	Space use ~ dispersal phase + area + season + sex
Model 2	Space use ~ dispersal phase + area + season + sex + season*sex
Model 3	Space use ~ dispersal phase + area + season + sex + season*phase
Full	Space use ~ dispersal phase + area + season + sex + season*sex + season*phase

Landscape metrics: forest_PLAND, forest_PD, agriculture_ED, forest_AREA_MN, forest_ENN_MN, agriculture_ENN_MN, and forest_CLUMPY

Anthropogenic disturbances: distance to human settlement + distance to railway + Road density + Population density

5.4.2 Effect of variables on the movement rate

Movement rate (m/h) was estimated by scaling the step length (Euclidean distance between successive locations) divided by the time the individual took to complete the distance due to the varying interfix intervals (Hussain et al., 2022; Leblond et al., 2016). Movement rate was included as the response variable and dispersal phase, area, sex, season, time of day, vegetation cover (ndvi), forest fragmentation index, and anthropogenic variables were included as fixed factors. An animal's movement rate varies according to the time of day and changes in the physical environment during the season. Therefore, I included the interaction terms season and time of day. The zero-inflated negative binomial model was selected as the response variable (i.e. the movement rate) was zero-bounded.

5.4.3 Effect of variables on the daily distance

Variation in distance coverage, with daily distance (sum of displacement in 24-h) as the response variable and sex, phase (pre-dispersal, dispersal, and post-dispersal), and season as fixed factors. An animal's behaviour may vary with dispersal phase and sex owing to changes in the physical environment of the habitat and biological requirements across seasons. Therefore, I included the interaction terms season, dispersal phase, and sex. Therefore, a generalised linear model (GLM) framework with gamma distribution was used to analyse how various factors affected the daily distance travelled.

Table 5.5: A *priori* hypotheses and five candidate models to determine the parameters influencing daily distance travelled to dispersal phase, sex, and season

Hypothesis	**Model structure**
Null	Daily distance ~ 1
Model 1	Daily distance ~ phase + sex + season
Model 2	Daily distance ~ phase + sex + season + season*sex
Model 3	Daily distance ~ phase + sex + season + season*phase
Model 4	Daily distance ~ phase + sex + season + season*sex + season*phase

5.4.4 Effect of variables on the daily displacement

Variation in daily displacement (linear distance between the start and end locations for each 24-h period) as the response variable, and sex, area, phase, and season were fixed factors. An animal's behaviour may vary with dispersal phase and sex owing to changes in the physical environment of the habitat and biological requirements across seasons. I included the interaction terms season, dispersal phase, and sex. Therefore, a generalised linear model (GLM) framework with gamma distribution was used to analyse the effects of various factors on the daily displacement.

Table 5.6: A *priori* hypotheses and five candidate models to determine the parameters influencing daily displacement to dispersal phase, sex, and season

Hypothesis	**Model structure**
Null	Daily displacement ~ 1
Model 1	Daily displacement ~ phase + area + sex + season
Model 2	Daily displacement ~ phase + area + sex + season + season*sex
Model 3	Daily displacement ~ phase + area + sex + season + season*phase
Model 4	Daily displacement ~ phase + area + sex + season + season*sex + season*phase

5.4.5 Effect of variables during the dispersal phase

The effects of movement, environmental factors, anthropogenic disturbances, and fragmentation on dispersal were evaluated. I used the binary response as the life-stage (dispersal phase and non-dispersal phase) as the categorical response variable in the generalised linear model (GLM) framework with the binomial family. The time of day, season, movement rate, NDVI, anthropogenic disturbance, fragmentation, and straightness index were used as fixed factors. The straightness index measures the shape of animal movement paths to quantify disturbances caused by human activities and fragmentation (Batschelet, 1981).

Table 5.7: A *priori* hypotheses and five candidate models to evaluate the effect of environmental, anthropogenic and fragmentation on the life stage (dispersal and non-dispersal phase) of tigers in the Eastern Vidarbha Landscape

Hypothesis	**Model structure**
Null	Life stage ~ 1
Core	Life stage ~ tod + season + movement rate
Environmental	Life stage ~ core + ndvi
Anthropogenic	Life stage ~ core + dist.HS + dist.road + population count
Fragmentation	Life stage ~ core + large core + medium core + small core + straight index
Full model	Life stage ~ core + environmental + anthropogenic + fragmentation

5.4.6 Model selection

To investigate the influence of environmental, anthropogenic, and fragmentation factors on space use and movement, a combination of explanatory variables was used to test our hypotheses. Models were fitted through a generalised linear model (GLM) using the package “lme4” (Bates et al., 2015) in R 4.2.2 (R Core Team, 2022). Model selection was based on Akaike's Information Criterion (AIC), with the smallest value (Burnham & Anderson, 2002).

5.5 Result

GPS data from 15 tigers were collected from the Eastern Vidarbha Landscape of Maharashtra, which were tracked for 2,282 days. In 2016, four tigers were captured, two each from the Umred-Karhandla Wildlife Sanctuary and the Brahmapuri Forest Division. Two tigers from each year were captured in the TATR in 2017 and 2018. In 2019, seven tigers collared, three in Brahmapuri, two in Tipeshwar, and two in TATR. Additionally, four tigers were re-collared between 2016 and 2020. Throughout the study period from January 2016 to March 2022, 46, 158 high-quality GPS locations were obtained. The tracking duration for the individual tigers varied from two months to 23 months.

5.5.1 Identifying movement into different life stages: pre-dispersal, dispersal, and post-dispersal phase

The tiger movement trajectory in the Eastern Vidarbha Landscape is shown in Figure 5.3. The movement modes of tigers were analysed using semi-variogram plots (Figure 5.4) and categorised into individual tigers as either dispersing (non-resident) or non-dispersing (territorial). Semi-variogram plots are shown in Figure 5.3. Of the tigers, nine individuals were identified as dispersing, while three females exhibited philopatric behaviour. Tigers were classified into three distinct behavioural phases: pre-dispersal (n=14), dispersal (n=6), and post-dispersal (n=8). The pre-dispersal phase is characterised by the movement of individuals within their natal areas. The dispersal phase involved moving from the birth area to a new habitat, where they reproduced and established a new territory.

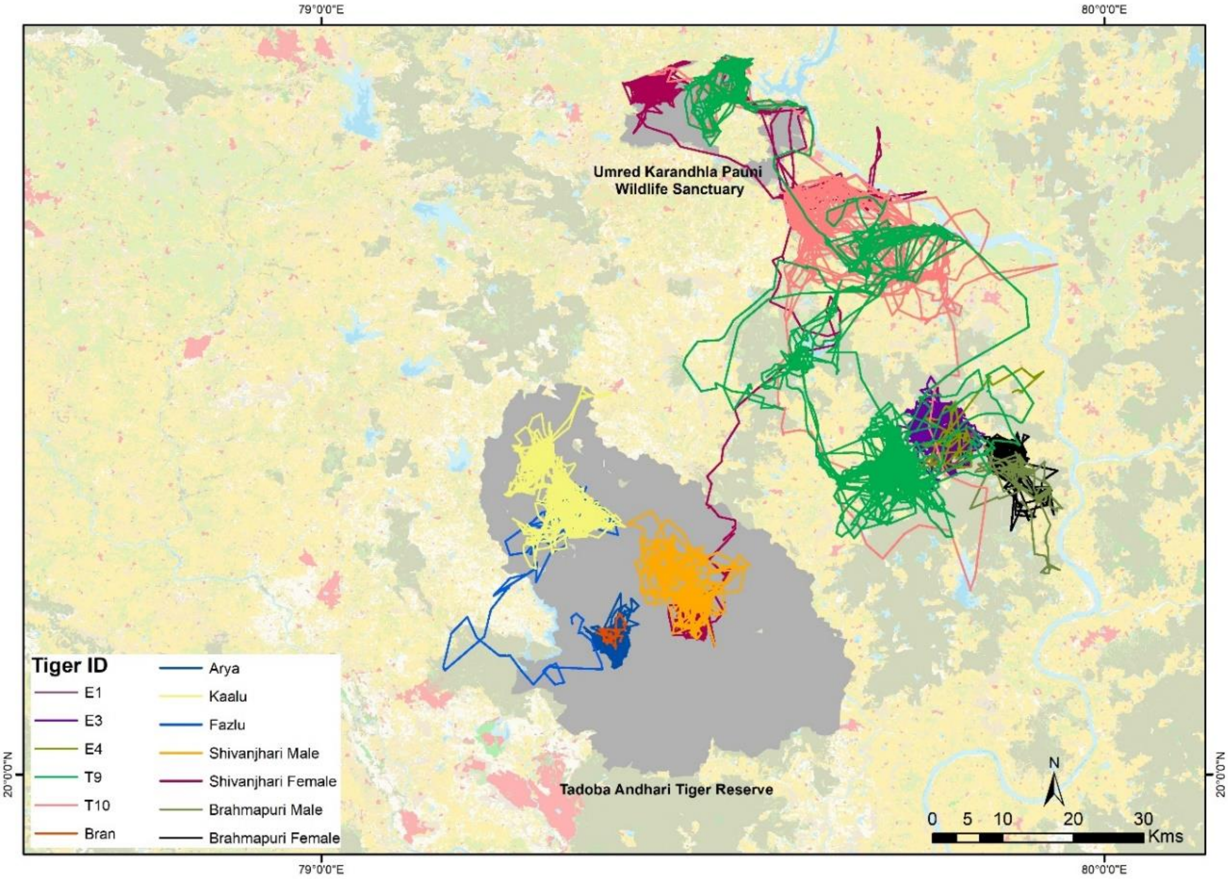
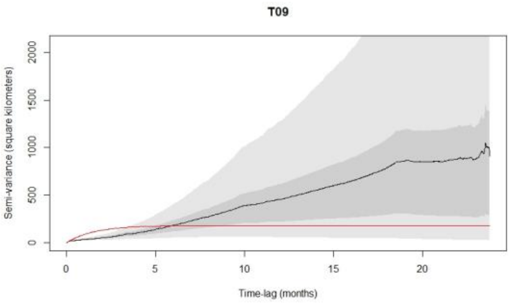


Figure 5.3: Trajectory of collared tigers in the Eastern Vidarbha Landscape of Maharashtra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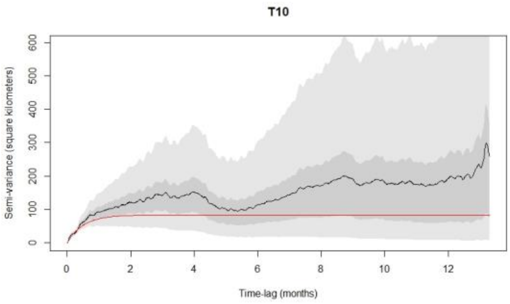
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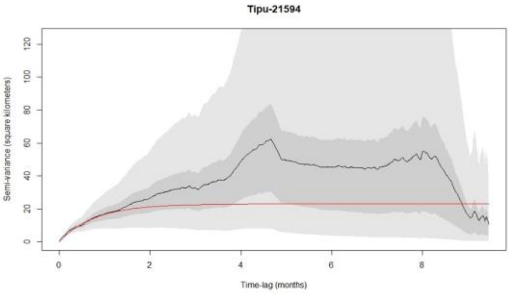
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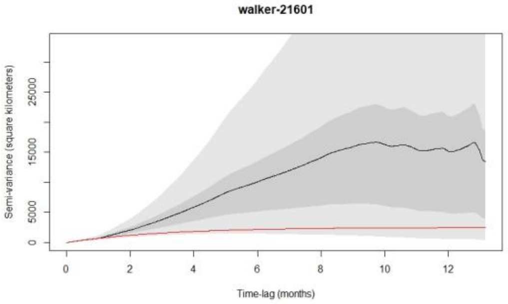
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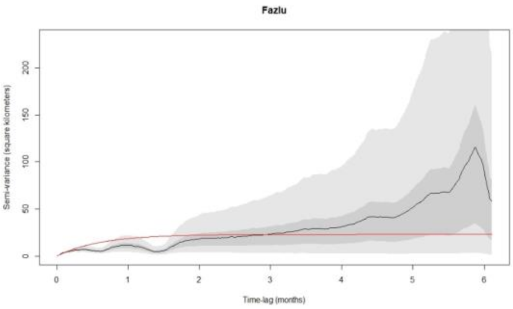
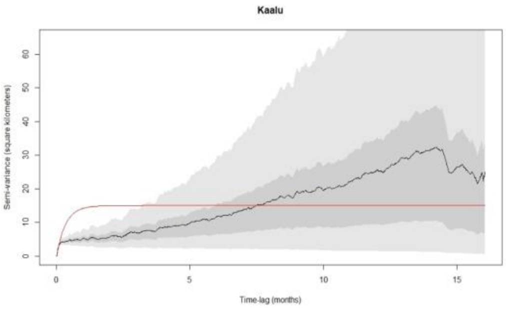
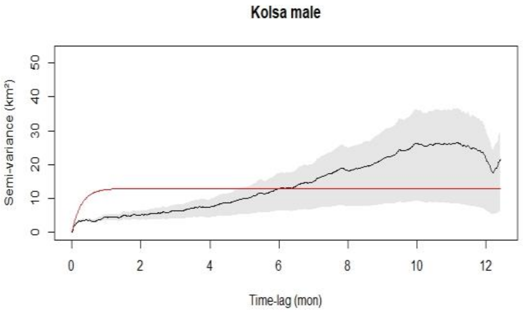
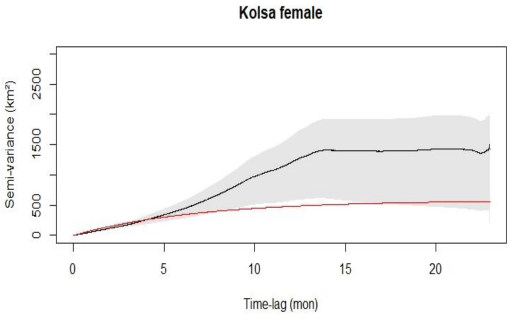
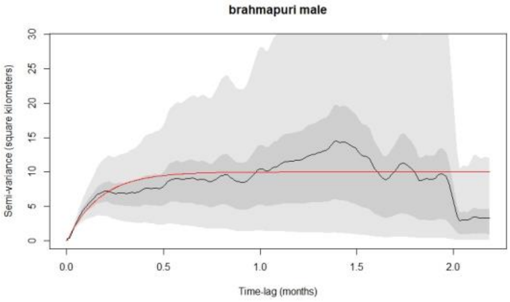
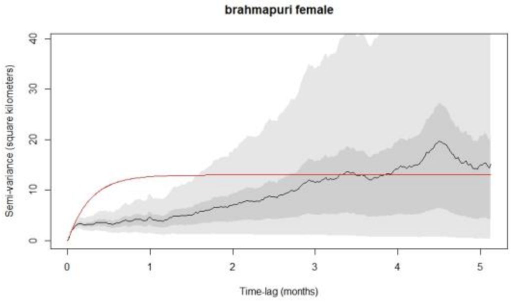

Fazlu


Kaalu


Kolsa male


Kolsa female


brahmapuri male


brahmapuri female

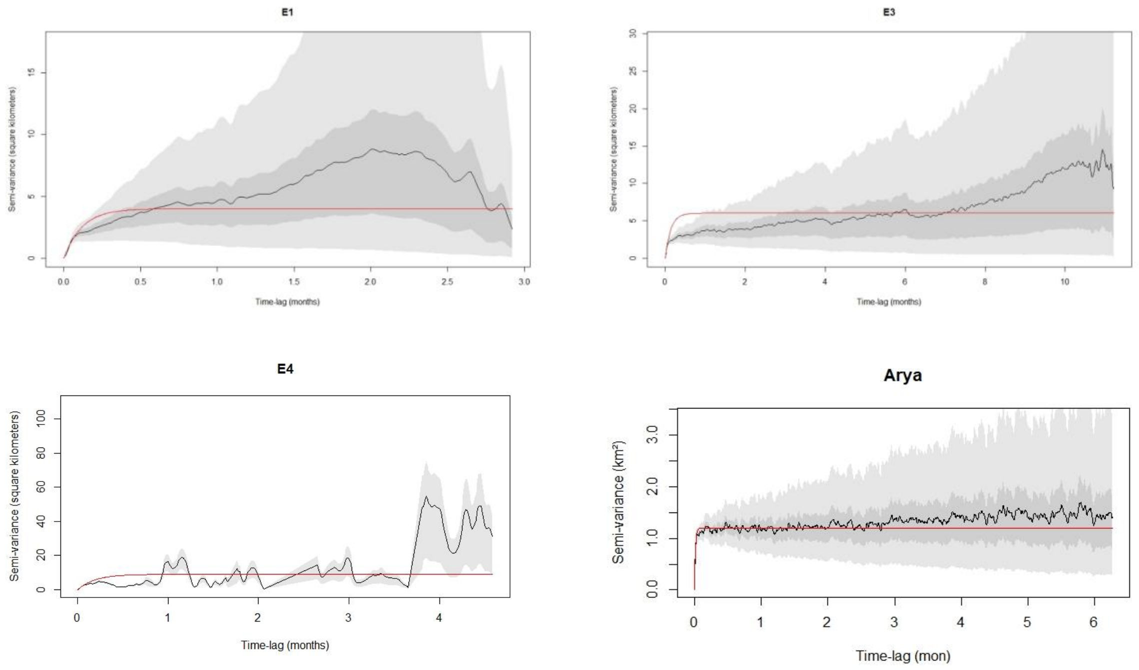


Figure 5.4: Semi-variance graph to identify collared tigers into dispersing and non-dispersing individuals from the Eastern Vidarbha Landscape of Maharashtra

5.5.2 Spatial and seasonal variability in space use

The space use of tigers varied across spatial scales during the three behavioural phases (Table 5.8). During the pre-dispersal phase, the median space use was 43.57 km^2 (95% UD, range = 7 – 75.74 km^2), and the core range was 4.08 km^2 (50% UD, range = 0.45 – 10.08 km^2). During the dispersal phase, tigers exhibited a larger space use, with a median space use of 325.71 km2 for 95% UD and a core area of 10.91 km^2. In the post-dispersal phase, space use decreased compared to the dispersal phase but remained higher than the pre-dispersal phase. The median space use was 60.74 km^2 (95% UD), with 5.45 km^2 as the core area. Tiger space use also showed considerable variation in size between dBBMM and MCP estimates. The MCP estimates were significantly larger than the corresponding dBBMM estimates at 95% UD ($p < 0.05$). The post-dispersal phase showed a decrease in space use compared to dispersal, but this was not significant. However, space use significantly differed between the pre-dispersal and dispersal phases across 99% and 95% UD (Figure 5.5; Kruskal–Wallis rank sum test, $p < 0.05$). Information on space use within and outside protected areas during the pre- and post-dispersal phases is given in Table 5.9. Tigers outside protected areas generally had larger space requirements, suggesting the influence of protected areas on the spatial requirements of tigers.

Across the sexes, male tigers generally required larger areas than females (Table 5.10). During the pre-dispersal, both sexes had similar space requirements in the landscape. However, males had significantly larger space use at all three spatial scales during post-dispersal.

Table 5.8: Space use (median) of tigers during pre-dispersal, dispersal, and post-dispersal phase from the Vidarbha Landscape of Maharashtra, India

Phase	**Space use (km^2)**			
	99% dbbmm	**95% dbbmm**	**50% dbbmm**	**95% MCP**
Pre-dispersal	62.88	43.57	4.08	42.72
Dispersal	596.17	325.71	10.91	1175.98
Post-dispersal	112.94	60.74	5.45	80.82

Table 5.9: Space use (median) of tigers between PA and outside PA during the pre-dispersal and post-dispersal phase

Phase	**Area**	**Space use (km^2)**			
		99% dbbmm	**95% dbbmm**	**50% dbbmm**	**95% MCP**
Pre-dispersal	PA	52.15	23.35	1.93	32.66
	Outside PA	68.10	45.03	6.15	68.28
Post-dispersal	PA	79.48	49.76	4.27	40.56
	Outside PA	264.72	118.01	9.34	322.59

Table 5.10: Space use (median) of tigers across sexes during the pre-dispersal, dispersal, and post-dispersal phase

Phase	**Sex**	**Space use (km^2)**			
		99% dbbmm	**95% dbbmm**	**50% dbbmm**	**95% MCP**
Pre-dispersal	Male	69.83	42.80	4.57	41.50
	Female	57.66	44.34	3.59	52.29
Post-dispersal	Male	264.72	118.01	9.34	322.59
	Female	38.48	26.07	4.83	30.82

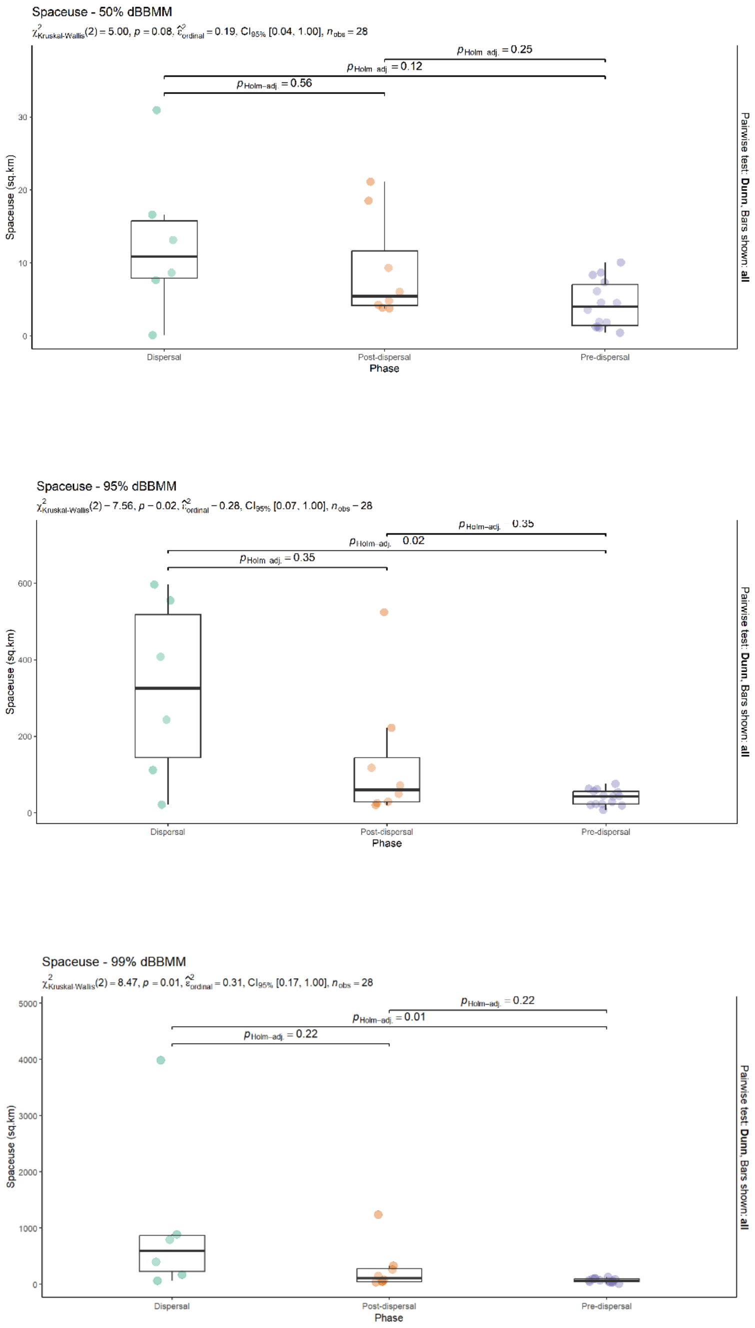


Figure 5.5: Non-parametric Kruskal-Wallis test between the space use of tigers (50% dBBMM and 95% dBBMM) during the pre-dispersal, dispersal, and post-dispersal phases. Further, the post hoc Dunn test revealed a significant difference in space use (99% and 95% dbbmm) between the dispersal and pre-dispersal phase ($p < 0.05$). However, no significant difference was found in the space use (50% dbbmm)

Seasonal space use

I estimated the seasonal space use by tigers during three distinct seasons: summer (1st April to 30th June), monsoon (1st July to 30th September), and winter (1st October to 30th March). In the pre-dispersal phase, tigers exhibited greater space during the monsoon season, with 95% UD of 31.43 km^2 and 50% UD of 3.98 km^2. In contrast, during the dispersal and post-dispersal phases, tigers occupied larger areas during winter (Table 5.11).

Table 5.11: Seasonal space use (median) of tigers during the three dispersal phases in the astern Vidarbha Landscape of Maharashtra

Phase	**Season**	**Space use (km^2)**			
		99% dbbmm	**95% dbbmm**	**50 % dbbmm**	**95% MCP**
Pre-dispersal	Summer	35.90	19.95	0.97	26.29
	Monsoon	47.21	31.43	3.98	46.81
	Winter	35.73	23.32	2.17	23.18
Dispersal	Monsoon	344.23	198.21	10.47	1674.11
	Winter	398.34	243.42	10.83	792.58
Post-dispersal	Summer	62.20	36.84	3.66	52.57
	Monsoon	44.15	27.64	3.49	38.49
	Winter	180.98	101.67	4.83	183.30

5.5.3 Effect of landscape metrics and anthropogenic disturbances on space use

The top model describing the variability in space use included landscape metrics and anthropogenic disturbances within and outside the PAs during the three dispersal phases (Table 5.12). At 99% dbbmm, the proportion of forest (PLAND) showed high explanatory variation in the space use of tigers across all three dispersal phases (Table 5.13; Figure 5.6). At 95% UD and 50% core area, an increase in patch density indicated a more fragmented landscape, corresponding to decreased space use of tigers (Figure 5.6). When accounting for anthropogenic disturbances, space use increased with population density at all three spatial scales (Table 5.13; Figure 5.6). Furthermore, the core area was significantly smaller during the pre-dispersal phase (β =-1.32, p=0.01).

Table 5.12: Results of *a priori* models of tiger's space use selected within the three spatial scales (99%, 95% and 50% dbbmm) in the Eastern Vidarbha Landscape

Spatial Scale	Model structure	df	AIC
99% dbbmm	Full model	16	322.45
95% dbbmm	Full model	16	303.84
50% dbbmm	Full model	16	134.22

**Full model: Space use ~ dispersal phase + area + landscape metrics + anthropogenic disturbances*

Table 5.13: Effects of predictors including dispersal phase, area type, landscape metrics and anthropogenic disturbances on space use of tigers in the Eastern Vidarbha Landscape

Parameters	Estimate	SE	Z value	p
99% dbbmm				
Proportion of forest (PLAND)	-1.21	0.30	-4.04	0.00
Population density	0.61	0.17	3.54	0.00
95% dbbmm				
Patch density (forest)	-0.70	0.30	-2.37	0.03
Population density	0.60	0.27	2.25	0.04
50% dbbmm				
Patch density (forest)	-1.28	0.17	-7.47	0.00
Population density	0.45	0.19	2.32	0.04
Pre-dispersal phase	-1.32	0.44	-3.03	0.01

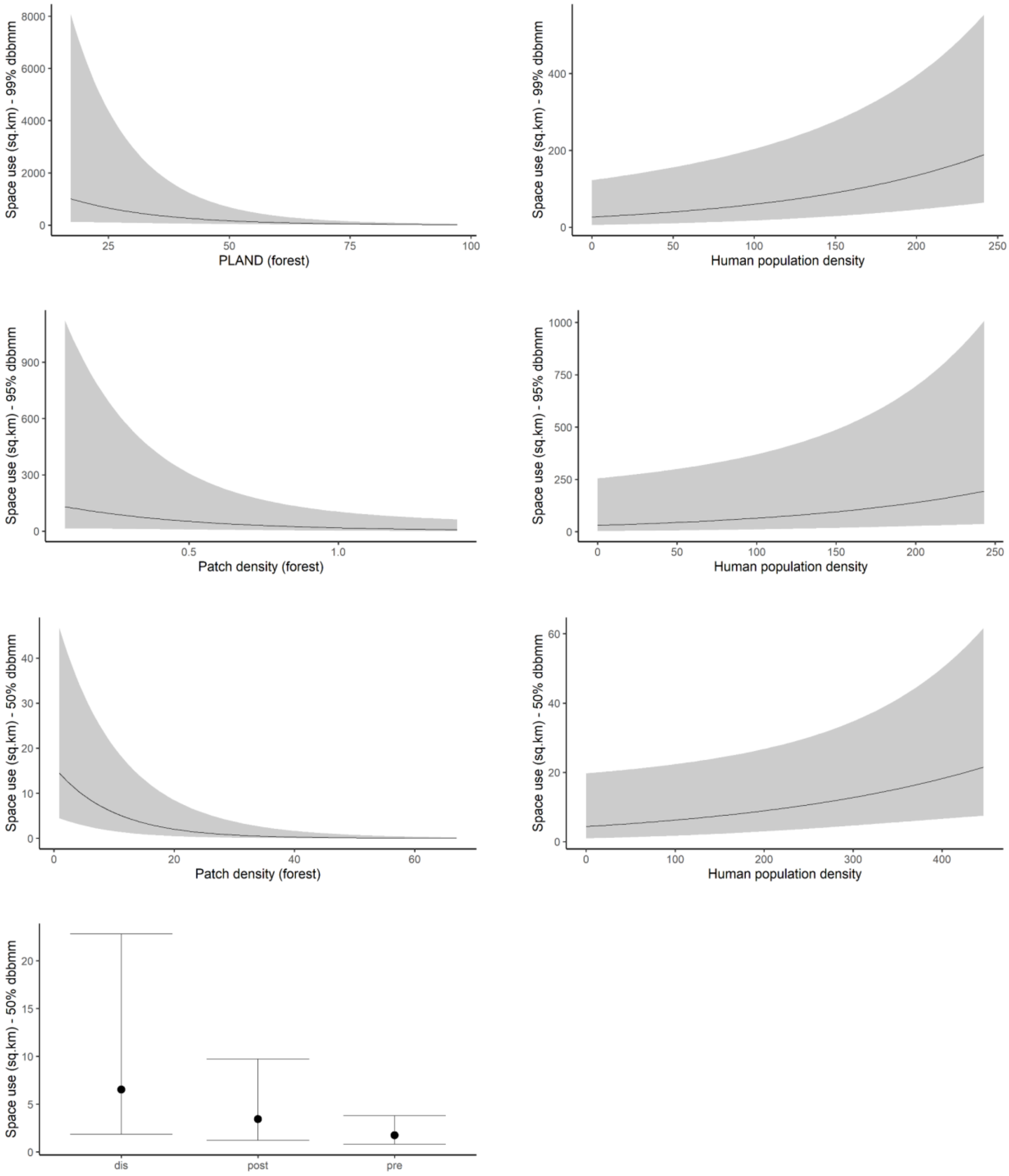


Figure 5.6: The plots are based on the prediction of a generalised linear model showing the relationship between space use at three spatial scales (99%, 95% and 50% dbbmm) to landscape metrics and human disturbances

The variability in seasonal space use was explained by the season across sexes within and outside the PAs during the three dispersal phases (Table 5.14). For 99% and 95% UD, the seasonal space use of males and females differed across the dispersal phases (Table 5.15; Figure 5.7). The interaction model showed that space use was greater in all three seasons during the dispersal phase (Table 5.15; Figure 5.7). The results of the core area analyses showed that season and sex were key determinants during the three dispersal phases across the landscape (Table 5.15; Figure 5.7).

Table 5.14: Results of *a priori* models of seasonal space use within the three spatial scales (99%, 95% and 50% dbbmm) in the Eastern Vidarbha Landscape

Spatial Scale	Model structure	df	AIC
99% dbbmm	Model 3	11	575.46
95% dbbmm	Model 3	11	522.99
50 % dbbmm	Model 1	8	273.71

Model 1: Space use ~ dispersal phase + area + season + sex
*Model 3: Space use ~ dispersal phase + area + season + sex + season*phase*

Table 5.15: Effects of predictors including dispersal phase, area type, season, and sex on seasonal space of tigers in the Eastern Vidarbha Landscape

Parameters	Estimate	SE	Z value	p
99% dbbmm				
Male	0.63	0.25	2.44	0.01
Post-dispersal*winter	1.57	0.64	2.42	0.01
95% dbbmm				
Male	0.55	0.24	2.21	0.03
Post-dispersal*winter	1.44	0.62	2.32	0.02
50 % dbbmm				
Pre-dispersal	-0.96	0.35	-2.69	0.00
Summer	-0.73	0.30	-2.44	0.01

**Reference category was dispersal phase for interaction model between phase*season*

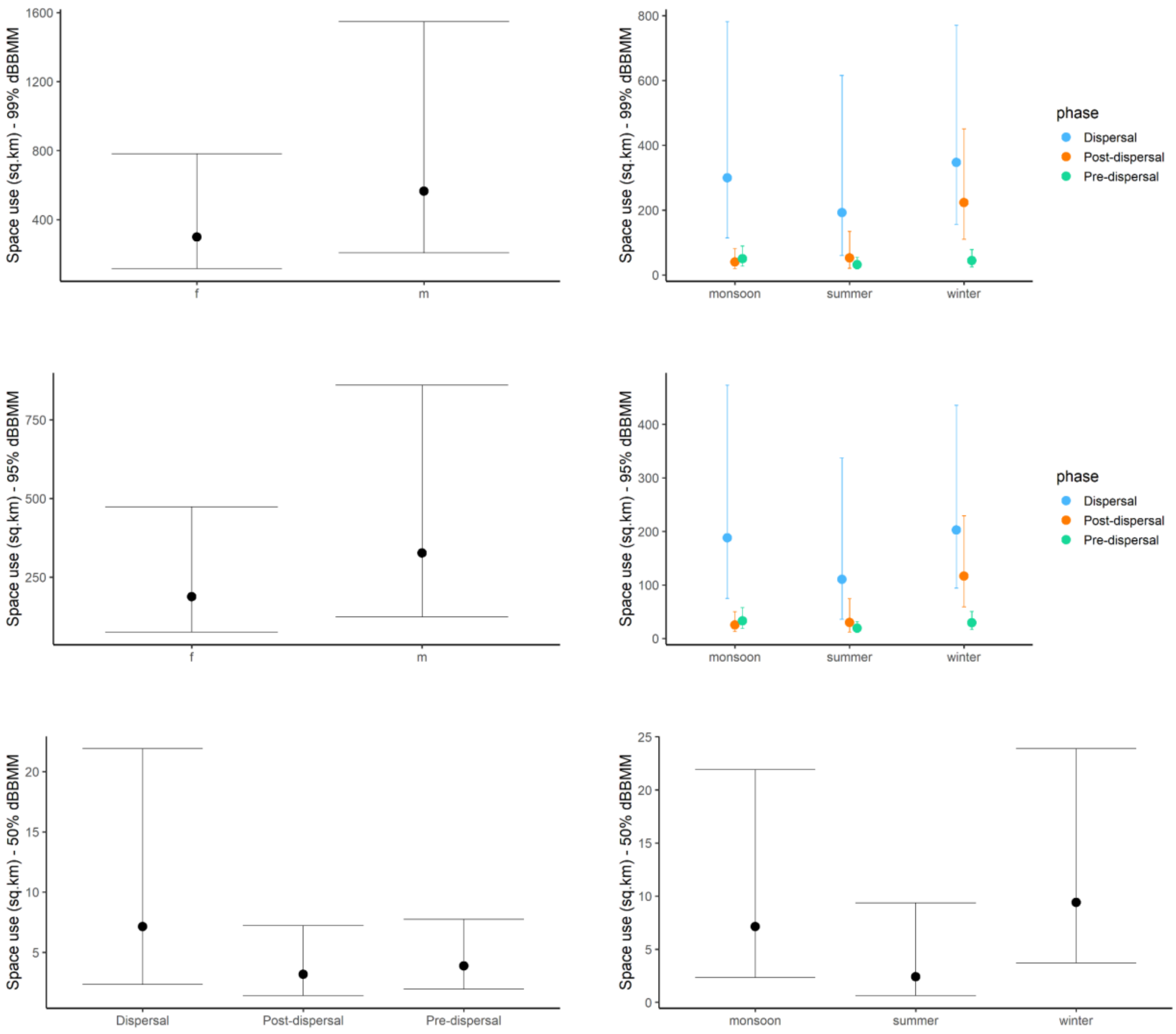


Figure 5.7: The plots are based on the prediction of a generalised linear model showing the relationship between seasonal space use at three spatial scales (99%, 95% and 50% dbbmm) to dispersal phase, area type, season, and sex

5.5.4 Movement rate and effect of variables

The movement rates of tigers were compared within and outside protected areas (PA) during the pre-dispersal, dispersal, and post-dispersal phases (Table 5.16). The results suggest that tigers moved significantly faster outside the PA (Figure 5.8a; $p<0.05$). Specifically, during the daytime, tigers outside PAs moved faster than those within PAs during the pre-dispersal and post-dispersal phases ($p<0.05$). However, no difference in the movement rate was observed between dispersing tigers within and outside the PAs. At night, the movement rate was higher outside the PAs during all three dispersal phases ($p<0.05$). Moreover, individuals outside PAs showed faster movement at night than during the day (Figure 5.8b). Across the sexes, male tigers showed significant differences in movement rates and moved faster outside the PAs ($p<0.05$). Similarly, during the pre-dispersal phase, female tigers exhibited faster movement outside PAs (mean = 210.08 m/h), whereas no difference was found during the dispersal and post-dispersal phases.

Table 5.16: Movement rate (m/h) of tigers between PA and outside PA during the pre-dispersal, dispersal, and post-dispersal phase

Phase	Area	Overall SL	Day	Night	Male	Female
Pre-dispersal	PA	136.66	120.91	152.89	138.51	125.32
	Outside PA	211.59	179.26	245.81	219.79	210.08
Dispersal	PA	241.89	261.46	219.30	248.88	224.30
	Outside PA	325.59	222.13	430.21	333.94	253.23
Post-dispersal	PA	210.94	209.95	212.01	203.28	216.35
	Outside PA	326.64	245.67	401.24	367.78	209.57

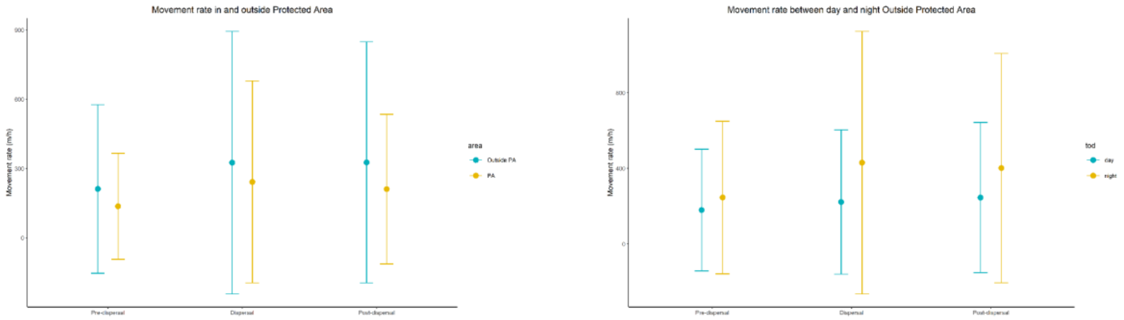


Figure 5.8: Mean movement rate with error bars of 95% CI (a) Movement of tigers within and outside protected areas during pre-dispersal, dispersal, and post-dispersal phase (b) The difference in movement during the diel cycle in outside protected area

The best-fit model that explains the variation in movement rate includes several factors, such as sex, season, time of day, land use, landscape fragmentation, and human disturbances within and outside the PA (Table 5.17). The coefficients of the fixed effects that influence movement rate are shown in Figure 5.9. Tiger movement significantly increased during dispersal and moved longer steps outside the PA (Figure 5.10). While moving in a high vegetation cover or an increase in NDVI, they decreased their movement rate ($\beta = -0.07$, $p<0.05$). In contrast, the movement rate increased as they traversed agricultural landscapes ($\beta = 0.23$; $p<0.001$). Owing to human-induced disturbances, tigers moved faster when approaching roads and slowed down in areas close to human settlements. Landscape fragmentation classes negatively influenced movement rate (Table 5.18; $p < 0.05$). Tigers also showed seasonal variations in movement during the day and night (Figure 5.10). They were most active in summer and winter at night, whereas the opposite was observed in the monsoon season.

Table 5.17: Models describing variables affecting the movement rate of tigers in the Eastern Vidarbha Landscape

Name	**Model structure**	**df**	**AIC**
Model 3	Movement rate (m/h) ~ phase + area + sex + season + tod + ndvi + tod * season + agri + large core + medium core + small core + perforated + edge + dist.HS + dist.road	20	425364.4
Model 2	Movement rate (m/h) ~ phase + area + sex + season + tod + ndvi + tod * season + agri + forest + grassland + large core + medium core + small core + perforated + edge + dist.HS + dist.road	22	425368.2
Model 1	Movement rate (m/h) ~ phase + area + sex + season + tod + temp + ndvi + tod * season + straight.index + builtup + agri + forest + grassland + water + large core + medium core + small core + perforated + edge + patch + dist.HS + dist.road + population count	26	425369.7
Null	Movement rate (m/h) ~ 1	2	427553.1

Table 5.18: Effects of predictors and estimates on the movement rate of tigers in the Eastern Vidarbha Landscape

Parameters	Estimate	Std. Error	z value	Pr(>|z|)
Post-dispersal	-0.03	0.03	-1.16	0.25
Pre-dispersal	-0.40	0.03	-12.89	0.00
Protected area	-0.37	0.02	-15.65	0.00
Male	0.08	0.02	3.99	0.00
Vegetation cover (NDVI)	-0.07	0.01	-7.17	0.00
Agriculture	0.23	0.05	4.67	0.00
Large core	-0.15	0.04	-3.79	0.00
Medium core	-0.78	0.19	-4.17	0.00
Small core	-0.44	0.08	-5.81	0.00
Perforated	-0.24	0.07	-3.64	0.00
Edge	-0.13	0.05	-2.76	0.00
Distance to human settlement	0.04	0.01	3.30	0.00
Distance to road	-0.04	0.01	-3.22	0.00
Summer*night	0.48	0.04	11.22	0.00
Winter*night	0.46	0.04	11.33	0.00

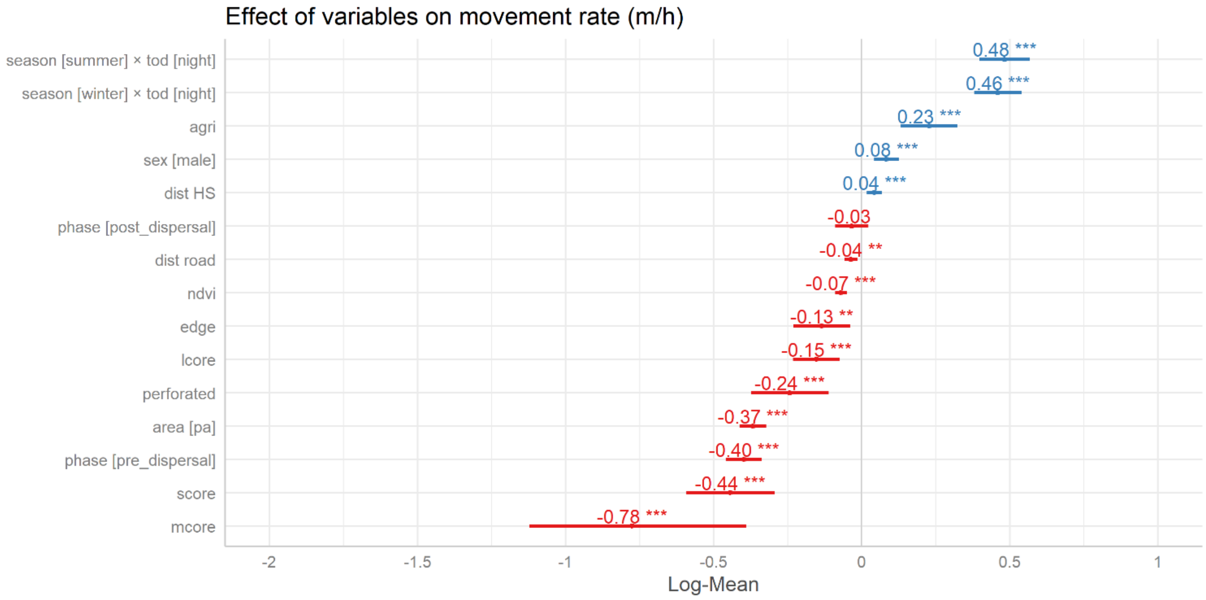


Figure 5.9: Parameter estimates of variables affecting tigers' movement rate (m/h). Estimates are based on a set of top models with ΔAIC < 2. The grey line represents the zero effect. Significant responses are highlighted by asterisks. The x-axis depicts the estimates, and the y-axis represents the variables. Asterisks indicate significance level: * = 0.05, ** = 0.005, *** = 0.0005

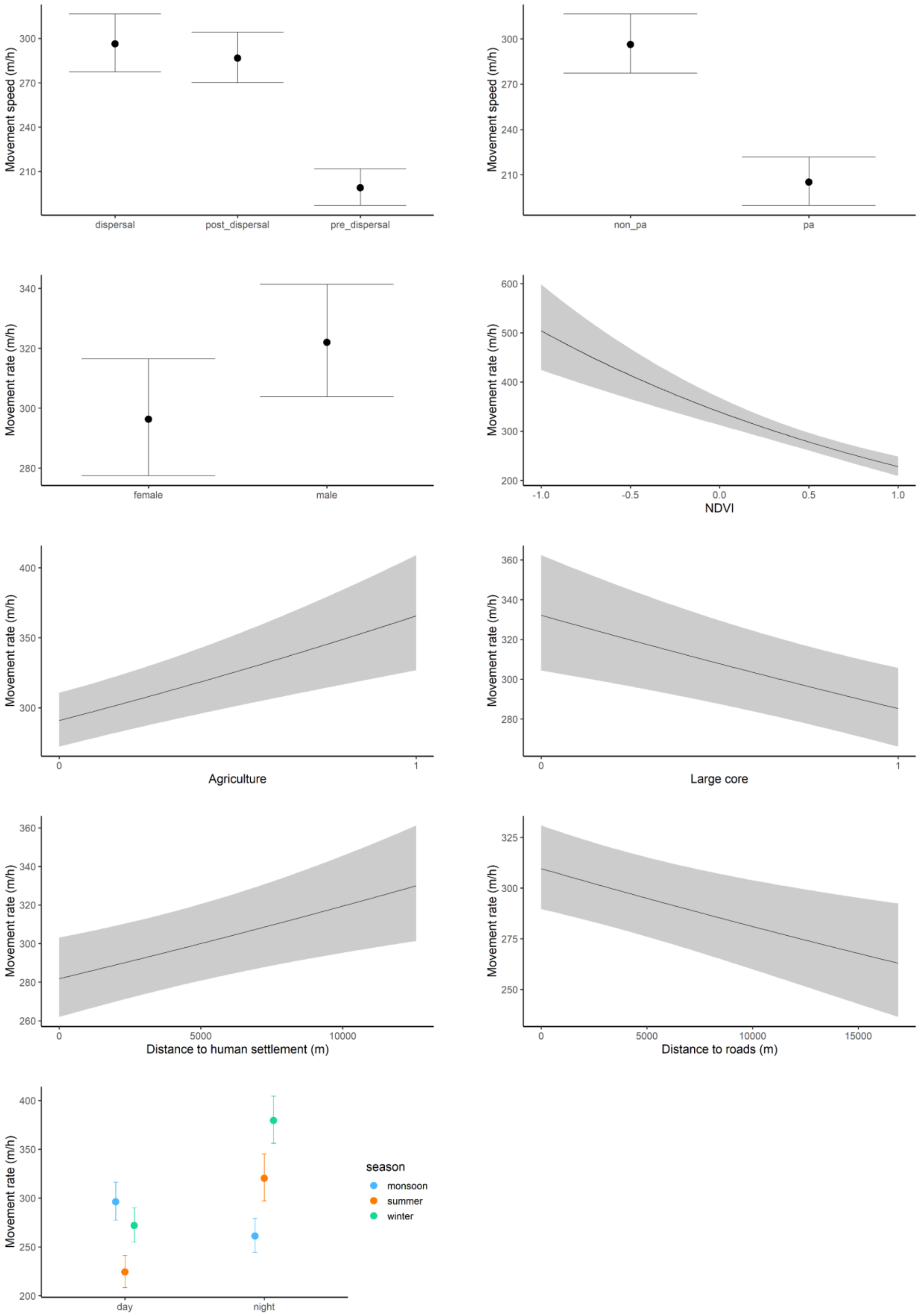


Figure 5.10: The effect plots are based on the prediction of a generalised linear model showing the relationship between the movement speed of tigers to environmental and anthropogenic variables

5.5.5 Effect of variables on the daily distance

The model showed a clear relationship between daily distance travelled, sex, and season during the pre-dispersal, dispersal, and post-dispersal phases (Table 5.19). The results indicated that males travelled longer distances during the winter (Table 5.20; p<0.001), with no significant difference observed between sexes during the monsoon and summer seasons. The interaction between dispersal phases and seasons exhibited a strong association with daily distance travelled (Figure 5.11). They travelled long distances during the monsoon season during the dispersal phase (Figure 5.12). In contrast, tigers displayed longer movements during the summer and winter in the post-dispersal phase.

Table 5.19: Models describing variables affecting the daily distance travelled by tigers in the Eastern Vidarbha Landscape

Name	Model structure	df	AIC
Model 4	Daily distance ~ phase + sex + season + season*sex + season*phase	13	81037.3
Model 2	Daily distance ~ phase + sex + season + season*sex	9	81059.5
Model 3	Daily distance ~ phase + sex + season + season*phase	11	81075.4
Model 1	Daily distance ~ phase + sex + season	7	81106.5
Null	Daily distance ~ 1	2	81630.7

Table 5.20: Effects of predictors and estimates on the daily distance travelled by tigers in the Eastern Vidarbha Landscape. The dispersal phase was considered the reference category in the regression analysis

Parameters	Estimate	Std. Error	t value	Pr(>|t|)
Male*summer	2.866e-05	8.901e-05	1.44	0.15
Male*winter	-7.402e-05	2.069e-05	-4.33	0.00
Pre-dispersal*summer	-2.375e-04	8.860e-05	-2.68	0.01
Pre-dispersal*winter	-6.518e-05	-2.927	-2.93	0.00
Post-dispersal*summer	-1.744e-04	8.826e-05	-1.98	0.05
Post-dispersal*winter	-6.743e-05	1.745e-05	-3.86	0.00

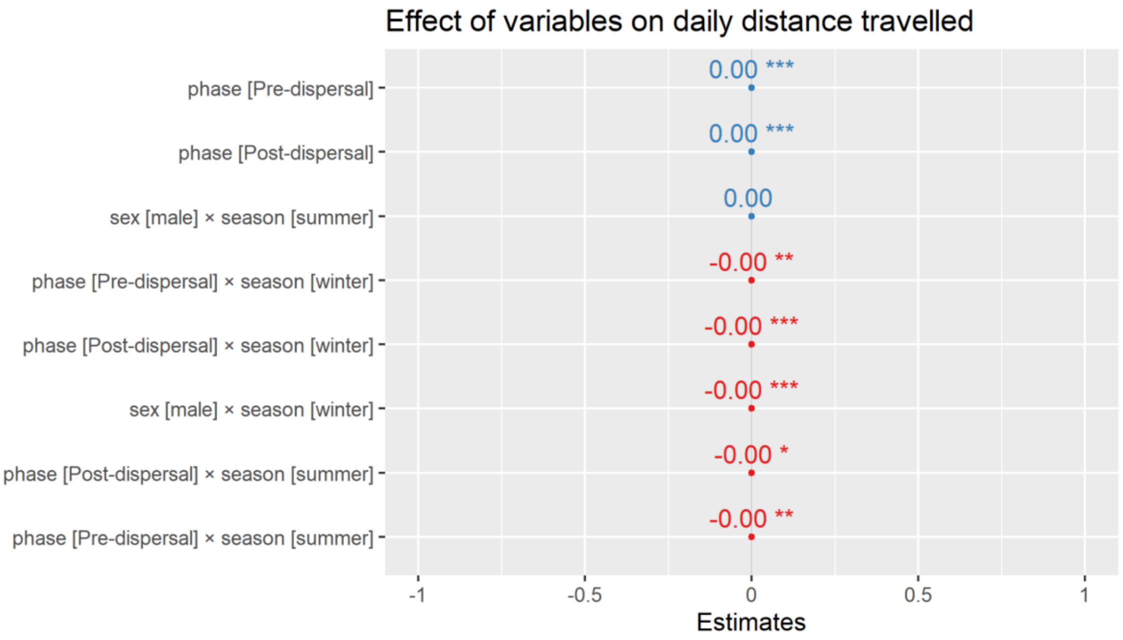


Figure 5.11: Parameter estimates of variables affecting daily distance travelled. Estimates are based on a set of top models with ΔAIC < 2. The grey dotted line represents the zero effect. Significant responses are highlighted by asterisks. The x-axis depicts the estimates, and the y-axis represents the variables. The error bars depict the standard error of the standardised coefficients

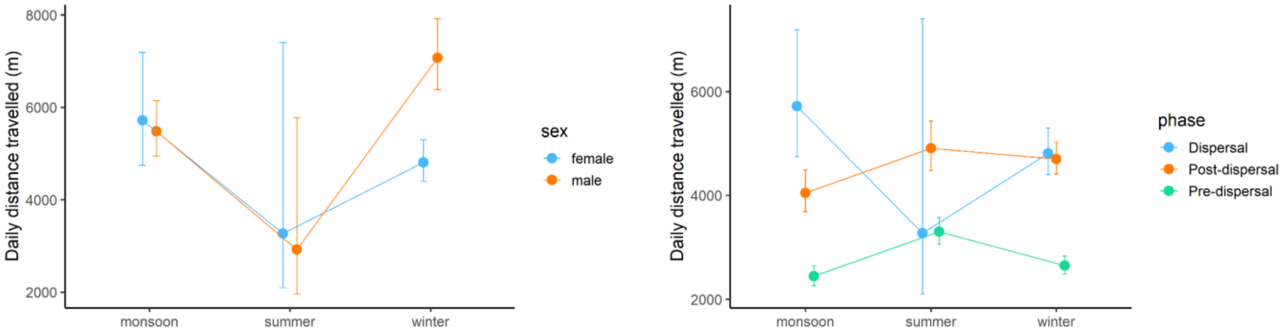


Figure 5.12: The interaction plots are based on the prediction of a generalised linear model showing the relationship between sexes, season, and dispersal phases (pre-dispersal, dispersal, and post-dispersal) to daily distance travelled

5.5.6 Effect of variables on the daily displacement

The daily distance covered by tigers, both within and outside protected areas, was influenced by factors such as sex, season, and dispersal phase (Table 5.21). The coefficients of the fixed effects that contribute to the daily displacement are shown in Figure 5.13. The results showed that the daily displacement of tigers was significantly higher outside the PAs ($\beta = -0.37$; $p<0.001$). Across the sexes, there were variations in the daily displacement between males and females during the winter season (Table 5.22; $\beta = 0.49$; $p<0.001$). During the summer, displacement significantly differed between the pre-dispersal and post-dispersal phases, as shown in Figure 5.14. Tigers exhibited less displacement during winter than during the dispersal and post-dispersal phases. However, no significant difference in the daily displacement was observed across the three dispersal phases during the monsoon season.

Table 5.21: Models describing variables affecting the tiger's daily displacement in the Eastern Vidarbha Landscape

Name	Model structure	df	AIC
Model 4	Daily displacement ~ phase + area + sex + season + season*sex + season*phase	14	60951.9
Model 2	Daily displacement ~ phase + area + sex + season + season*sex	10	60957.8
Model 3	Daily displacement ~ phase + area + sex + season + season*phase	12	60974.6
Model 1	Daily displacement ~ phase + area + sex + season	8	60980.2
Null	Daily displacement ~ 1	2	61493.0

Table 5.22: Effects of predictors and estimates on the daily displacement of tigers in the Eastern Vidarbha Landscape. The dispersal phase was considered the reference category in the regression analysis

Parameters	Estimate	Std. Error	t value	Pr(>|t|)
Protected area	-0.37	0.04	-10.16	0.00
Male*summer	0.07	0.09	0.77	0.44
Male*winter	0.49	0.09	5.64	0.00
Pre-dispersal*summer	1.22	0.33	3.70	0.00
Pre-dispersal*winter	-0.26	0.12	-2.19	0.03
Post-dispersal*summer	1.36	0.33	4.07	0.00
Post-dispersal*winter	0.00	0.12	0.03	0.97

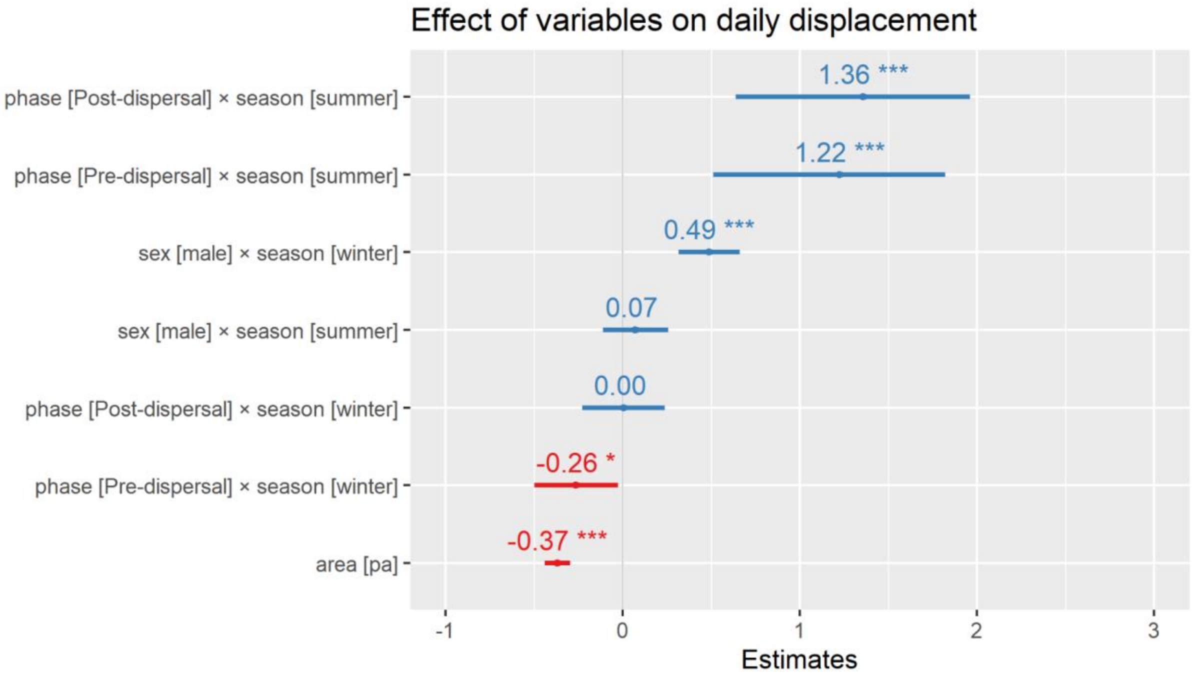


Figure 5.13: Parameter estimates of variables affecting the daily displacement of tigers in the Eastern Vidarbha Landscape. Estimates are based on a set of top models with ΔAIC < 2. The grey dotted line represents the zero effect. Significant responses are highlighted by asterisks. The x-axis depicts the estimates, and the y-axis represents the variables. The error bars depict the standard error of the standardised coefficients

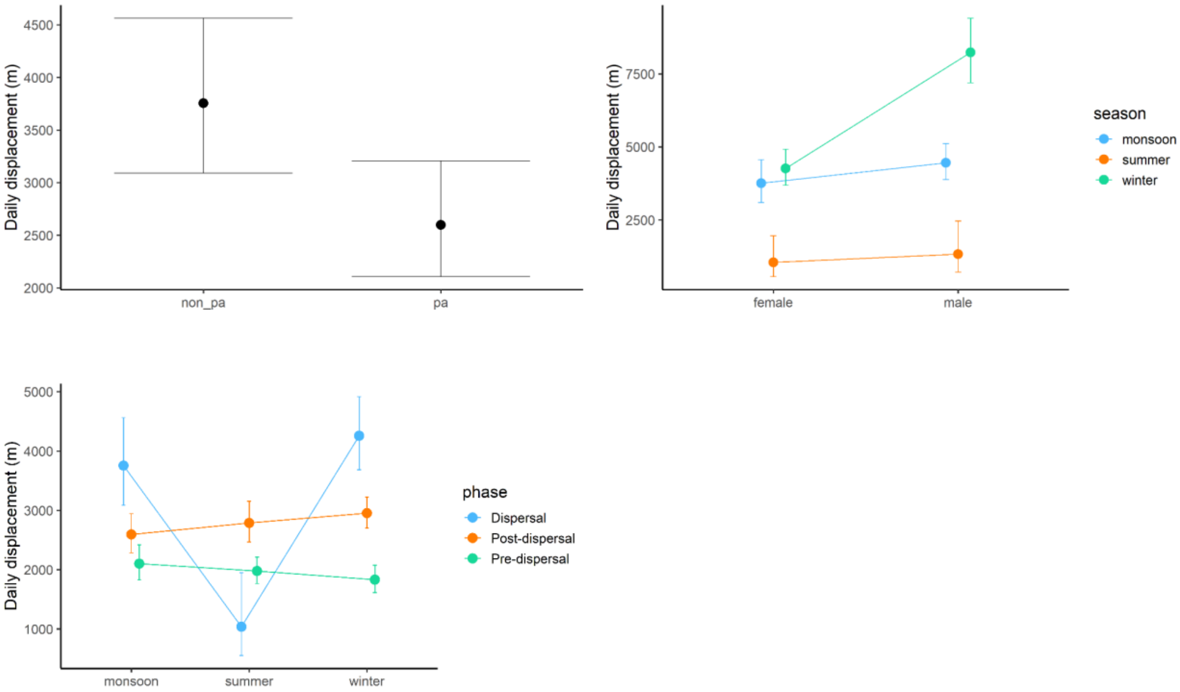


Figure 5.14: The interaction plots are based on the prediction of a generalised linear model showing the relationship between sexes, season, and dispersal phases (pre-dispersal, dispersal, and post-dispersal) to daily displacement

5.5.7 Effect of variables during dispersal phase

The model with the lowest AIC value included movement metrics, environmental factors, anthropogenic disturbance, and fragmentation to explain the variation observed between dispersing and non-dispersing tigers (Table 5.23). Dispersing tigers exhibited faster movement when traversing a landscape dominated by human activity. They also showed a strong affinity for areas with high vegetation cover (NDVI) during the monsoon season (Table 5.24, Figure 5.15). Although dispersing tigers positively affected human settlements, they tended to avoid areas with a human presence (Figure 5.16). In addition, their responses to roads were negatively associated. Furthermore, dispersing individuals exhibited a negative relationship with medium-sized habitat patches but preferred smaller patches. Regarding human activities and fragmentation, dispersers were positively associated with the straightness index, indicating more directional movement in the landscape.

Table 5.23: Models describing variables affecting the dispersal phase of tigers in the Eastern Vidarbha Landscape (dispersal phase was considered as a reference during the regression analysis)

Name	Model structure	df	AIC
Full	Life stage ~ core + environmental + anthropogenic + fragmentation	13	7003.0
Fragmentation	Life stage ~ core + large core + medium core + small core + straight index	9	8256.3
Anthropogenic	Life stage ~ core + dist.HS + dist.road + population count	8	22296.9
Environmental	Life stage ~ core + ndvi	6	25775.4
Core	Life stage ~ tod + season + movement rate	5	25781.7
Null	Life stage ~ 1	1	29888.8

Table 5.24: Effects of predictors and estimates on dispersing tigers in the Eastern Vidarbha Landscape

Parameters	Estimate	Std. Error	z value	Pr(>|z|)
Winter	-2.30	0.08	-28.32	0.00
Summer	-6.85	0.19	-36.54	0.00
Movement rate	0.00	0.00	3.18	0.00
Night	0.04	0.06	0.70	0.48
Vegetation cover (NDVI)	0.39	0.03	12.47	0.00
Distance to human settlement	-2.46	0.09	-28.65	0.00
Distance to road	0.84	0.05	17.13	0.00
Population count	-0.43	0.07	-6.14	0.00
Large core	0.13	0.11	1.24	0.21
Medium core	-1.89	0.27	-6.89	0.00
Small core	1.35	0.20	6.72	0.00
Straight index	4.24	0.07	57.17	0.00

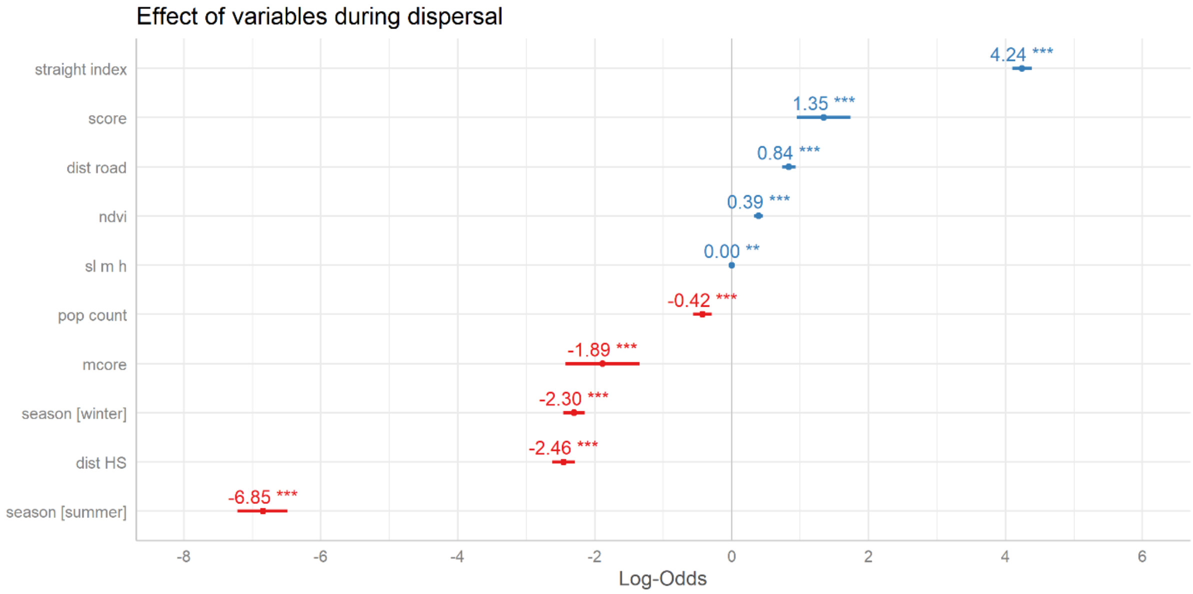


Figure 5.15: Parameter estimates of variables affecting the dispersing tigers in the Eastern Vidarbha Landscape. Estimates are based set of a priori models with the lowest AIC value. Significant responses are highlighted by asterisks. The x-axis depicts the estimates, and the y-axis represents the variables. Asterisks indicate significance level: * = 0.05, ** = 0.005, *** = 0.0005

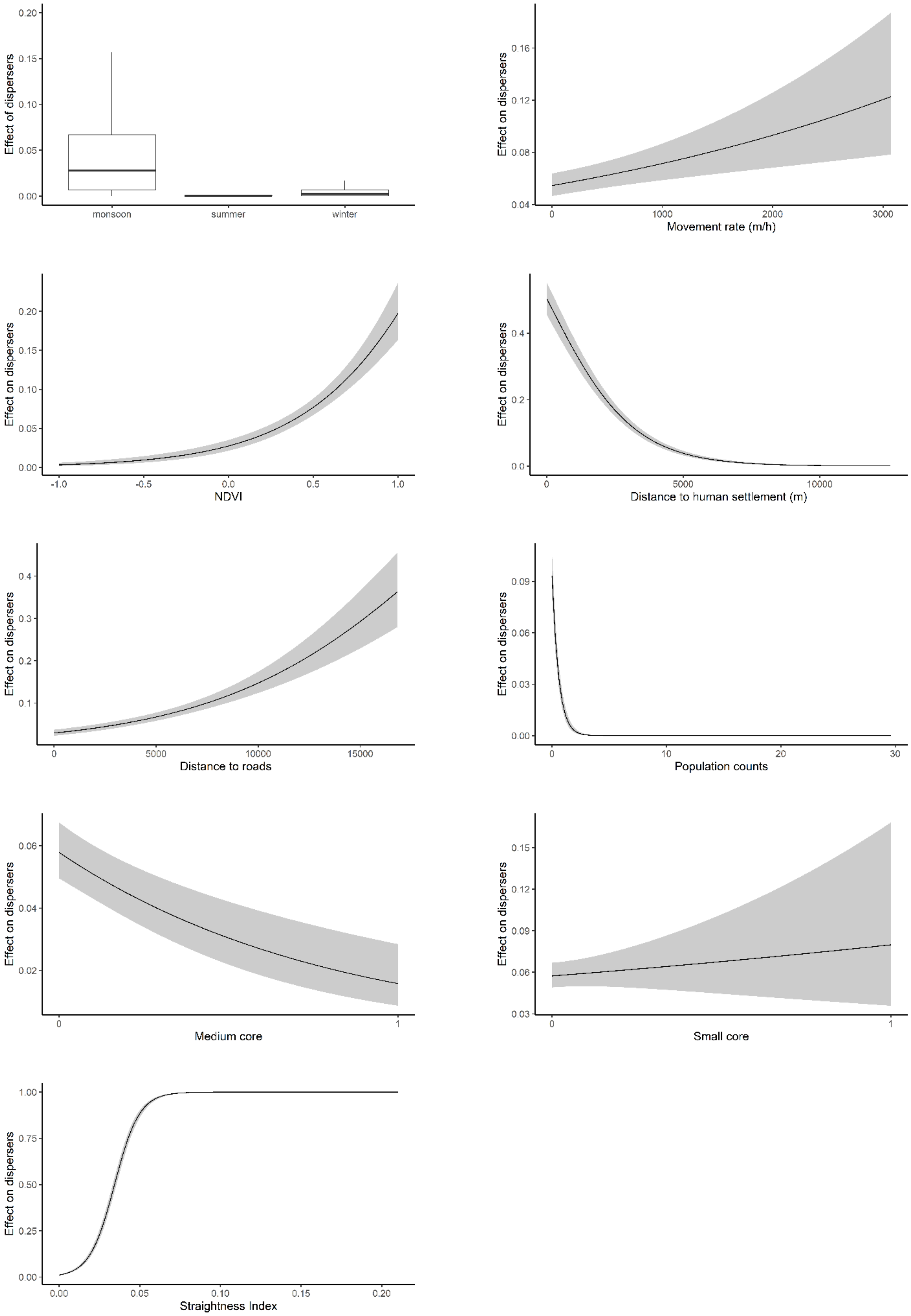


Figure 5.16: The plots are based on the prediction of a generalised linear model showing the effect of environmental, anthropogenic and fragmentation on dispersing and non-dispersing tigers in the Eastern Vidarbha Landscape

5.6 Discussion

Animal movement and space use are crucial aspects of ecological research and provide valuable insights into various ecological processes and conservation strategies. Several studies have investigated animal movement and space use across diverse taxa and ecosystems. For example, with the advancement of GPS technology, studies on radio-telemetry have been widely used to track individual animals and gather fine-scale movement data (Bista et al., 2021; Goodall et al., 2019; Goodheart et al., 2022; Habib, Ghaskadbi, et al., 2021b; Hussain et al., 2022; Kays et al., 2015; Kertson et al., 2011; Tucker et al., 2018). Moreover, there has been a shift in the study of animal movement, behaviour, and spatial use at different temporal scales. In the Indian subcontinent, few studies have utilised such technological inputs to understand tiger ecology, dispersal movement, and home ranges (Athreya et al., 2014; Chundawat et al., 2016; Habib et al., 2021b; Karanth & Sunquist, 2000; Naha et al., 2016; Sarkar et al., 2016). These studies were primarily conducted in protected areas, and the available information on tiger ecology has mainly focused on adults. Furthermore, existing information on movement patterns, behaviour, or space use is limited, leaving a significant gap in our understanding of dispersing tigers.

This study focused on movement patterns, space use, and factors influencing the dispersal process in tigers. The life stages of sub-adult tigers were classified into three behavioural phases, i.e., pre-dispersal, dispersal, and post-dispersal phase. The findings suggest that males and females disperse over long distances, with males moving greater distances than females. The observed pattern of natal dispersal in both sexes is influenced by behavioural adaptability, which various ecological and anthropogenic factors can trigger. Previous studies on tigers have shown a general pattern of sex-biased natal dispersal (Smith, 1993; Goodrich et al., 2010), attributed to factors such as competition for mates, inbreeding avoidance, and resource competition (S. F. Dobson, 1982; Greenwood, 1980; Sutherland et al., 2000). However, more recent studies indicate behavioural plasticity in sex-biased dispersal, which challenges the notion that a single factor can fully explain the interspecific patterns of dispersal (Lambin et al., 2001). Dispersal can also be influenced by ecological and proximate factors, including social pressures resulting from increased population density (Snyder, 1961) and food resources (Messier, 1985; Harrison, 1992). Additionally, dispersal may be influenced by environmental factors, such as habitat fragmentation and human activities, rather than solely driven by population dynamics and mating systems. Species that persist in fragmented landscapes exhibit interpopulation variation in dispersal traits related to landscape structure. For example, studies on birds have revealed that individuals of the same species exhibit differences in the maximum distance they disperse, based on whether they inhabit forest fragments or continuous habitats (Van Houtan et al., 2007). Our understanding of the dispersal mechanism has advanced significantly because of radio-telemetry, enabling us to observe the process at a fine temporal scale.

Tigers in the dispersal phase exhibited the highest utilisation of space use, followed by the post-dispersal and pre-dispersal phases. There was also variation in space use within and outside protected areas, with individuals outside of protected areas requiring larger territories. This can be attributed to the environmental characteristics and mosaic of landscape habitats that influence their movement. Tigers outside protected areas utilise larger fragmented areas in the landscape, including forests and agricultural fields, which also influence the movement pattern. Similarly, studies on cougars and lions have shown increased speeds while traversing fragmented human-dominated areas to minimise the time spent in multiple-use areas (Kertson et al., 2011; Valeix et al., 2012). Across the sexes, male tigers usually require larger areas than females, although the requirements are similar during the pre-dispersal phase. This is because male tigers compete to access resources, find mates, and establish exclusive home ranges that can encompass the home ranges of one to several females (Sunquist, 1981). Female tigers maintain home ranges of adequate size to fulfil the energetic requirements associated with cub rearing (Smith et al., 1987; Miller et al., 2014). Previous studies have shown that the distribution of resources influences female spatial organisation in tigers, while male spatial patterns are determined by the distribution of females (Sandell, 1989; Macdonald, 1983). Moreover, the relatively small adult female home range can be attributed to spatially homogenous and abundant prey species (Sunquist, 1981; Smith et al., 1987; Sandell, 1989; Macdonald, 1983).

Variations in seasonal space utilisation were also observed across different life stages. During the pre-dispersal phase, tigers exhibited greater space utilisation during the monsoon season. Their movement can explain this behaviour in the search for new habitats and the establishment of new territories. Because of increased movement and activity during the season, there is an increase in space requirements. Moreover, tigers are mostly dispersed during the monsoon season, making tiger movement more permeable to the landscape. High vegetation cover, water availability, and increased productivity in dry deciduous habitats during this season make dispersal more permeable in human-dominated landscapes. Agricultural fields with growing crops act as cover for dispersal. Furthermore, livestock availability increases as they are allowed to graze in forested areas, providing easy prey for dispersing tigers.

The study also highlights the factors that influence the spatial and seasonal variability of space use in the landscape. Factors such as land use composition, landscape configuration, and anthropogenic disturbances primarily drive patterns of tiger space use. These findings suggest that the proportion of forest cover, habitat patch density, and the human population within the daily movement range of the tiger influenced the spatial patterns. Moreover, these relationships were evident at different spatial scales, represented by 99%, 95%, and 50% isopleths of utilisation distribution. The scale at which landscape structure is measured is crucial for species persistence and for guiding management strategies. Previous studies have indicated that the effect of scale varies across spatial scales, and is linked to ecological processes and species dependency (Gestich et al., 2019; Jackson & Fahrig, 2012; Miguet et al., 2016). For example, at a larger scale (99% isopleth), tiger space utilisation decreases as the proportion of forest cover increases. Landscape configuration affects movement because different habitats offer varying levels of benefits and risks. Increased forest cover in undisturbed and contiguous habitats supports more resources, resulting in smaller tiger space requirements. Moreover, good-quality habitats and high prey abundance may increase tiger density, resulting in less space for conspecifics. However, in 95% isopleths and core areas, space use decreased with increased forest fragmentation. As forest patches become more disaggregated, movement within these patches may increase the likelihood of exposure to human-induced effects, leading to increased human-animal interactions. Consequently, tigers restrict their movement and reduce the space required to minimise the risk of anthropogenic disturbances. In contrast, no significant fragmentation effect was observed at the larger spatial scale of 99% isopleth. This suggests that individuals compensate for fragmentation by maintaining the required space on a larger scale and shows that the scale effect depends on species mobility. When accounting for anthropogenic disturbances, the human population is an important predictor of space utilisation in a human-dominated landscape.

Space use within and outside protected areas varied between sexes and seasons. At 99% and 95% isopleths, males exhibited more space utilisation, suggesting important physiological requirements for males and females in different seasons. Furthermore, dispersing tigers showed the highest space use across all seasons, particularly during the winter. Dispersing tiger movements primarily occur outside PAs, searching for new habitats and mates. Movement occurs between a matrix of fragmented forests and agriculture with high human density and road networks (Habib et al., 2021b), which may explain the larger space use of tigers. The core area sizes were similar across the sexes, suggesting that males and females maintain habitat-specific resource-rich areas for daily requirements (Kernohan et al., 2001). This also suggests that tigers exhibit less plasticity while maintaining their core area size in a human-dominated landscape. However, across seasons, the core area was significantly smaller in summer, as tiger movement was mostly restricted by high temperature and water availability.

This study also highlighted the factors influencing the movement rate, daily distance travelled, and daily displacement of tigers. The tiger movement was generally faster and had a longer displacement outside the protected area. This was probably due to the environmental features and mosaic of landscape habitats that influence movement. The landscape outside the PA encompasses a larger fragmented area, including forests and agricultural fields. The habitat patches in such landscapes are at varying distances from each other and are interspersed with human settlements. Thus, they adapt movements to cover a more extensive area while crisscrossing agricultural and forested areas in a human-dominated landscape. Similarly, studies on cougars and lions have shown higher speeds while traversing fragmented human-dominated areas to reduce the time spent in multiple-use areas (Kertson et al., 2011; Valeix et al., 2012). A difference in movement patterns was also observed across sexes, with males moving faster and covering more distance in winter. Owing to their larger home ranges, male tigers require longer distances to cover the habitat matrix. In addition, there is strong heterogeneity of food and resources in the landscape during winter. I also found that tigers moved faster at night during summer and winter, and vice versa during the monsoon season. Similarly, seasonal variability also influenced tiger movement, dispersing tigers travelling more and covering greater distances in the monsoon and winter. As human activity decreases at night, animals can move between forest fragments situated far away from each other, thereby perceiving a low risk attributed to human activity and anthropogenic disturbances. The habitat is contiguous in forested areas, making movement more conducive during day and night. During the monsoon season, with high resource availability, movement becomes restricted. However, tiger movement during the post-dispersal phase was higher in summer, as the movement was similar to that of an established tiger and had to defend the territory. Tiger movement slowed down when traversing areas with dense vegetation cover and large core forests. In contrast, they increased their movement rate when encountering anthropogenic features such as agricultural areas and roads. However, their movement rate decreases when moving close to human habitation. This variability in movement behaviour can be attributed to behavioural plasticity while moving through a human-dominated landscape, thus minimising human encounters, and reducing anthropogenic pressures.

Altered movement patterns owing to habitat fragmentation and human pressure have been observed in many carnivorous species worldwide (Poessel et al., 2014; Tigas et al., 2002; Tucker et al., 2018). Thus, the energetic cost, resource availability, and anthropogenic risk that vary across landscapes might affect animal movement patterns. Our findings provide new insights into the factors influencing the dispersion of tigers in the landscape. The cost of dispersal varies depending on environmental factors, anthropogenic disturbances, and fragmentation. Dispersing tigers moved faster with high vegetation cover during the monsoon season, probably facilitating dispersers to move in a fragmented habitat and navigate more easily in landscapes dominated by human activities. Moreover, it reduces the risk of encountering humans when travelling through areas with high vegetation cover. I also observed that dispersing tigers avoided roads, as some species perceived landscapes negatively. Roads usually have reduced forest cover, higher grazing disturbance, high vehicle traffic, and human presence, possibly making tigers perceive them as risky. Tigers may slow down to become more vigilant when close to human settlements and used areas away from high human presence. This also suggests a tiger's ability to differentiate between risky and undisturbed areas. Roads with high traffic volumes can act as barriers to animal movement, leading to mortality, displacement, or behavioural avoidance, depending on specific landscape conditions (Anderson, 2002; Carter et al., 2023; Forman et al., 2003; Scrafford et al., 2018; Shepard et al., 2008). Moreover, these animals crisscrossed the fragmented landscape with more directional movement to minimise human-induced interference. These findings demonstrate the risk-avoidance behaviour of dispersers while travelling through a human-dominated landscape.

The findings of this study significantly enhance our understanding of the complex relationships between tigers and their surrounding landscape. Specifically, this study emphasises the influence of habitat fragmentation, resource availability, and anthropogenic disturbances on the movement patterns exhibited by tigers. The risk-avoidance behaviour of dispersing tigers highlights the importance of conserving and restoring suitable habitats outside PAs and reducing human-induced pressures to facilitate their dispersal and ensure long-term survival.

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CHAPTER 6

TO IDENTIFY THE BEHAVIOURAL PATTERN OF TIGERS IN THE EASTERN VIDARBHA LANDSCAPE

Chapter 6

To identify the behavioural pattern of tigers in the Eastern Vidarbha Landscape

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6.1 Introduction

Large carnivore populations face significant challenges in an increasingly fragmented world owing to their diverse behaviours (Ripple et al., 2014). Habitat loss, habitat degradation, and increased human land use are major contributors to changes in species movement and behaviour (Tucker et al., 2018). Large carnivores have extensive home ranges; thus, their space use includes a multi-use landscape in a heterogeneous human-dominated environment (Crooks et al., 2011; Dobson, 1982; Ripple et al., 2014) and modifies their movement patterns. As a result, the success of their movement and behaviour determines their ability to survive and persist in a human-dominated landscape (Carter & Linnell, 2016; Gantchoff et al., 2020; Tucker et al., 2018).

Human activities have accelerated fragmentation and habitat loss worldwide, thereby impeding animal movement (Anadón et al., 2012; Shepard et al., 2008). High-quality habitats are often separated into small patches, surrounded by unsuitable habitats and anthropogenic features (van der Ree et al. 2015). Consequently, species are forced to alter their movement in a matrix of fragmented habitats. For example, carnivorous species such as tigers move faster in fragmented and high human presence (Habib et al., 2021c). Moreover, linear features such as roads have multiple negative impacts on terrestrial wildlife populations (Barrientos et al. 2021), including increased wildlife mortality (Ascensão et al. 2014; Grilo et al. 2018), which hampers the ecological connectivity (Carvalho et al. 2016; Chen and Koprowski 2016; Ascensão et al. 2017) or affecting species activity and individual behaviour (Kociolek et al. 2011; Medinas et al. 2019). While moving or dispersing through a habitat matrix, tigers may change their movement behaviour in response to environmental and anthropogenic factors. For example, land use changes and anthropogenic features, such as roads, affect animal movement and behaviour in various habitat matrices (Scrafford, 2017). However, understanding animal movement behaviour is complex and a key environmental challenge (Zeller et al. 2012; McClintock et al. 2020).

More recently, fine-scale movement data have made it possible to understand animal behaviour (Gardiner et al. 2019). For example, Hidden Markov models (HMMs) are used to interpret and classify behavioural states from movement data depending on the specific characteristics of individual movement paths (Patterson et al. 2017; McClintock et al. 2020). The outcomes of the HMM analysis include movement parameters (such as mean step length) for each behavioural state and an estimated state for each observation time. HMMs have been used to investigate how covariates, including age, sex, and environmental and anthropogenic factors, affect state transition probabilities, i.e., state-switching behaviour (Morales et al., 2004; Grecian et al., 2018). Thus, it is possible to evaluate its effect on the behavioural dynamics of animals, which is often of great ecological interest.

Understanding the behavioural ecology of large carnivores, especially those inhabiting complex and dynamic environments, presents many data collection and analysis challenges. Mainly, when animals are elusive and live in habitats where direct observation of their behaviour is complex. Furthermore, the ability of large carnivores to persist in human-dominated landscapes may be critical to their conservation, as human land use continues to expand and encroach on wildlife habitats (Carter & Linnell, 2016). Thus, understanding behavioural mechanisms in a habitat matrix is essential for the long-term coexistence and conservation of species.

Here, I studied the movement behaviour of sub-adult tigers during three dispersal phases, i.e., pre-dispersal, dispersal, and post-dispersal, in the central Indian landscape. I used conventional and generalised HMMs on GPS data collected from sub-adult tigers during 2016-2020. I investigated how intrinsic and extrinsic factors interact to shape movement patterns and how they are affected by life stage. In this chapter, I modelled tiger behavioural states to assess the relationship between behavioural states and different variables including ambient temperature, diel patterns, habitat type, and distance to roads. Specifically, it aimed to (i) identify and describe the behavioural states displayed by dispersing and non-dispersing sub-adult tigers and (ii) understand how environmental factors (ambient temperature, time of day, and habitat) and linear features (proximity to roads) influence behavioural states.

6.2 Methods

6.2.1 Study area

This study was conducted in the Vidarbha Landscape (EVL) of Maharashtra, part of the Central Indian Tiger Landscape. The landscape encompasses an area of approximately 97,320 km^2, with forest cover accounting for 27.5% of the total area (Habib et al., 2021). Tiger-bearing PAs in our study area include Tadoba-Andhari Tiger Reserve (TATR), Bor Tiger Reserve, Umred-Karhandla Wildlife Sanctuary (UKWLS), and Tipeshwar Wildlife Sanctuary (TWLs). The area outside the PA comprises the Brahmapuri Forest Division, which is interspersed with urban and semi-urban regions comprising 8,540 villages. The vegetation of the landscape is primarily dry deciduous, with teak (*Tectona grandis*) and bamboo *(Dendrocalamus strictus*) being the dominant flora. Faunal species include the tiger (*Panthera tigris*), estimated to be around 350 (Habib et al., 2022), co-occurring with other species such as leopard (*Panthera pardus*), dhole (*Cuon alpinus*), sloth bear (*Melursus ursinus*), gaur (*Bos gaurus*), and several ungulate species.

6.2.2 Telemetry data collection

Between 2016 and 2020, 15 tigers were captured and fitted with GPS collars from the Eastern Vidarbha Landscape in Maharashtra. Ten tigers were captured from PAs (eight males and two females) and five from outside PAs (one male and four females) across age and sex classes. Collaring was conducted within PAs in the Tadoba-Andhari Tiger Reserve (TATR) and two Wildlife Sanctuaries (Umred-Karhandla and Tipeshwar Wildlife Sanctuary). In TATR, sub-adult tigers were captured from both core and buffer areas. Core areas are critical tiger habitats without human activities, whereas buffer areas lie on the periphery of the core zones and include a matrix of human-wildlife habitats. Sub-adult collared tigers were from the same litter in a combination of male-male, male-female, and female-female from different mothers. All subadults were >1 year old and were in their natal areas during collaring. Collars were padded with foam layers to allow the neck to grow to adulthood. Individual tigers were tracked via VHF ground tracking until they established territory and the collar was removed using a drop-off mechanism.

Tigers were captured and immobilised using a combination of Medetomine hydrochloride, Ketamine hydrochloride, and Xylazine (dosages based on body weight, age, and sex). The animals were fitted with GPS collars (GPS Plus, Vectronic Aerospace, Berlin, Germany) and received fixes at different time intervals according to the dispersal phase. The animals were fitted with Iridium GPS radio-collars (Vectronics, Germany) with a high spatial location accuracy (± 5 m). The collar was programmed to obtain locations every 1-5 h depending on the dispersal behaviour of the individual. During the pre-dispersal phase, locations were received every 2-5 h intervals when the tiger was within its natal area. When tigers moved out of their natal areas during dispersal, the collars were programmed to receive intensive location every 1-h. During the post-dispersal phase, locations were received every 2-5 h interval.

6.2.3 Hidden Markov Model (HMM)

Hidden Markov models (HMM) were used to investigate the relationship between different behavioural states with environmental and anthropogenic covariates. The HMM parameters are defined based on a learning set of trajectories for which the movement pattern is known. Trajectories are translated from an array of positions to an array of angles and distance intervals (Figure 6.1). Given a trajectory with an unknown pattern and a defined model, the most probable set of hidden states is reconstructed using the Viterbi algorithm. I investigated the behavioural patterns of tigers using conventional and generalised HMM. The conventional HMM allows covariates to affect the stationary probabilities (i.e., probability of remaining in the same behavioural state) and state transition probabilities (i.e., the probabilities of switching between behavioural states) but not the state-dependent probability distribution parameters of the movement characteristics (i.e., step lengths and turn angles). In other words, within the conventional model, the covariates (including *time*) could affect the probability of switching between states, but not the distribution of movement metrics that inform the states that remain stationary. The generalised HMM is an extension of the conventional HMM, which explicitly models covariates acting on the state transition probabilities (as in the conventional HMM) and state-dependent probability distribution parameters of the movement characteristics. The framework allows testing the impact of covariate effects on the state-dependent probability distribution parameters for step lengths and turn angles and the state transition probability.

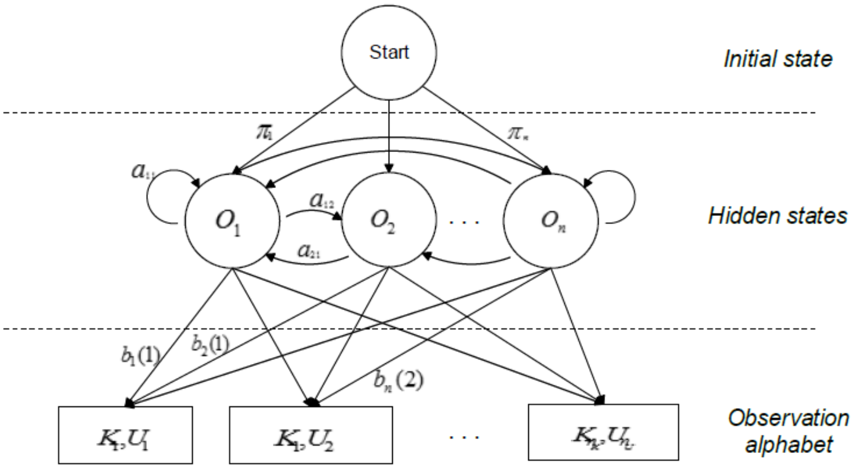


Figure 6.1: Schema of Hidden Markov model for discovery of movement patterns

6.2.4 Processing of movement data

HMMs assume that animal locations are observed at regular intervals with no errors. Because the parameters to fit the HMM depend on the sampling scale, movement data were filtered into 2-h and 3-h data for different individuals. Data from the first 48-h following animal collaring were deleted to ensure behavioural bias in model fitting. Separate models for the two temporal scales were analysed, i.e., 2-h and 3-h. Moreover, location data with 2-h and 3-h were combined to predict locations and uncertainty at 2-h time steps for the three dispersal phases, i.e., pre-dispersal, dispersing and post-dispersal. A two-stage approach was applied to regularise the movement data and missing locations. First, the *"crawl"* package accounted for missing spatial locations in R software. It fits the continuous-time correlated random walk (CTCRW) model of Johnson et al. (2008) to one or more tracks (subject to location measurement error and temporal irregularity), and then predicts temporally regular tracks based on the CTCRW model output. Once the missing location was interpolated, I used the data to fit HMMs that accounted for observation errors, temporally irregular, or missing data (Hooten et al., 2017; McClintock, 2017). Models at different temporal scales were checked to determine if there were variations in the estimates through HMM using multiple imputation methods.

6.2.5 Environmental and anthropogenic covariates

A set of significant explanatory variables for tiger movement were calculated to investigate the effects of environmental and anthropogenic variables across the three dispersal phases. Time of day (hours), temperature, habitat (forest and non-forest), and distance to the road were used as predictor variables for each GPS fix. The Euclidean distance of each tiger location to the nearest road was calculated using the OpenStreetMap geospatial data repository (OpenStreetMap 2020) in the Google Earth Engine™ (Gorelick et al., 2017). These environmental and anthropogenic variables were used to investigate how state transition probabilities (i.e. the probabilities of switching between behavioural states) and state-dependent probability distribution parameters (step lengths and turn angles) were affected by covariates (Morales et al., 2004; Towner et al., 2016; van Beest et al., 2019). Habitat was used as a covariate to investigate the effect on the movement characteristics of behavioural states.

6.2.6 Statistical analysis

The behavioural states of tigers were inferred using HMM from movement data using the *'momentuHMM'* package (McClintock & Michelot, 2018) in the R software. Two movement parameters were considered: step length (the linear distance moved between two locations at a sampling interval of 2-h) and turning angles between steps in successive sampling intervals. HMMs were fitted by modelling the step length with a gamma distribution and turning angles using a von Mises distribution, which is a circular analogue of the normal distribution (Michelot et al. 2016). Significantly, their Markov property relaxes the assumption of serial dependence, thereby making HMMs well suited to highly autocorrelated movement data (Zucchini et al., 2017). The 3-state HMM included state transition probabilities and transition probabilities as functions of the environmental and anthropogenic covariates. I considered HMMs with three behavioural states since 3-state models are usually statistically well supported and biologically meaningful in terrestrial mammal studies (Gardiner et al., 2019; Farhadinia et al., 2020). The 3-state behaviour based on the time series of step lengths and turning angles is

- *State 1 (resting)*: trajectories with shorter step lengths and variable turning angles with slow and undirected movements.
- *State 2 (area restricted movement)*: trajectories with small step lengths and turning angles, suggesting that the movement is tortuous within a small area.

- *State 3 (travelling)*: Trajectories with longer step lengths and low turning angles indicate that movement is faster with high directional movement.

An example of animal trajectory with 3-state behaviour representing resting, area-restricted movement, and travelling patterns is shown in Figure 6.2

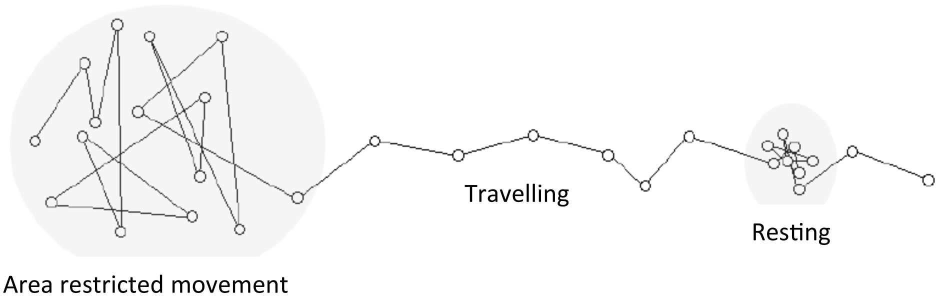


Figure 6.2: Illustration of animal trajectory and behaviour identified from the movement pattern (Source: Kosović & Fertalj, 2014)

Traditional applications of HMMs assume that state-switching dynamics do not change between or within individuals (Grecian et al., 2018; Carter et al., 2020); however, individual variation is explained by demographic covariates, such as sex, region, size, or life history stage. Therefore, I incorporated discrete-level random effects (hereafter referred to as "mixture") to account for potential individual variations in the initial state distribution and transition probabilities (DeRuiter et al., 2017; McClintock, 2021). When fitting the baseline models, mixtures = 1, i.e., no discrete-valued individual-level random effects, after which two models for each baseline were constructed using mixtures = 2 and mixtures = 3, respectively. I fitted 21 HMMs for each mixture, including all combinations and interactions between the covariates.

6.2.7 Model selection

The null model and models with covariates (time of day, temperature, distance to road, and habitat) were used to identify the different behavioural states of dispersing tigers. A description of the covariate type and model name is provided in Table 6.1.

Table 6.1: Description of covariates and model type used for HMM models

Model name	**Covariate type**
Null	No covariates
Environmental	Ambient temperature
Habitat	Forest and non-forest
Anthropogenic	Distance to road

The model comprised a three-way interaction of covariates (time of day, ambient temperature, and habitat) on 1) the state transition probabilities, 2) the distribution of mean step lengths, and 3) the distribution of angular deviation (on the state-dependent probability distribution parameters for step lengths and turn angles). Furthermore, to ensure optimal Maximum Likelihood, 25 HMM trials were run with different sets of randomly chosen starting values within a range of plausible values determined by inspecting histograms of the step length and turning angles. I found that the model output was robust to different starting values, reflecting a converging value of Maximum Likelihood. Therefore, the average values applied in the trials were used to construct the null model, confirming that it led to the same convergence value of the Maximum Likelihood. The most probable state sequence is decoded using the Viterbi algorithm (Zucchini et al., 2017). Model assumptions were checked by visual inspection of pseudo-residual plots (Zucchini et al., 2017) and verified that state characteristics were biologically interpretable in line with our data observations.

6.3 Result

Fifteen tigers were collared and tracked during three dispersal phases: pre-dispersal, dispersal, and post-dispersal. I fitted 3-state HMM for each dispersal phase (pre-dispersal, dispersal, and post-dispersal) with different predictor variables on the stationary state probabilities and transition probabilities with a fixed interval of 2-h. Conventional and generalised HMM were fitted to identify distinct movement patterns. The HMM indicated that the tiger movement patterns were composed of three behavioural states. Moreover, the 3-state behaviour is easy to interpret biologically, with the predicted state inferred to the animal being in "*resting*", "*area restricted movement (ARM)*", and "*travelling*", respectively. The lowest AIC value selected the best-fit model with covariates across all three dispersal phases (Table 6.2). The effect of temperature and time of day was evident for the pre-dispersal phase, while the time of day and habitat affected the 3-state behaviour during dispersal. Similarly, during the post-dispersal phases, the time of day and habitat influenced stationary and transition probabilities. Moreover, the pseudo-residuals of each model suggested that the goodness-of-fit was good for the step length and turning angle, capturing the autocorrelation in the movement parameters.

Table 6.2: Generalised HMM showing the best models with AIC, model weight, and heterogeneity models (K) for 3-state HMMs with different covariate dependencies of dispersing tigers based on 2-h time intervals. The effect of time of day was considered cyclical over 24-h

Phase	**HMM Model**	**Effect of covariates**	**Log-likelihood**	**AIC**
Pre-dispersal	Conventional HMM	Covariate effect on stationary state and transition probability: *Time of day + temperature*	-9667.22	15297.84
Dispersal	Generalised HMM	Covariate effect on stationary state and transition probability: *Time of day* State-dependent distribution parameter *Step length ~ Habitat*	-7573.23	15386.63
Post-dispersal	Generalised HMM	Covariate effect on stationary state and transition probability: *Time of day + Habitat* State-dependent distribution parameter *Step length and Turn angle ~ Habitat*	-18709.58	15393.7

6.3.1 Pre-dispersal phase

I analysed data from 10 individuals (6 males and 4 females) ranging from 15-154 days per individual and used 9420 GPS locations of tigers from the Eastern Vidarbha Landscape. State 1 (resting) corresponded to short step lengths (mean= 14.98 m) and variable turning angles (mean= 3.14; concentration= 0.08), indicating very slow and undirected movement. State 2 (area-restricted movement) had a small step length (mean= 102.73 m) and turning angle (mean= 0.10), suggesting that the movement was composed of tortuous movement within a small area. On the other hand, state 3 (travelling) had longer step lengths (mean= 749.92 m) and turning angles (mean= -0.03; concentration= 1.03), indicating faster movement with high directional movement (Figure 6.3). Tigers spent 41.20% of their time on area-restricted movement and 30.65% on travelling, while 28.13% were used to rest. There were also significant differences in how behavioural states were related to covariates. The best model was explained by time of day and temperature on stationary state probabilities and state-switching behaviour (i.e., transition probabilities). The final model had a K = 3 mixture, i.e., three different patterns of state-switching behaviour, including individual heterogeneity in the model.

Table 6.3: Parameter estimates of step length, turning angle, directionality, and temporal budget of the 3-state behavioural models during the pre-dispersal phase (n =10). The step lengths are modelled with gamma, and the turning angle with von Misses distribution based on the 2-h dataset for dispersing tigers

Parameters	**Resting**	**Area Restricted Movement**	**Travelling**
Mean step length (m)	14.98	102.73	749.92
Mean step length SD (m)	12.37	84.73	578.12
Mean angle	3.14	0.10	-0.03
Concentration	0.08	0.35	1.03
Proportion in each state (%)	28.13	41.20	30.65

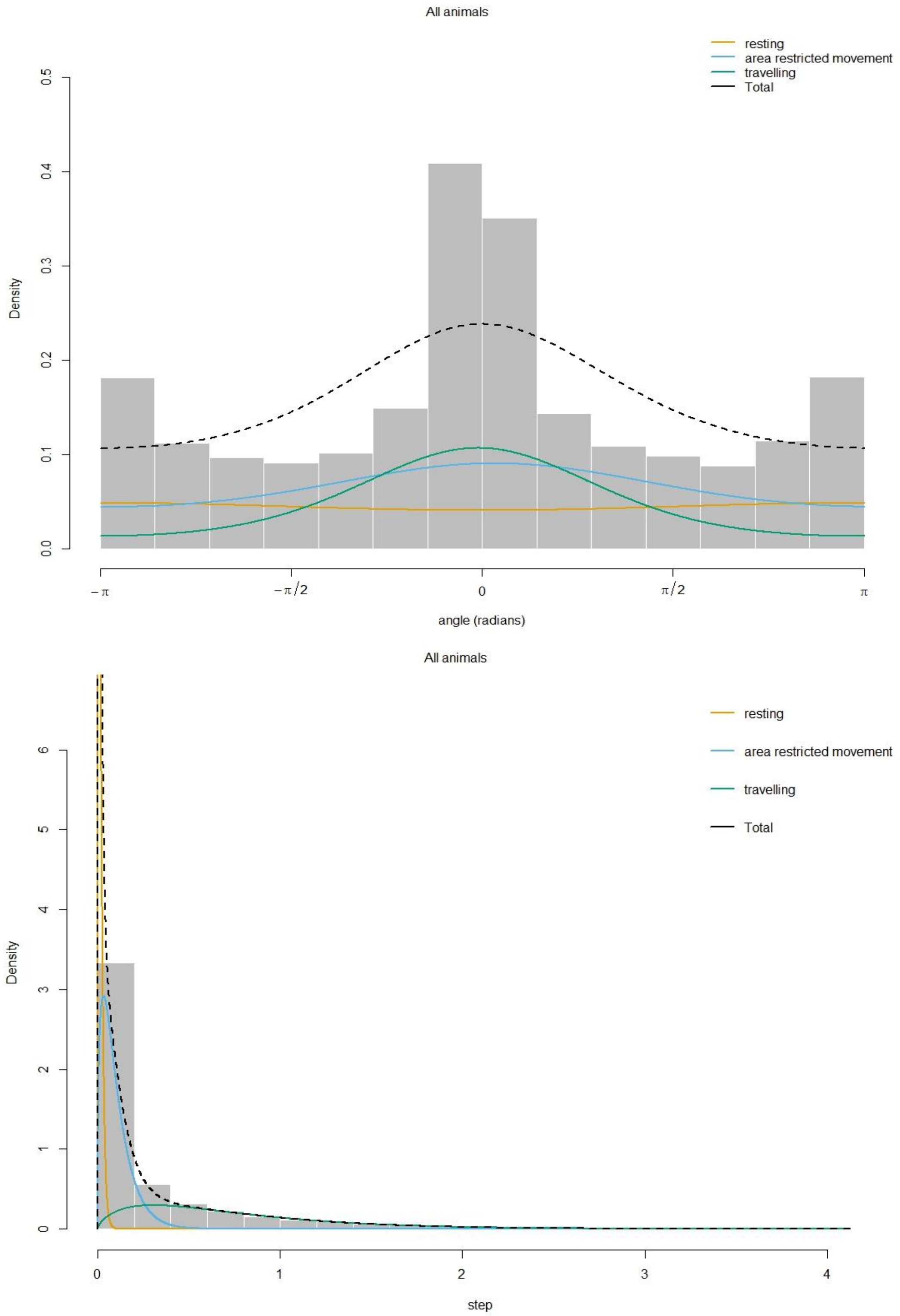


Figure 6.3: Histograms of observed step lengths and turning angles in a 3-state behaviour model during the pre-dispersal phase. The coloured lines are estimated densities of movement parameters in each state, and the dotted black line represents the sum of each parameter

Stationary state probability

The results indicated that tigers modulated their fine-scale behaviour in response to the time of day and temperature. The heterogeneity model with a mixture of k=3 was the best-fit model and three different state-switch patterns were observed (Figure 6.4). The effect of time of day on the state stationary probability remained the same across the three mixture groups. The area-restricted movement had the highest probability of occurring during the morning 9:00-10:00 h while travelling was most likely to occur in the early morning and late evening across all mixtures. The resting state had a low probability of occurrence and the trend was similar for all mixtures. The three-mixture model also supported the observation that ambient temperature strongly affected the stationary probability of tigers during the pre-dispersal phase (Figure 6.5). However, the effect of temperature on stationary state probability was prominent in mixtures 2 and 3. Individuals in these two mixtures had a higher probability of state-switching behaviour and were more likely to travel than rest with an increase in temperature. The probability of being in area-restricted movement peaks between 25-35 degrees and further decreases with an increase in temperature.

Transition probability

The transition probability matrix provides the probabilities of transitioning from one state to another, i.e. state-switching behaviour. The tigers' response to the time of day on the transition probability was similar across the three mixtures (Figure 6.6). When resting, the probability of shifting from resting to area-restricted movement peaked between 10:00-12:00 h and travelling early in the morning. The transition to resting remains low from area-restricted movement, while the travelling probability increases early in the morning and evening. Once in a travelling state, the transition probability to area-restricted movement peaks between 10:00-12:00 h during the day and shows a low transition for resting.

In contrast, the response of the transition probability to temperature varied among individual tigers when they were most active during the evening (Figure 6.7). The transition probability showed no clear trend in response to the temperature for mixture 1. For mixtures 2 and 3, the probability of switching from area-restricted movement to travelling increased with increasing temperature. In the travelling state, the most likely transition is to remain in the same state as the temperature increases.

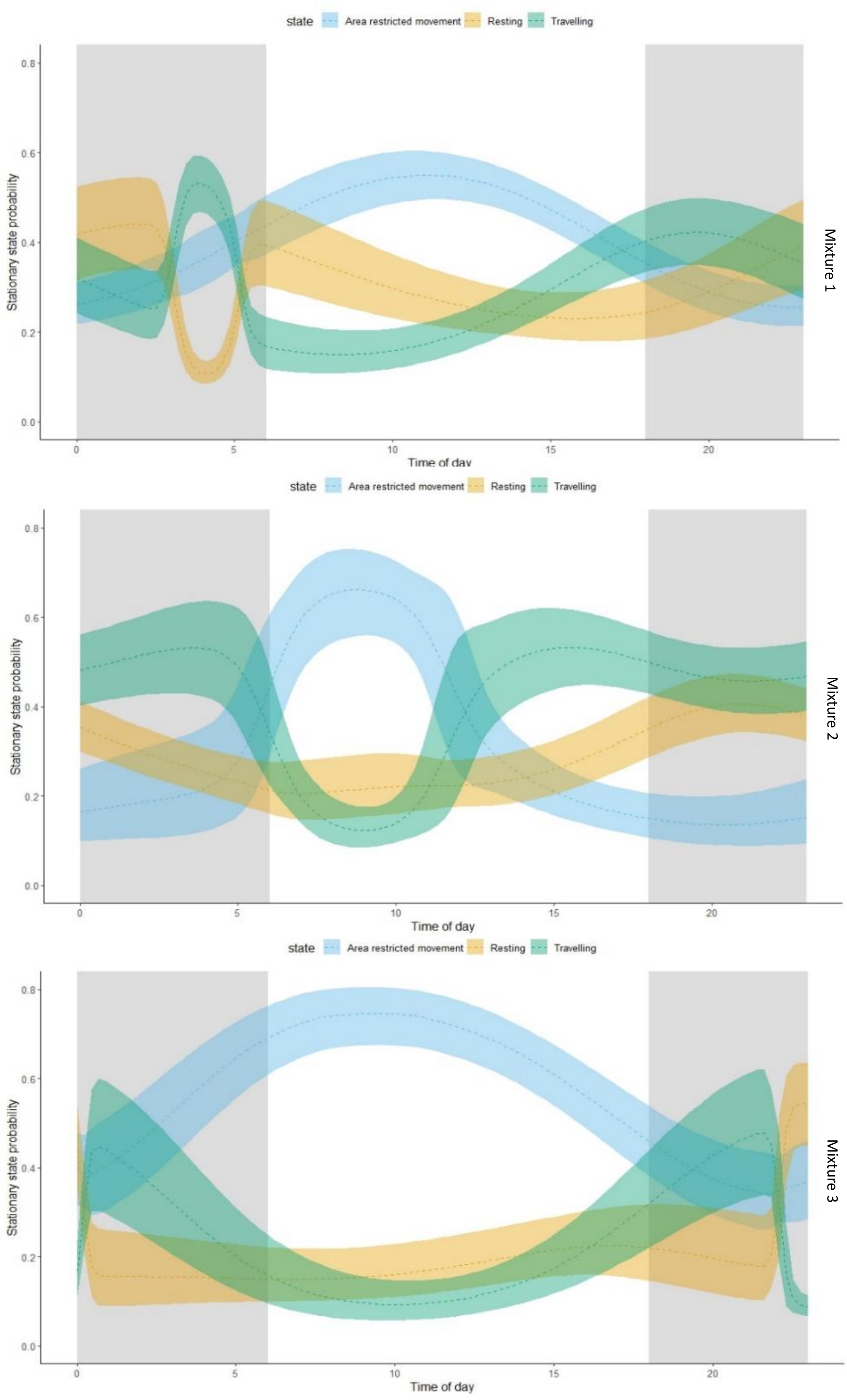
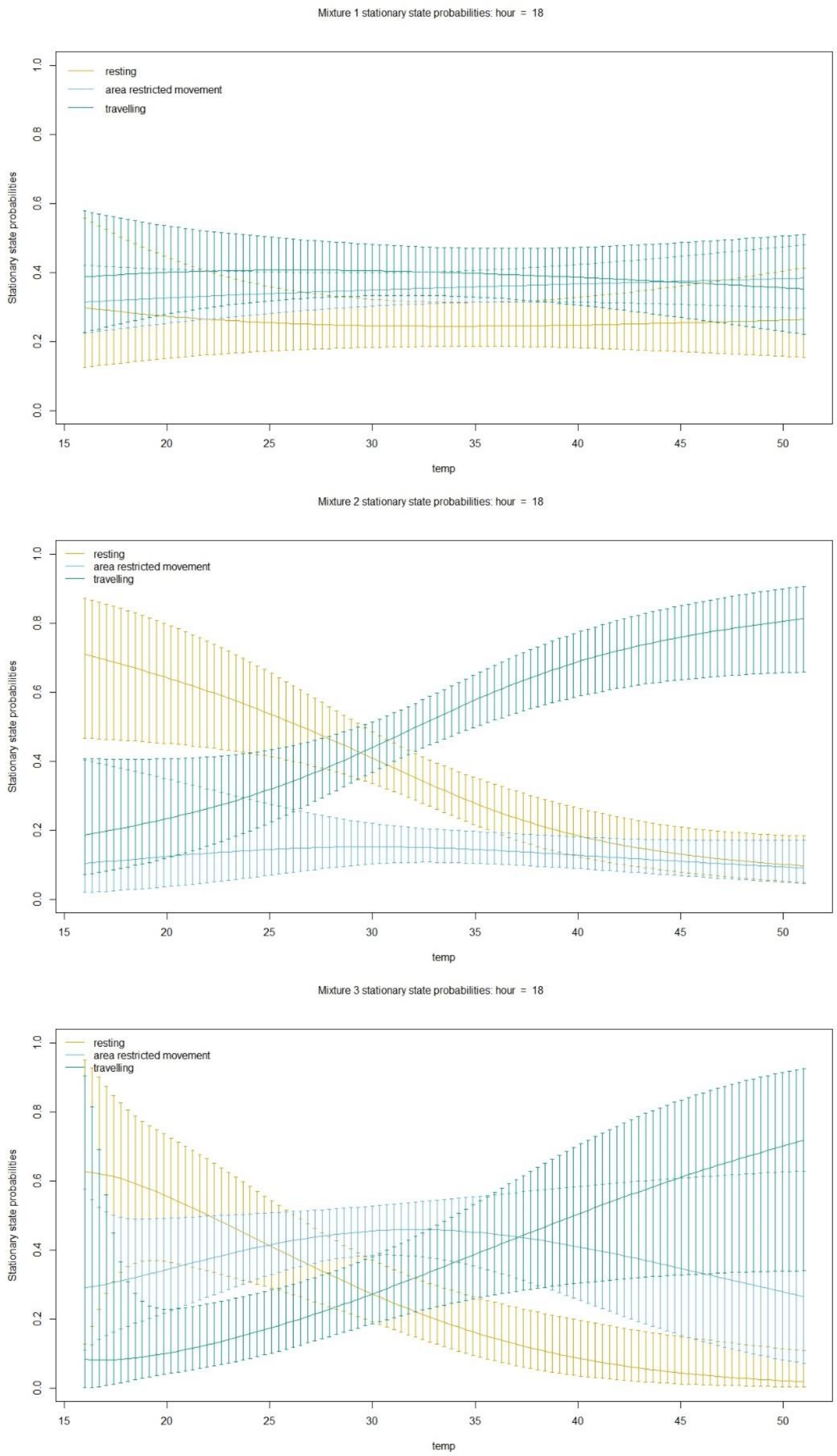


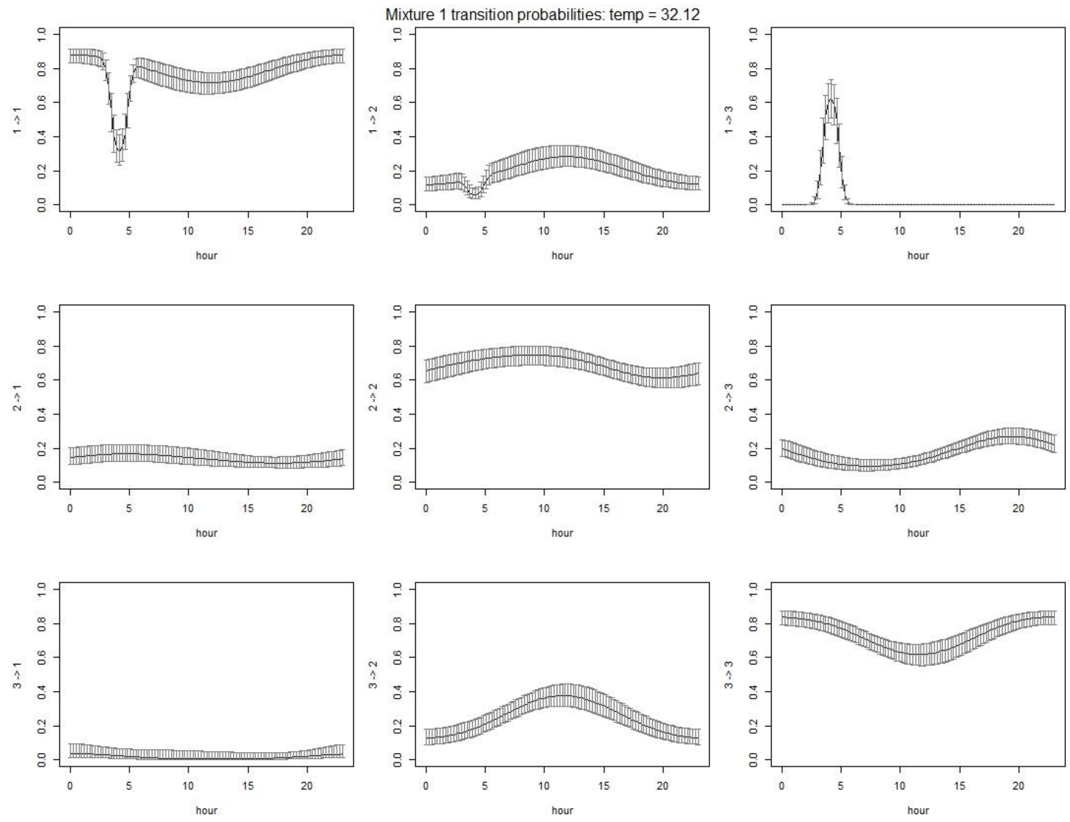
Figure 6.4: Effect of time of day (hour) on the stationary state probabilities (with 95% confidence intervals) during the pre-dispersal phase

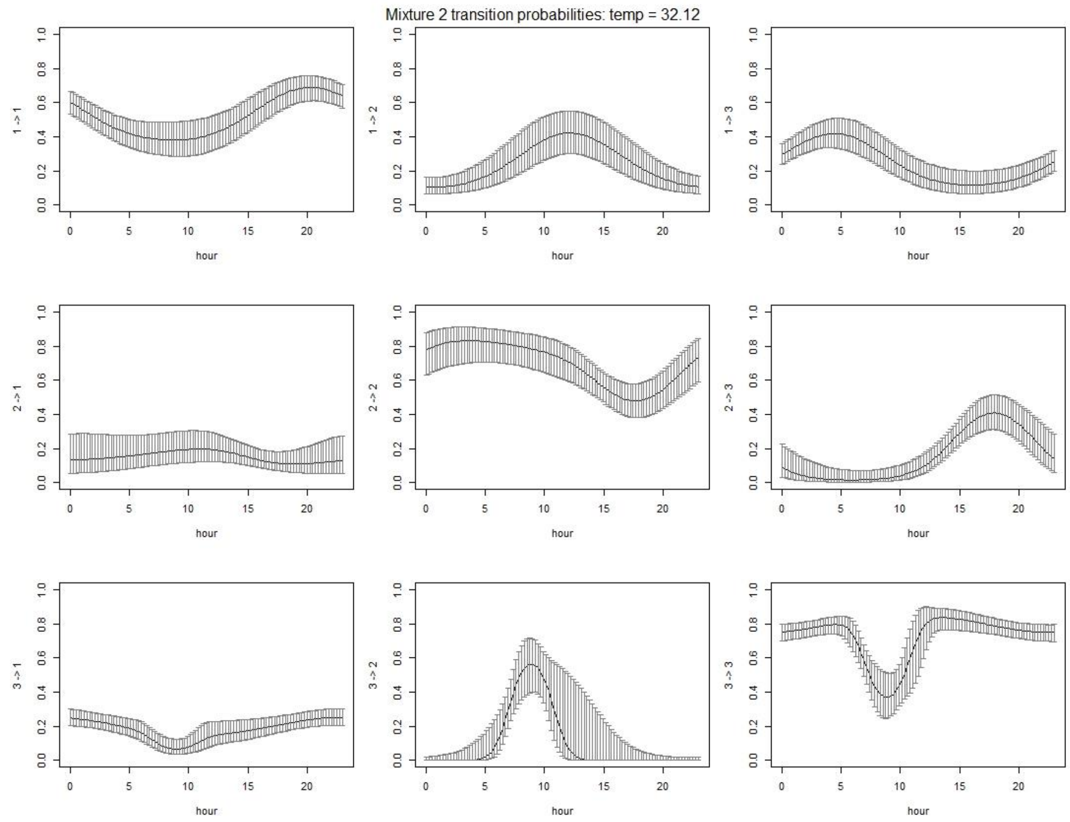

Mixture 1 stationary state probabilities: hour = 18

Mixture 2 stationary state probabilities: hour = 18

Mixture 3 stationary state probabilities: hour = 18

Figure 6.5: Effect of temperature on stationary probability probabilities (with 95% confidence intervals) during the pre-dispersal phase


Mixture 1 transition probabilities: temp = 32.12
1 -> 1
1 -> 2
1 -> 3
2 -> 1
2 -> 2
2 -> 3
3 -> 1
3 -> 2
3 -> 3
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
hour


Mixture 2 transition probabilities: temp = 32.12
1 -> 1
1 -> 2
1 -> 3
2 -> 1
2 -> 2
2 -> 3
3 -> 1
3 -> 2
3 -> 3
0.0
0.2
0.4
0.6
0.8
1.0
0
5
10
15
20
hour

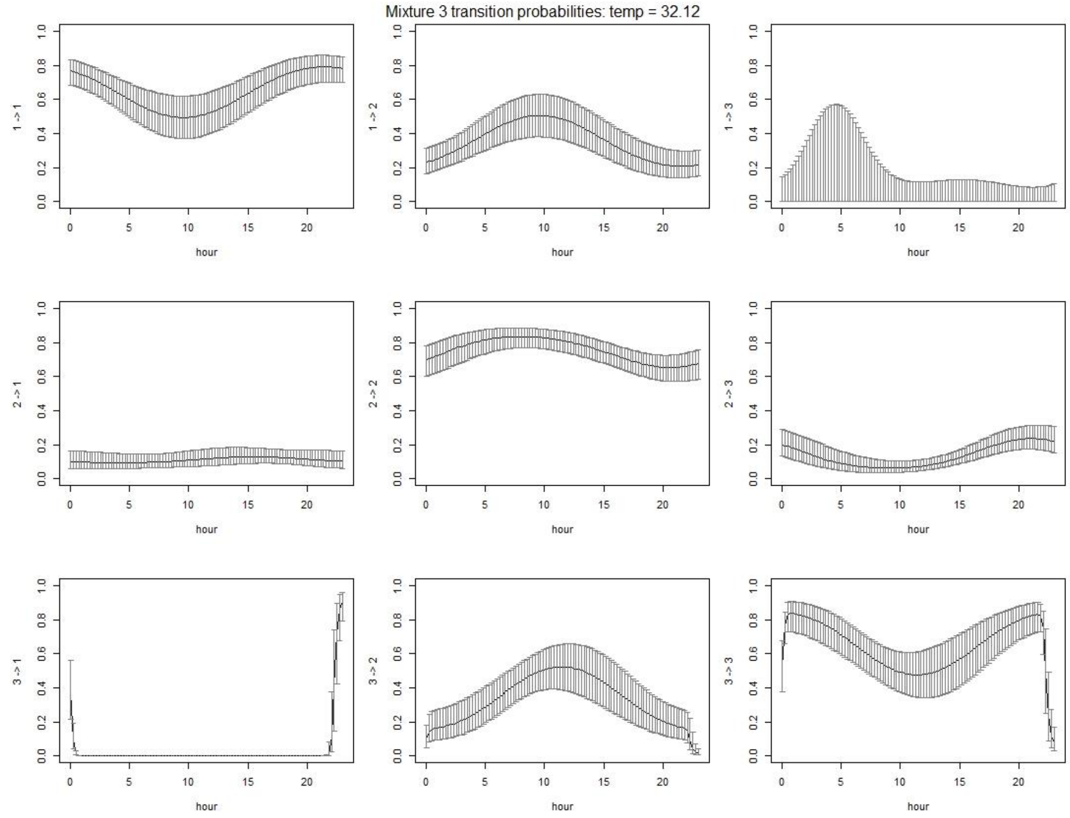
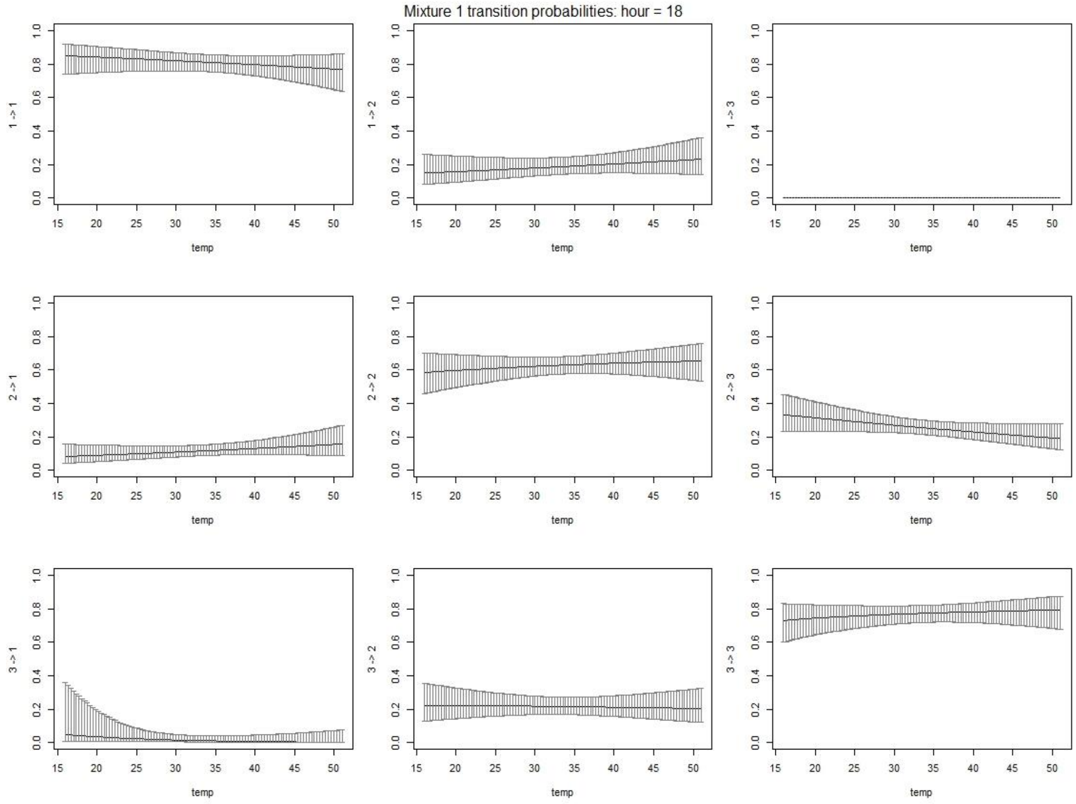
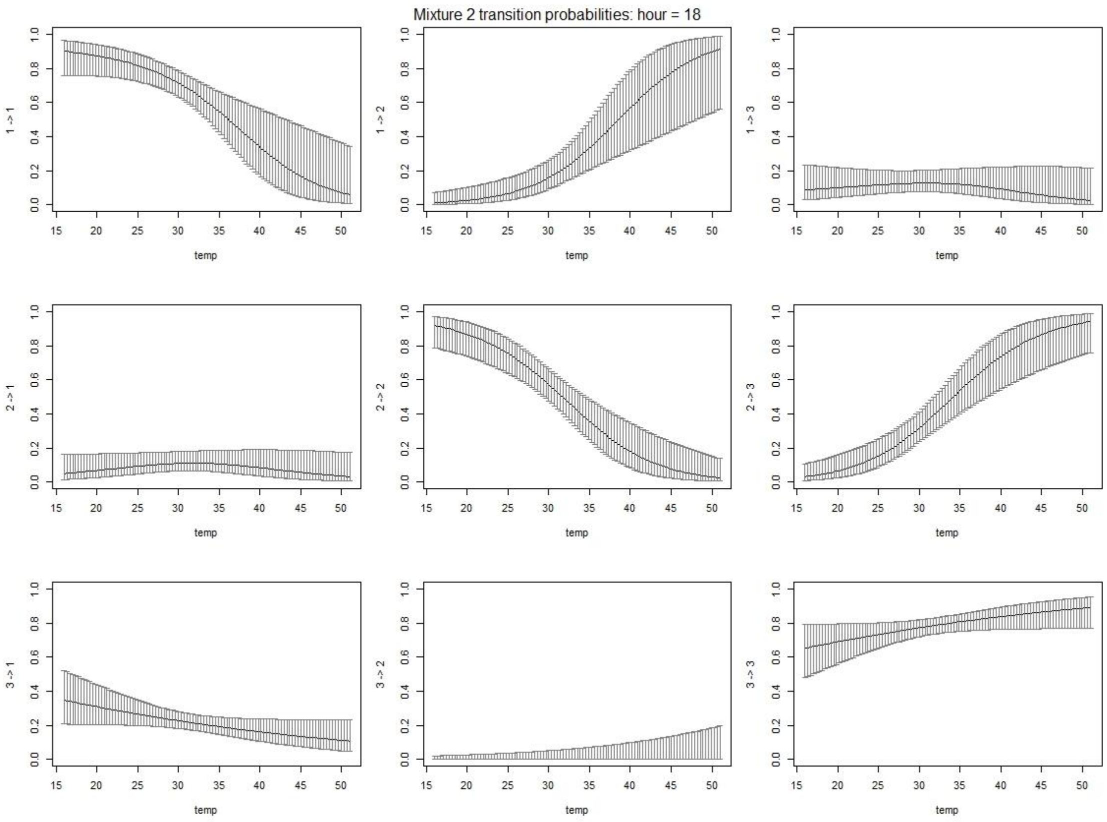


Figure 6.6: Effect of time of day (hour) on transition probability during the pre-dispersal phase





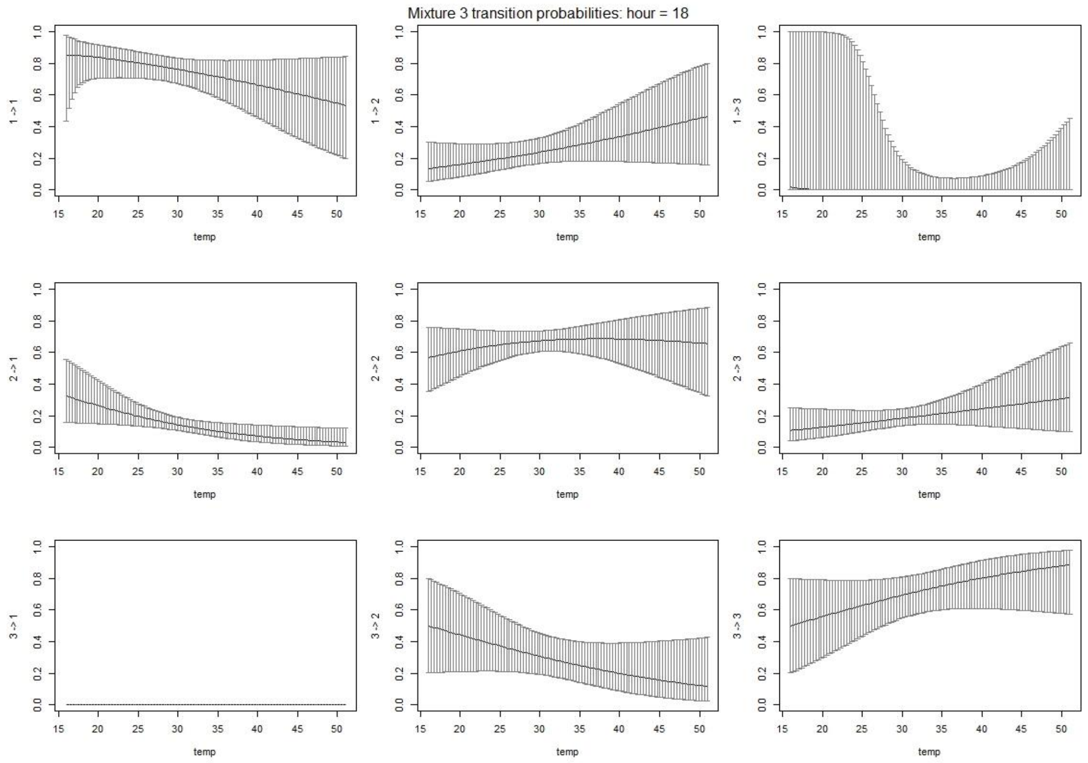


Figure 6.7: Effect of temperature on transition probability during the pre-dispersal phase

6.3.2 Dispersal phase

Data from six dispersing tigers (five males and one female) with 5400 GPS locations ranging from 19-162 days were analysed. State 1 (resting) corresponded to short step lengths (mean= 17.96 m) and variable turning angles (mean= 3.14; concentration= 0.16), indicating very slow and undirected movement. State 2 (area-restricted movement) had a moderate step length (mean= 229.63 m) and turning angle (mean= -0.13), suggesting that the movement was composed of tortuous movement within a small area. In comparison, state 3 (travelling) had longer step lengths (mean= 1404.39 m) and turning angle (mean= 0.02; concentration= 1.79), indicating movement to be faster with high directional persistence (Figure 6.8). Of the total activity budget, about 33.20% of time activity was classified as resting, 35.06% as area-restricted movement, and 31.72% as travelling. The generalised HMM was best explained by the time of day in the stationary state probability and transition probability matrix. Additionally, the movement characteristics (step length) within behavioural states (i.e. state-dependent parameter distributions) depended on the habitat (forest and non-forest) in the landscape.

Table 6.4: Parameter estimates of step length, turning angle, directionality, and temporal budget of the 3-state behavioural models for dispersing tigers (n =6). The step lengths are modelled with gamma, and the turning angle with von Misses distribution based on the 2-h dataset for dispersing tigers

Parameters	Resting	Area Restricted Movement	Travelling
Mean step length (m)	17.96	229.63	1404.39
Mean step length SD (m)	15.45	20.74	922.89
Mean angle	3.12	-0.13	0.02
Concentration	0.16	0.27	1.79
Proportion in each state (%)	33.20	35.06	31.72

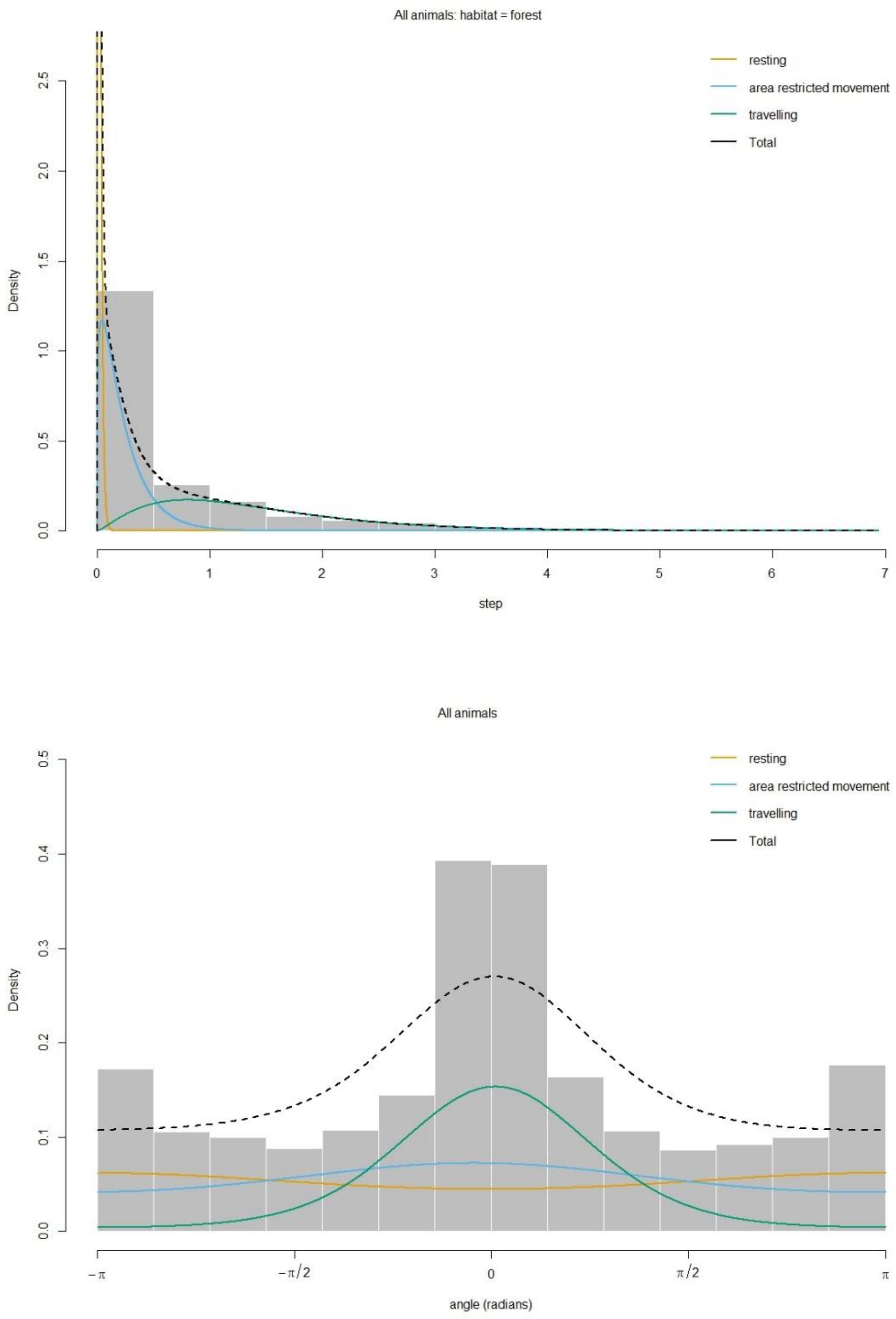


Figure 6.8: Histograms of observed step lengths and turning angles in a 3-state behaviour model of dispersing tigers. The coloured lines are estimated densities of movement parameters in each state, and the dotted black line represents the sum of each parameter

State-dependent distribution parameter (step length)

The movement parameter, i.e., step length in the 3-state HMM, differed between forest and non-forest (Figure 6.9). In the resting state, step length (mean= 18 m) was higher in the forest. Mean step length was higher in non-forested habitats during area-restricted movement than in forested habitats. Similarly, dispersing tigers in the travelling state moved longer in non-forested habitats (mean= 2400 m).

Stationary state probability

The stationary probability of dispersing tigers showed distinct individual variation in behaviour with time of day. The heterogeneity model with mixture k=3 was the best-fit model, and three different stationary-state patterns were observed (Figure 6.10). The relative role of time of day on the resting and area-restricted movement probability remains the same in the three mixtures and varies in the travelling state. A higher probability of area-restricted movement occurred during the late morning, reaching a maximum during 9:00-10:00 h, while the opposite was observed for the resting state. Individuals in mixtures 1 and 2 tended to travel more during dusk and the late evening, while mixture 3 had a lower probability.

Transition probability

When resting, the highest probability was to remain resting, with a low probability of shifting from resting to area-restricted movement for all mixtures (Figure 6.11). The most likely transition from area-restricted movement is to remain in the same state, followed by the resting state, and peaks between morning and mid-day. The travelling state was maximum from evening to midnight and showed a low transition probability to area-restricted movement and resting, respectively.

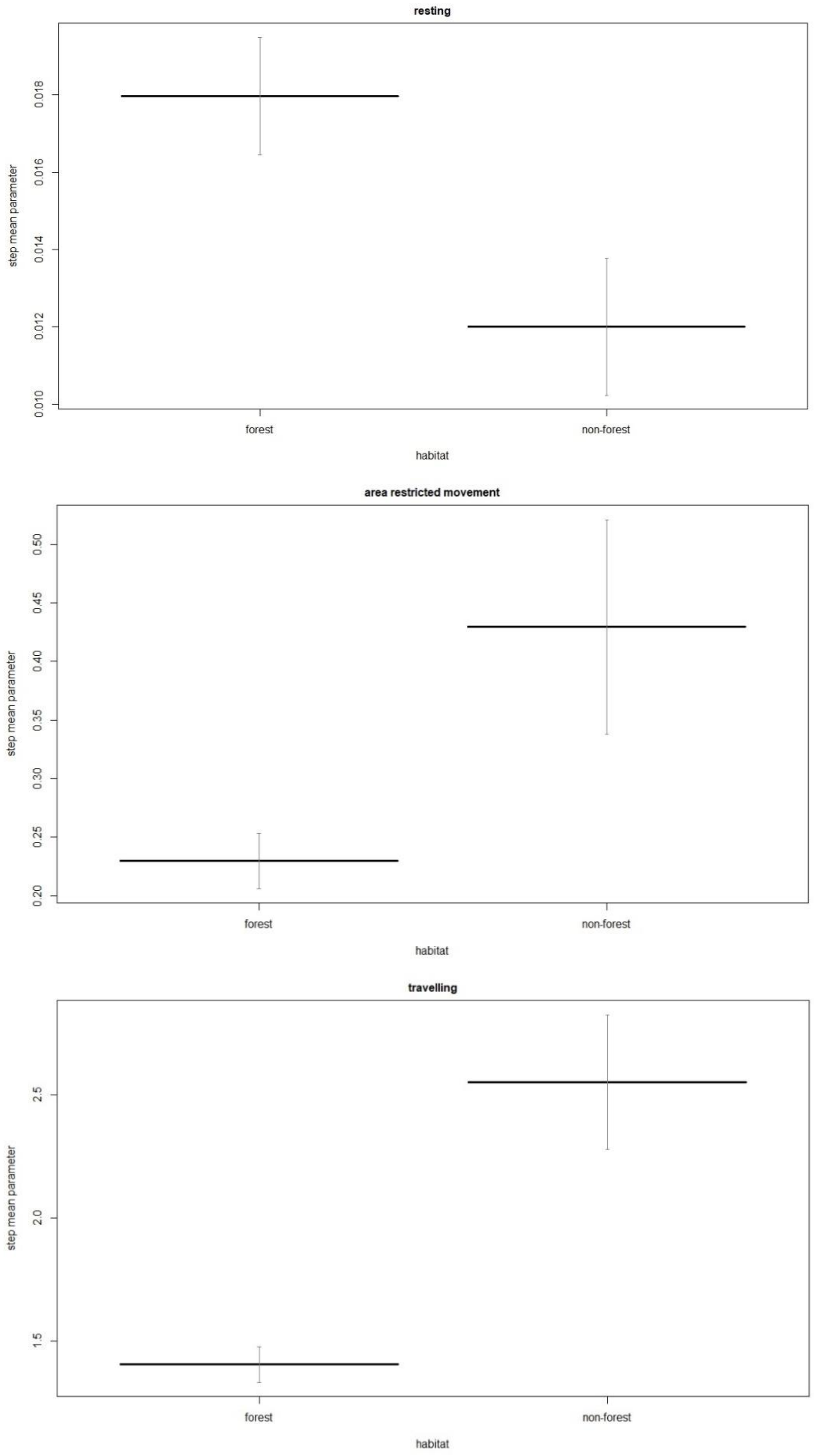


Figure 6.9: Effect of habitat on movement (step length) during the dispersal phase

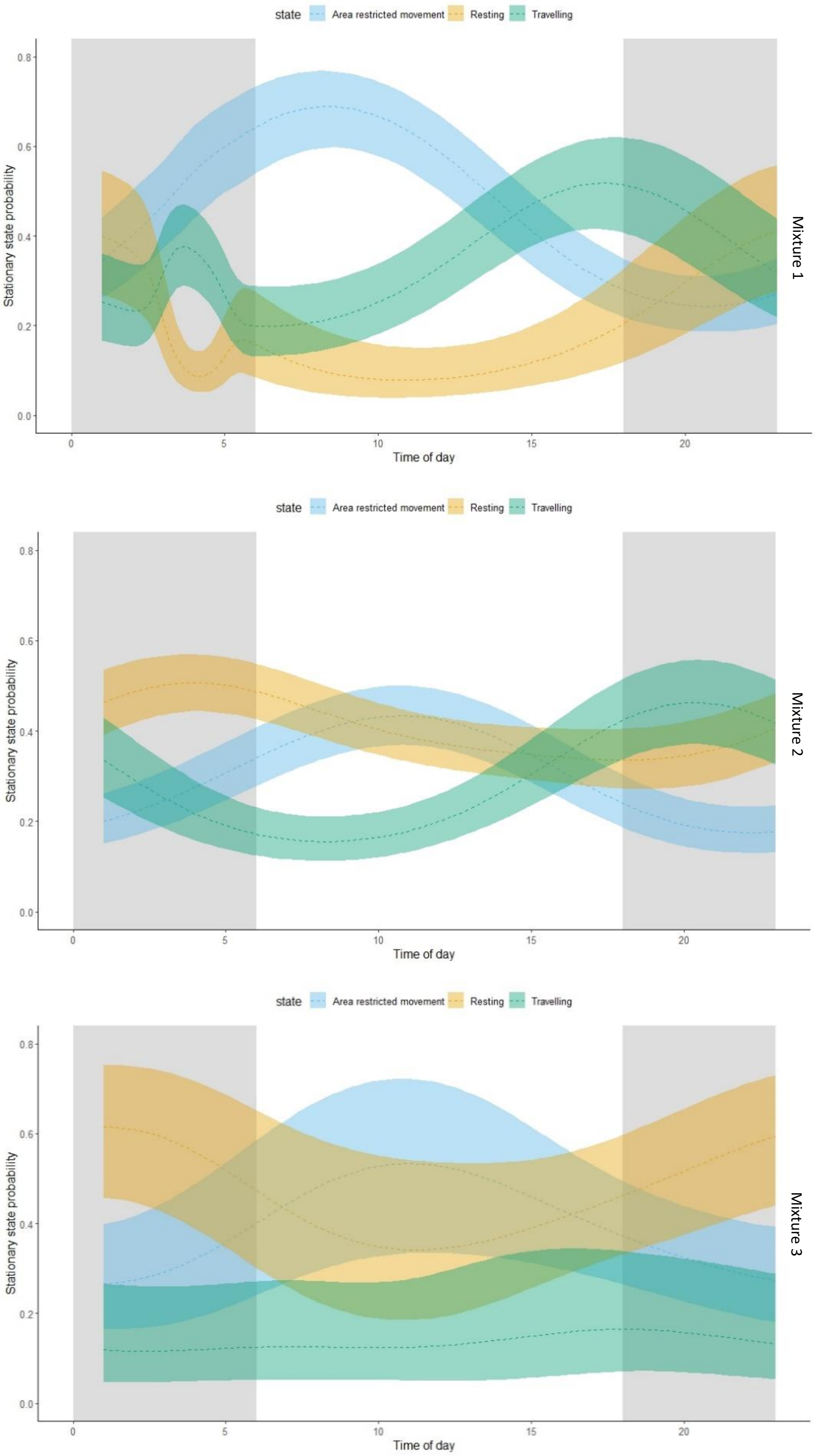
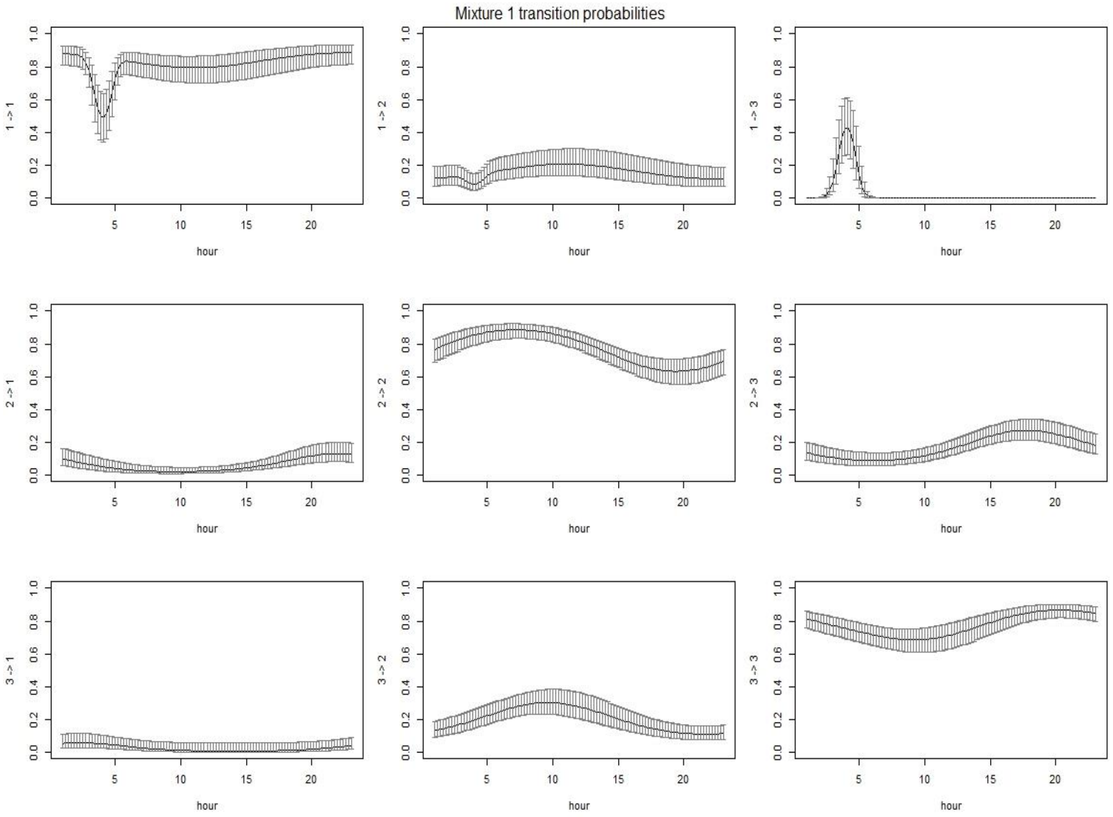
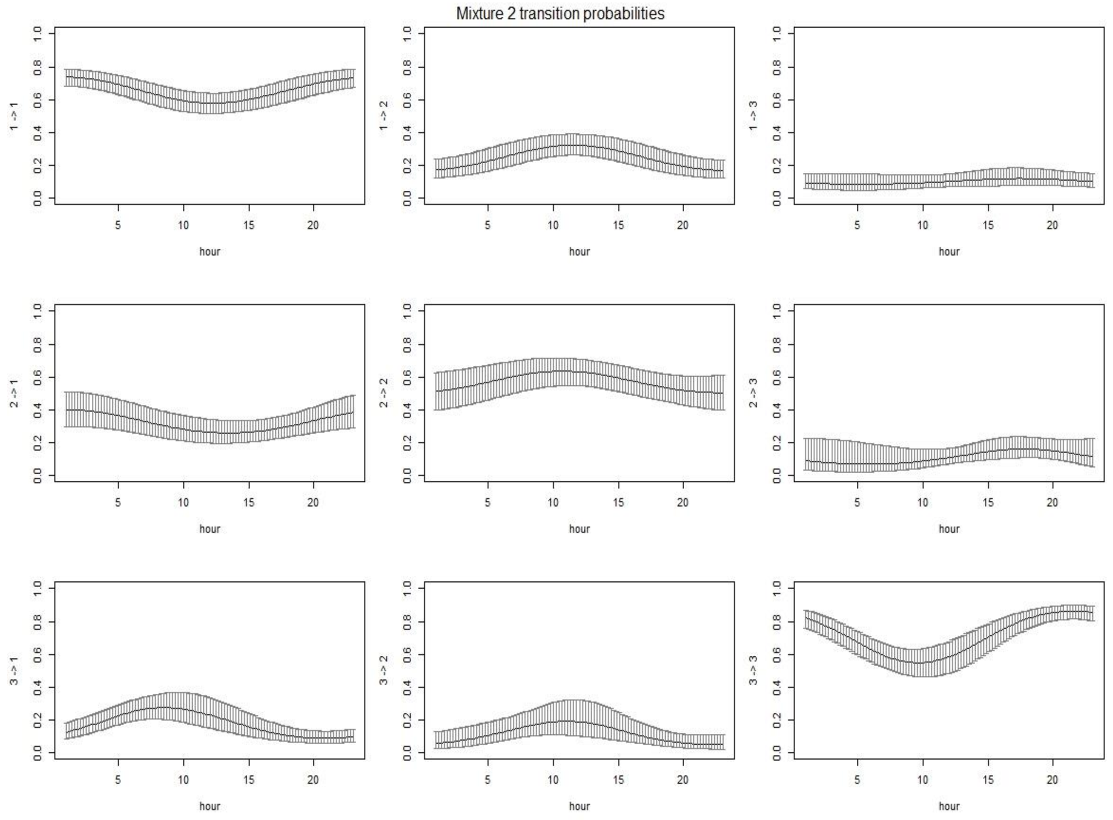


Figure 6.10: Effect of time of day (hour) on stationary probability (with 95% confidence intervals) during the dispersal phase


Mixture 1 transition probabilities
1 -> 1
1 -> 2
1 -> 3
2 -> 1
2 -> 2
2 -> 3
3 -> 1
3 -> 2
3 -> 3
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
hour


Mixture 2 transition probabilities
1 -> 1
1 -> 2
1 -> 3
2 -> 1
2 -> 2
2 -> 3
3 -> 1
3 -> 2
3 -> 3
0.0
0.2
0.4
0.6
0.8
1.0
5
10
15
20
hour

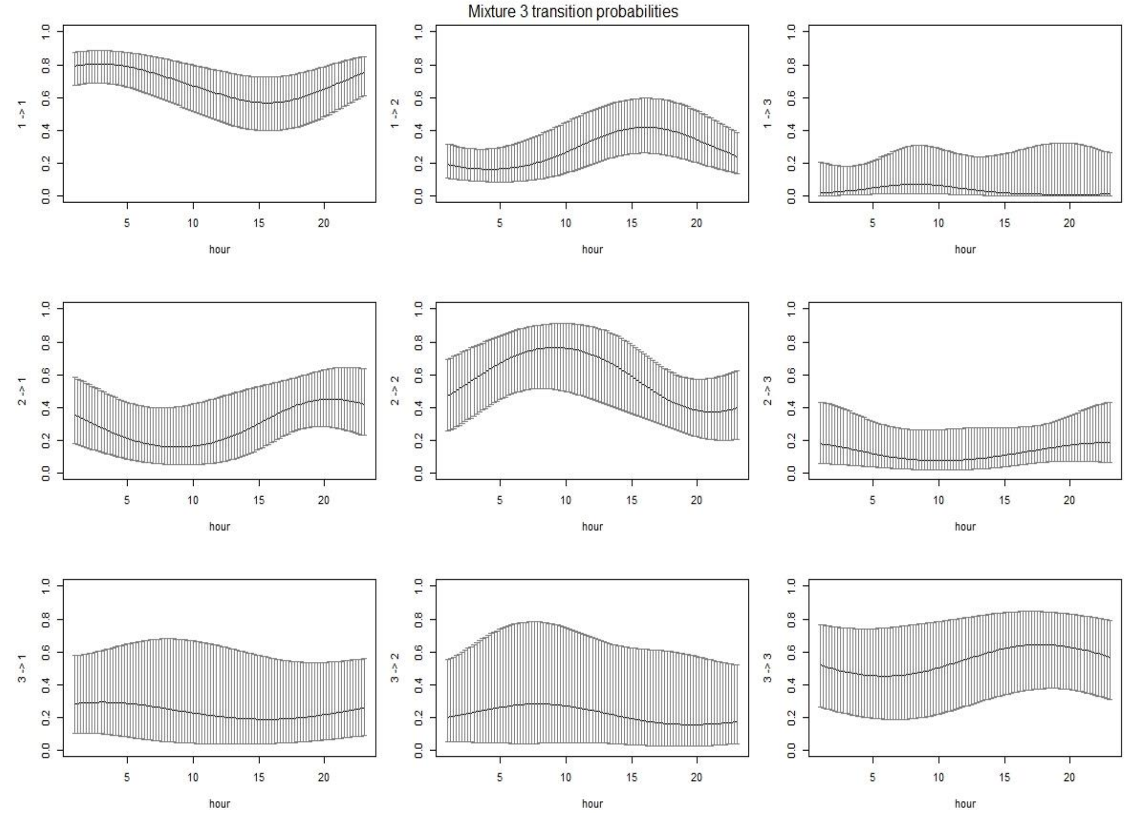


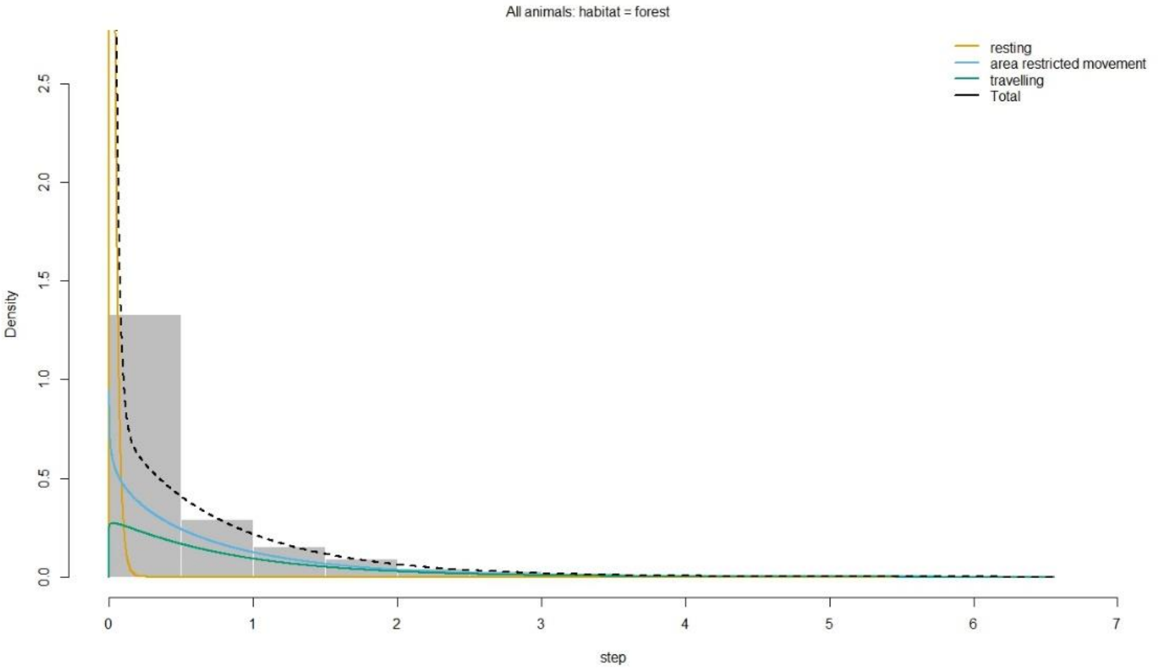
Figure 6.11: Effect of time of day (hour) on transition probability during the dispersal phase

6.3.3 Post-dispersal phase

The post-dispersal phase for HMM included seven individuals (five males and two females), with a fixed interval of 2-h. I used data from collared individuals ranging from 84-305 days per individual and 8980 GPS locations for male and female tigers in the landscape. State 1 (resting) had short step lengths (mean= 26.18 m) and variable turning angles (mean= 3.13; concentration= 0.09; Figure 6.12). State 2 (area-restricted movement) exhibited high step lengths (mean= 754.52 m) and turning angles (mean= 3.12), suggesting longer distances with directional persistence. State 3 (travelling) showed minimal variation from state 2 with a mean step length of 836.16 m and a strong sense of direction (mean= -0.004). Of the total activity budget, about 37.31% of time activity was classified as resting, 37.71% as area-restricted movement, and 24.97% as travelling. The time of day and habitat (forest and non-forest) influenced the stationary state probability and transition probability. Moreover, the habitat influenced the state-dependent movement parameters (step length and angle) in the 3-state model.

Table 6.5: Parameter estimates of step length, turning angle, directionality, and temporal budget of the 3-state behavioural models for tigers during the post-dispersal phase (n =7). The step lengths are modelled with gamma, and the turning angle with von Misses distribution based on the 2-h dataset for dispersing tigers

Parameters	**Resting**	**Area Restricted Movement**	**Travelling**
Mean step length (m)	26.18	754.52	836.16
Mean step length SD (m)	25.04	803.27	823.36
Mean angle	3.13	3.12	-0.004
Concentration	0.09	0.00	35.01
Proportion in each state (%)	37.31	37.71	24.97



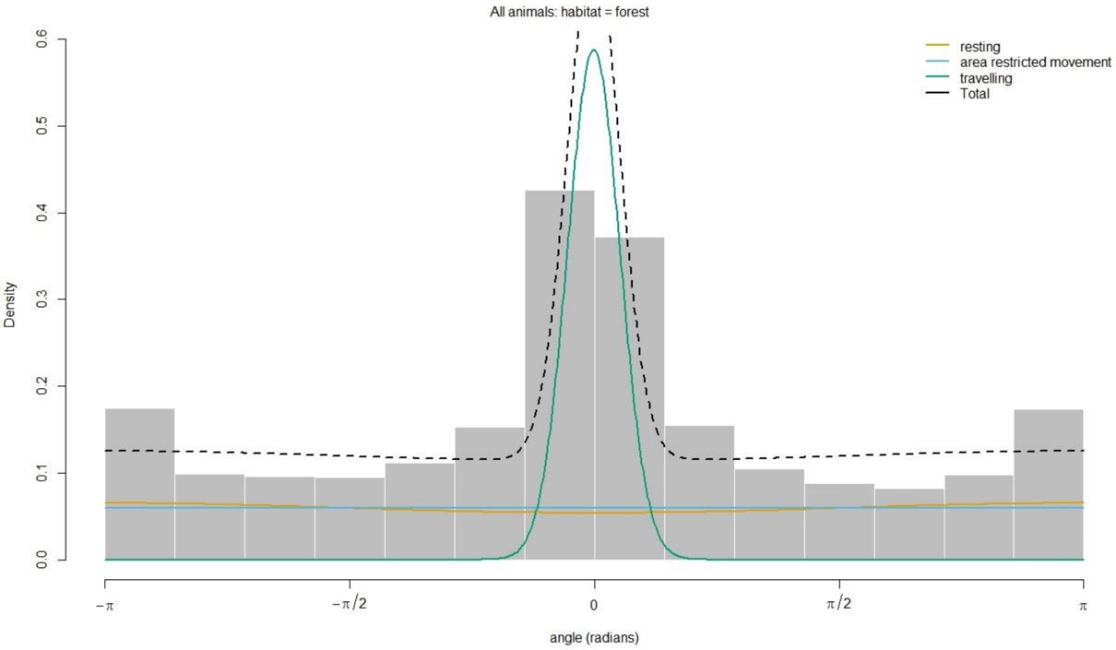


Figure 6.12: Histograms of observed step lengths and turning angles in a 3-state behaviour model during the post-dispersal phase. The coloured lines are estimated densities of movement parameters in each state, and the dotted black line represents the sum of each parameter

State-dependent distribution parameters (step length and turn angle)

In the resting state, the mean step length between the forest and non-forest did not differ significantly (Figure 6.13). During area-restricted movement, step length was greater in forested habitats (mean= 750 m). In the travelling state, the mean step length (2000 m) in the non-forested habitat was twice that in the forest habitat. The mean step length between area-restricted movement (750 m) and the travelling state (800 m) in the forest habitat was similar. However, the mean step length in the non-forest varied significantly between the area-restricted movement (400 m) and the travelling state (2000 m). Directional persistence also varied across the 3-states. The resting state differed in angle concentrations between the forest and non-forest habitats. There was no general directionality pattern in state 2 (area-restricted movement) among habitats. During the travelling state, tigers increased their directional persistence in response to habitat, with more directed or forward movement in forested habitats.

Stationary state probability

The stationary probability showed a distinct individual variation in behavioural states with habitat and time of day across the mixtures (Figure 6.14). In mixture 1, tigers in forest habitats showed the highest probability of area-restricted movement, followed by the travelling state. In contrast, the opposite was observed in non-forest habitats, with a higher persistence of travel. Individuals in mixture 2 responded similarly to forest and non-forest conditions, with resting being the highest probability state, followed by area-restricted movement and travelling. Moreover, the travelling probability in non-forest habitats was higher than that in forest habitats. In mixture 3, there was a higher probability of travelling than area-restricted movement in the forest. In contrast, in the non-forest area, area-restricted movement had the highest stationary probability.

The response of time of day to stationary state probability varied across individuals (Figure 6.15). Mixtures 1 and 3 responded similarly to the time of day, where area-restricted movement increased at dawn and dusk. The resting state was dominant throughout the day and decreased in the evening. The responses of individuals varied in mixture 2, with resting having the highest stationary probability and maximum at midnight. The area-restricted movement had a maximum probability between 10-15 h during the day. The travelling probability was low for all mixtures, with a peak in the evening.

Transition probability

The model predicted individual variations in state-switching behaviour with respect to habitat (Figure 6.16). Tigers differ in response to forests and non-forests, and are specific to the local context. The probability of remaining in the same resting state was high in non-forest habitats (mixtures 1 and 3), whereas individuals in mixture 2 tended to live in forest habitats. The transition from the resting state to area-restricted movement was only observed in mixture 1 in the forest habitat. The probability of remaining area-restricted was maximum in the forest for mixture 2, and non-forest for individuals in mixtures 1 and 3. The transition from area-restricted movement to travelling was highest in the forest (mixtures 1 and 3) and vice-versa for individuals in mixture 2. The travelling state showed the highest probability of travelling in non-forest areas across all mixtures. The second-highest transition probability from travelling to area-restricted movement was observed in the forest. The probability of transition from travel to rest was observed in the forest habitat.

The transition probability also varied with the time of day and among the individuals (Figure 6.17). The probability of switching from resting to area-restricted movement increased for all mixtures between 10-15 h. The transition probability showed no clear trends in response to the time of day for mixtures 1 and 2 for area-restricted movement and travel. For mixture 3, the most likely transition from area-restricted movement is to remain in the same state and show high nocturnal activity. The probability of switching from area-restricted movement to travelling increases during–15-20 h and eventually decreases. During the travelling state, the most likely transition is the area-restricted movement, with a maximum transition probability at night. The transition from the travelling state to resting state increased during the day and peaked at 10 h.

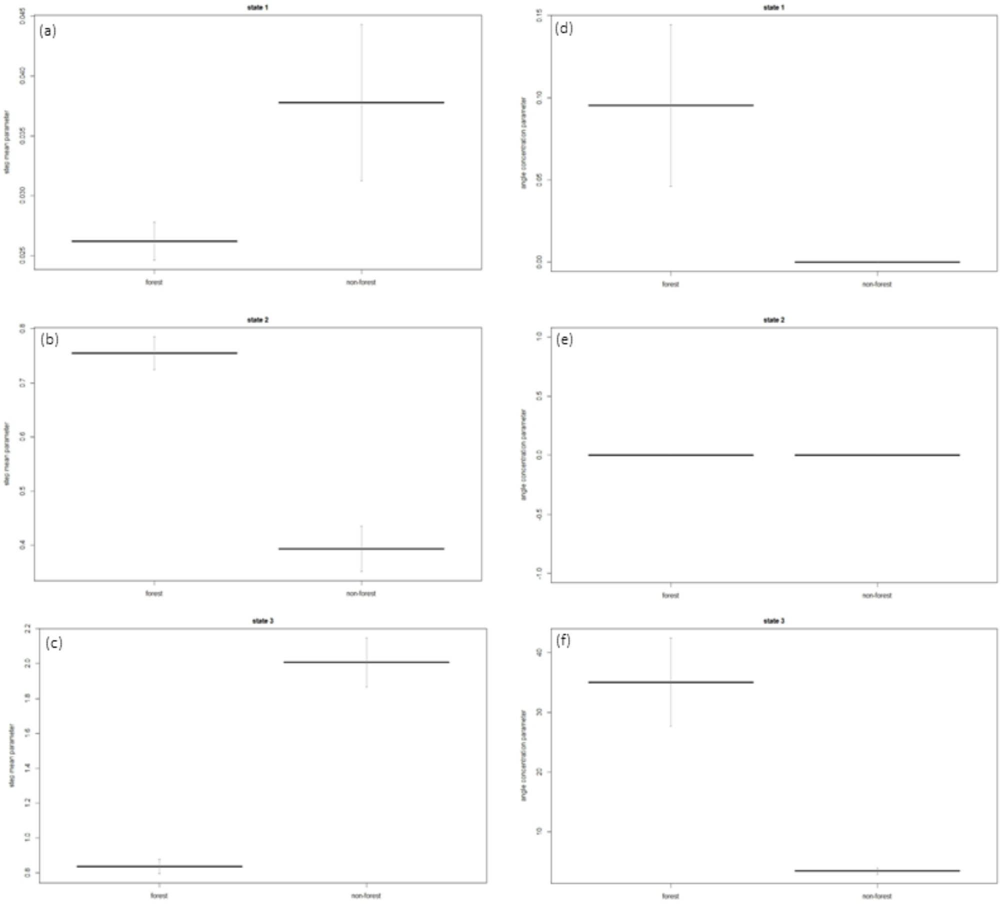
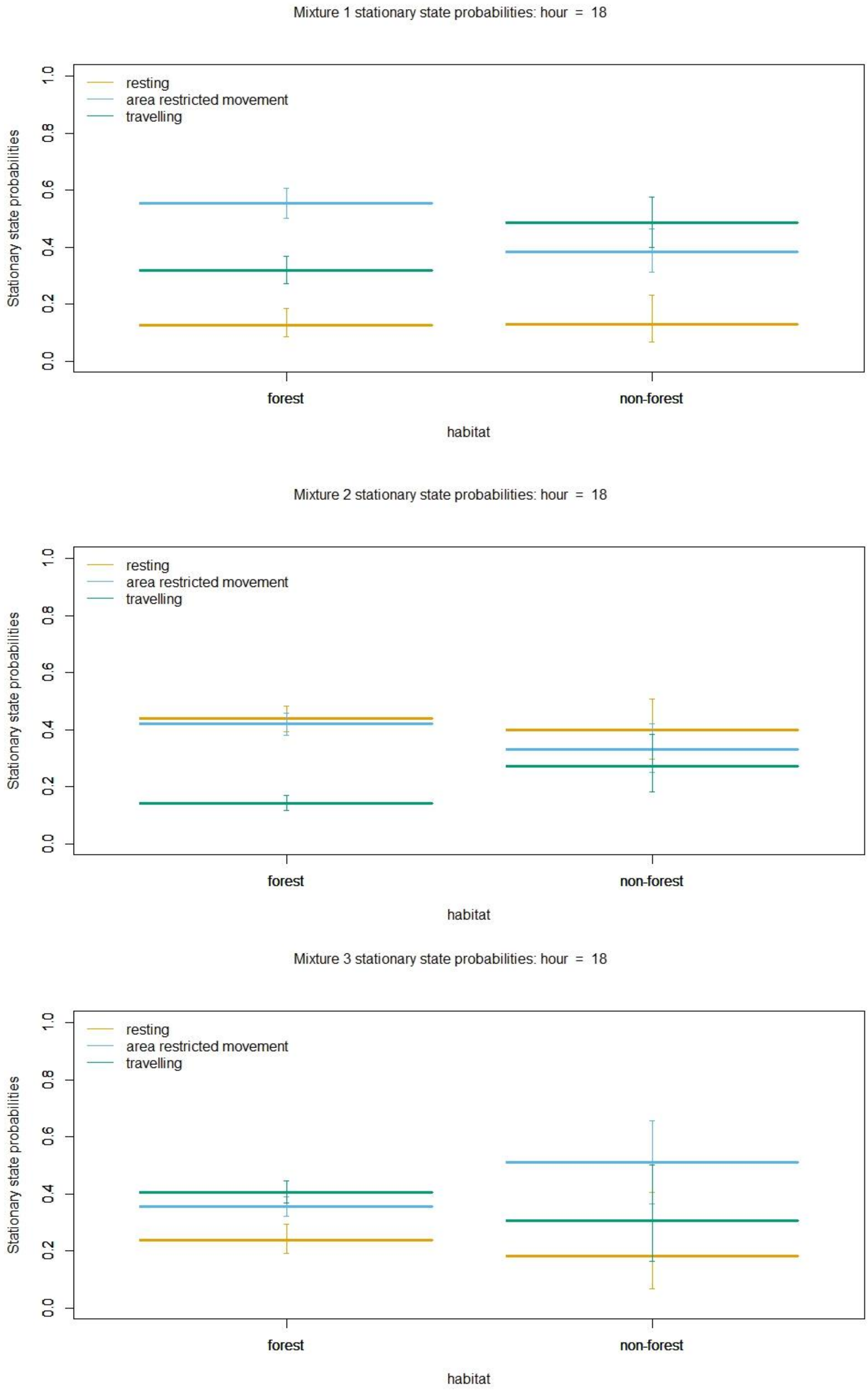


Figure 6.13: Effect of habitat on step length (a-c) and angle/directional persistence (d-f) across three behavioural states during the post-dispersal phase



Mixture 1 stationary state probabilities: hour = 18

Mixture 2 stationary state probabilities: hour = 18

Mixture 3 stationary state probabilities: hour = 18

Figure 6.14: Effect of habitat on stationary probability during the post-dispersal phase

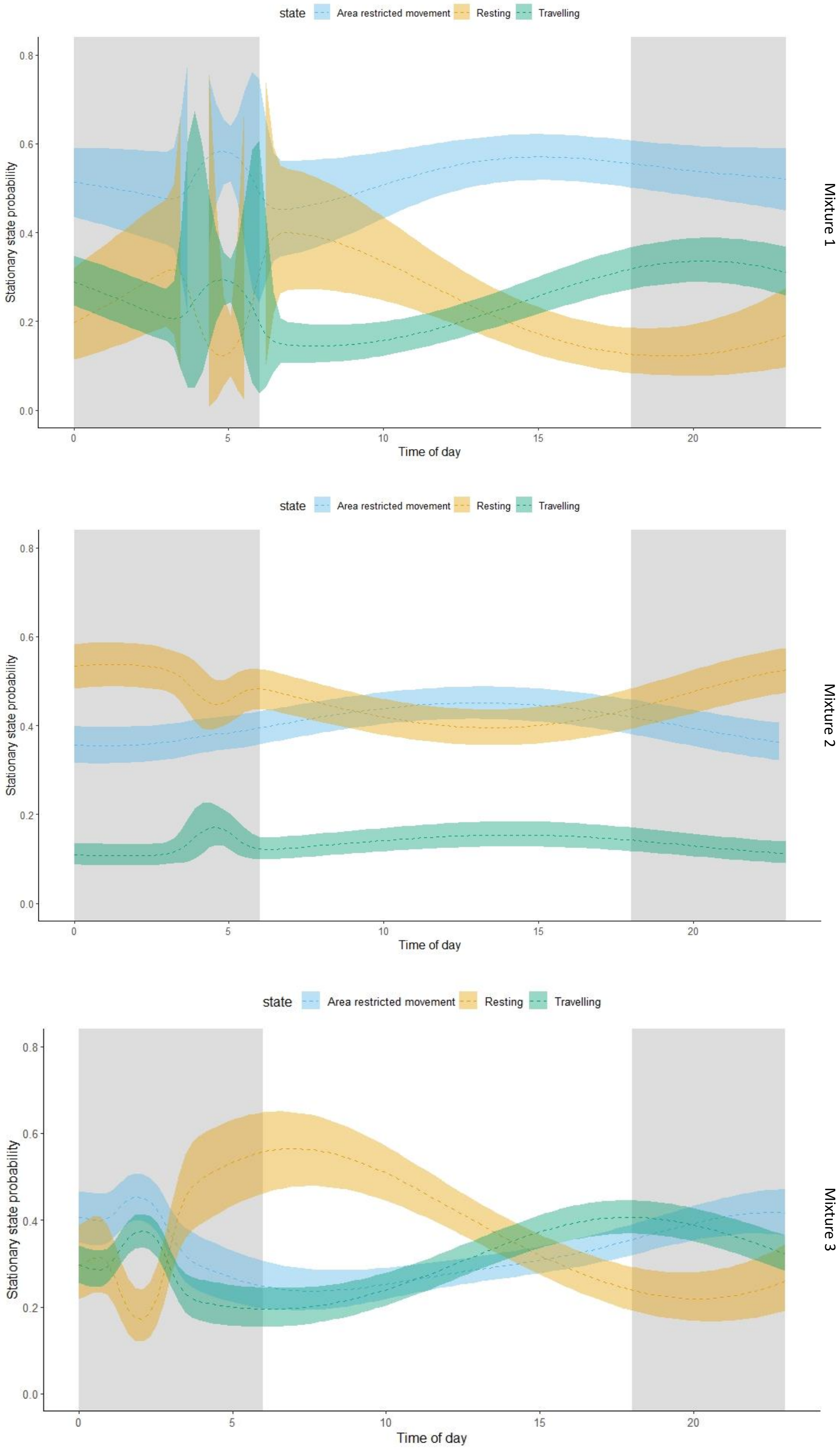
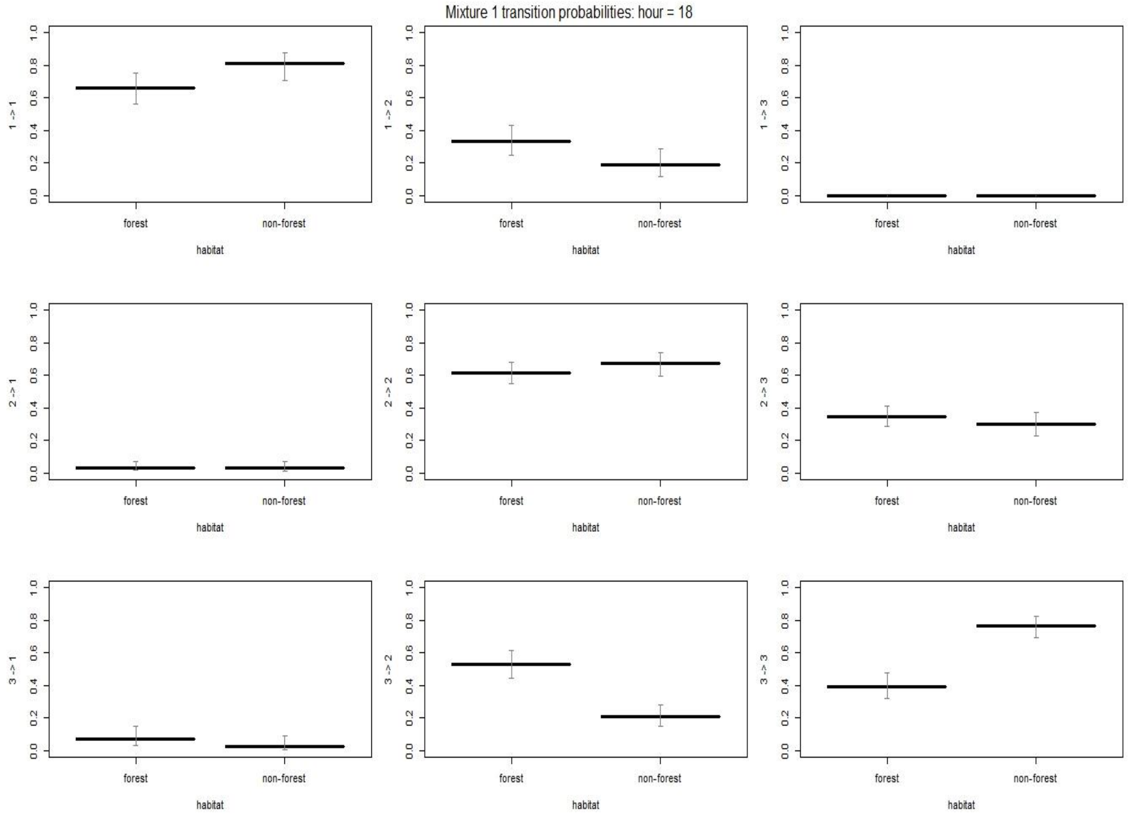
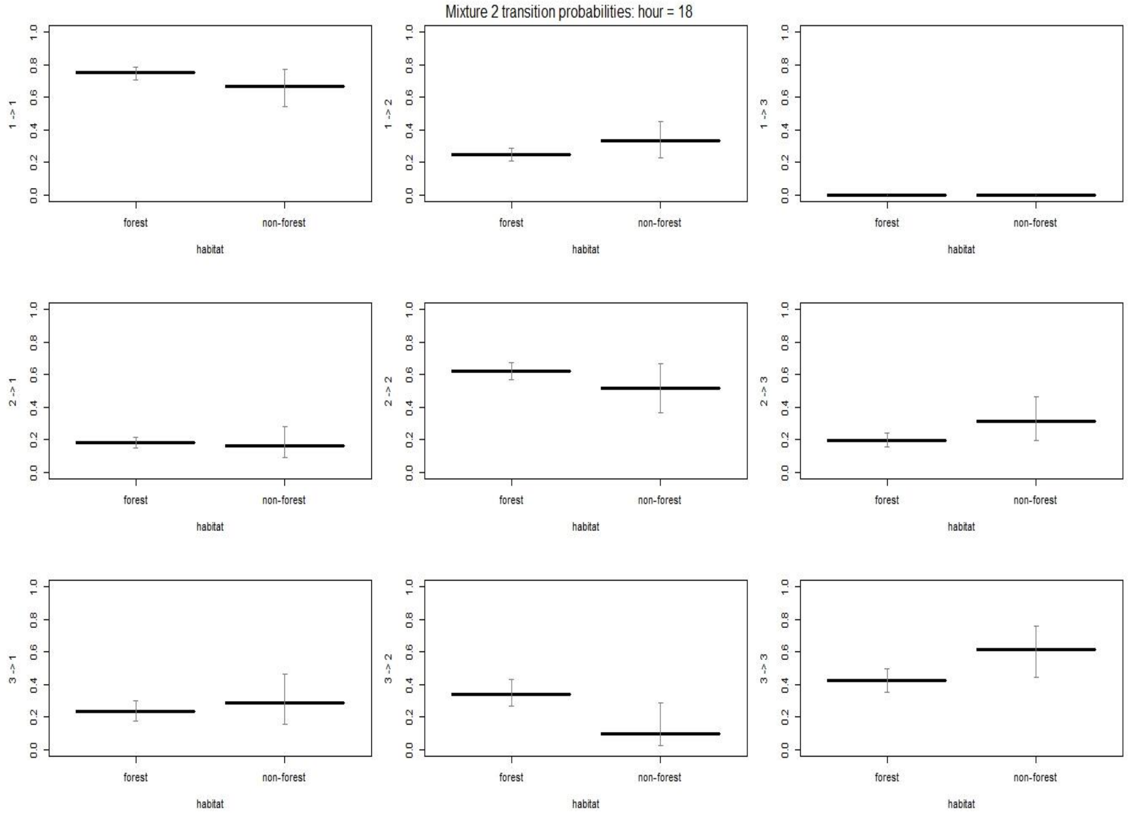


Figure 6.15: Effect of time of day (hour) on stationary probability during the post-dispersal phase


Mixture 1 transition probabilities: hour = 18
1 -> 1
1 -> 2
1 -> 3
2 -> 1
2 -> 2
2 -> 3
3 -> 1
3 -> 2
3 -> 3
0.0
0.2
0.4
0.6
0.8
1.0
forest
non-forest
habitat


Mixture 2 transition probabilities: hour = 18
1 -> 1
1 -> 2
1 -> 3
2 -> 1
2 -> 2
2 -> 3
3 -> 1
3 -> 2
3 -> 3
0.0
0.2
0.4
0.6
0.8
1.0
forest
non-forest
habitat

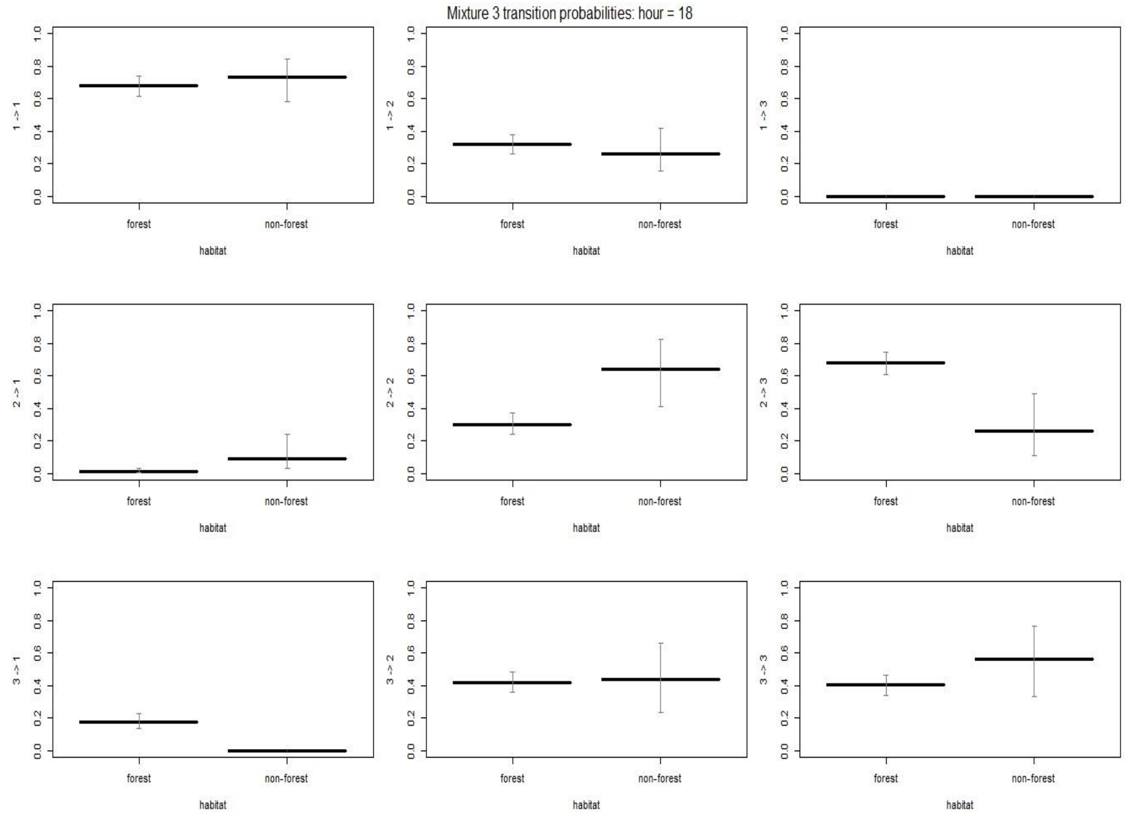
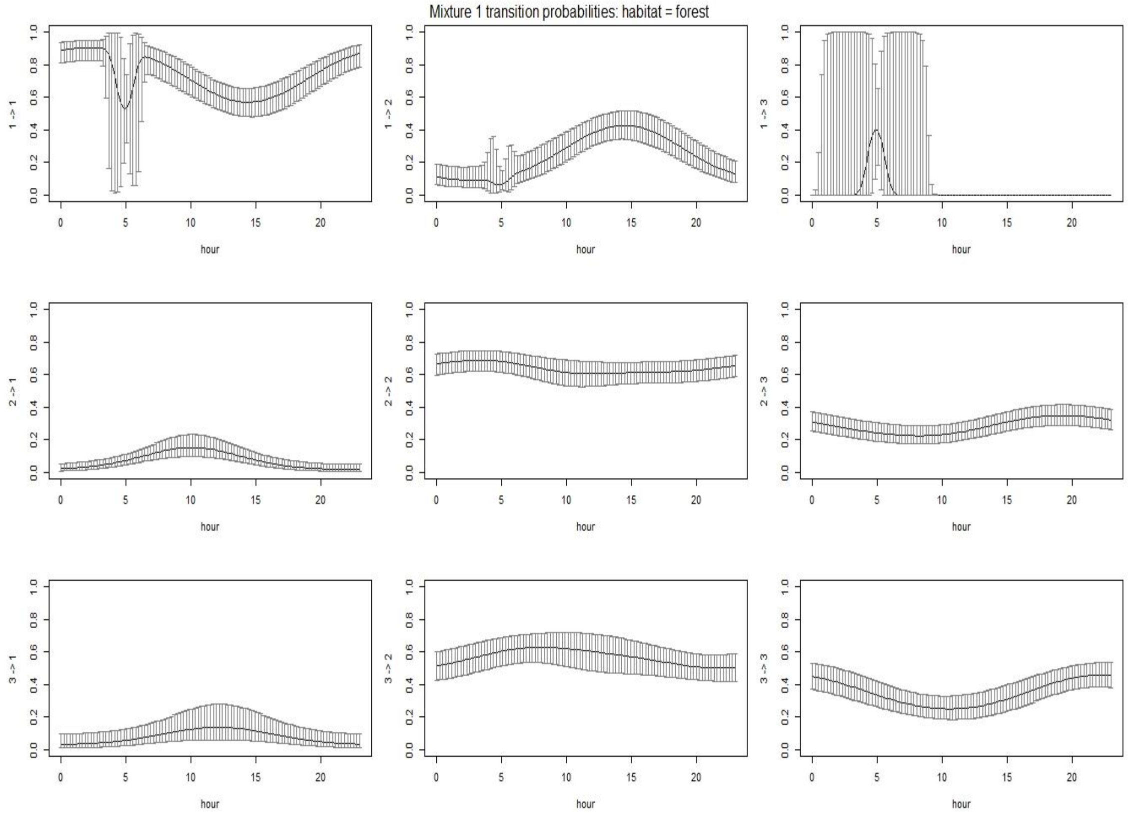
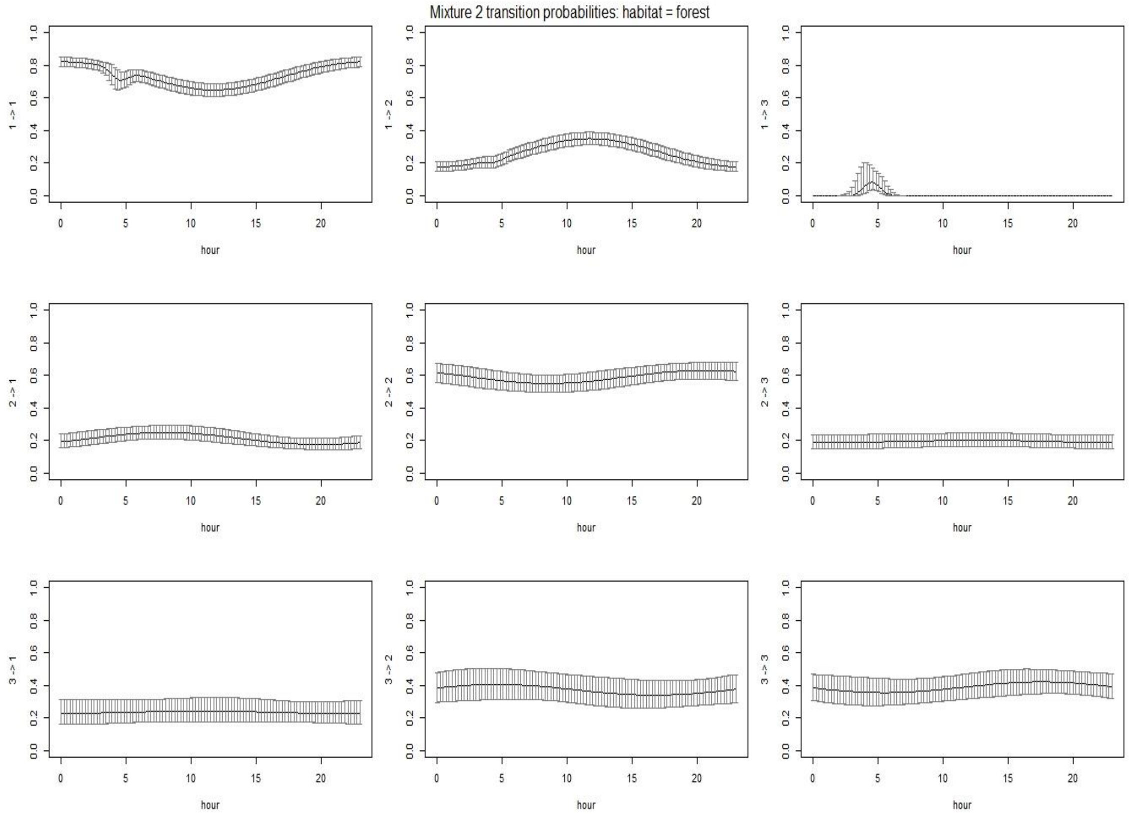


Figure 6.16: Effect of Habitat on transition probability during the post-dispersal phase





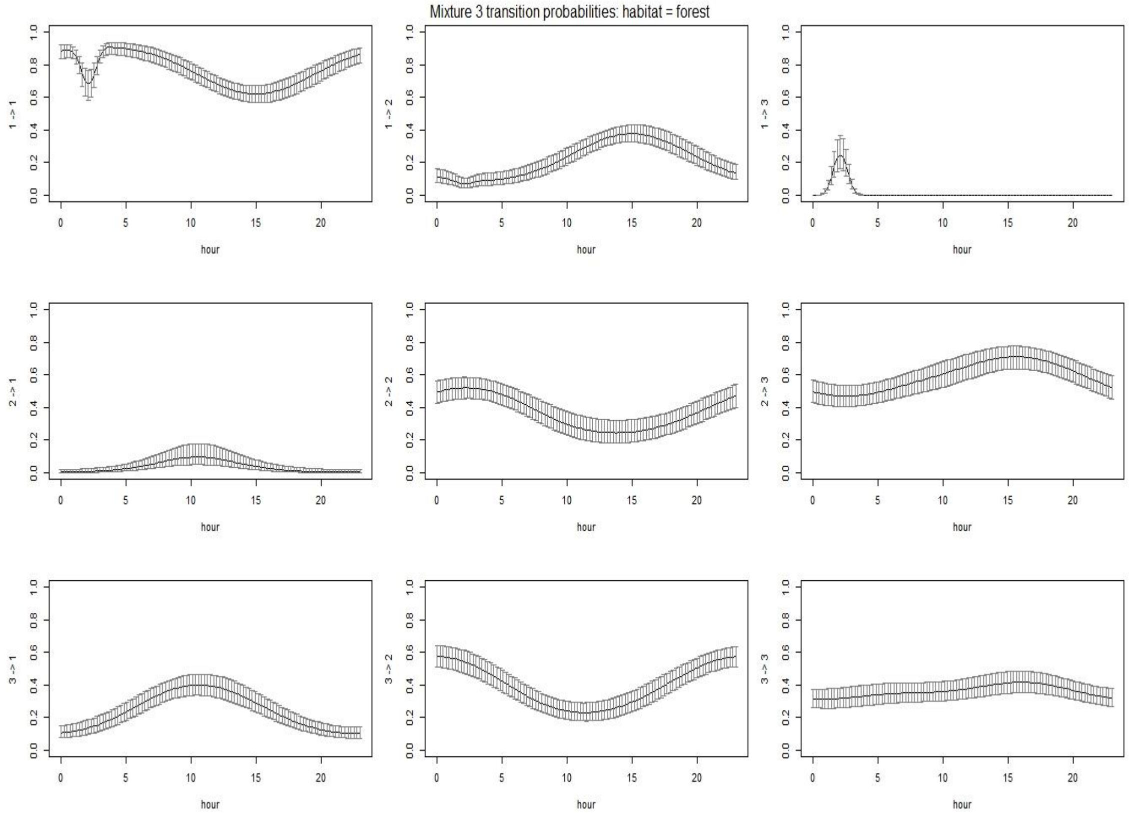


Figure 6.17: Effect of time of day (hour) on transition probability during the post-dispersal phase

6.3.4 Behaviour time allocation in different land use

Behavioural time allocation varied with land-use type across the dispersal phases (Figure 6.18). Tigers dedicated an equal proportion of their time to agriculture, regardless of their behavioural state in the pre-dispersal phase. The longest time was allocated to area-restricted movement in deciduous forests (43%) and plantations (46%). While travelling, the highest time allocation was observed in scrub forests (44%) and the lowest in plantations (22%). For grasslands, time allocation for all three behaviour types was equally allocated.

During the dispersal phase, tigers spent approximately 50% of their time travelling in agriculture. Resting behaviour was highest in grasslands (40%) and lowest in plantations (15%). However, the time allocated for area-restricted movement and travelling showed similarities between deciduous and scrub forests. In plantations, the highest proportion of time spent travelling (46 %), while the lowest was allocated to resting (15%). Resting accounted for the highest proportion (40%) of time in grasslands, whereas the least (29%) was assigned to area-restricted movement.

In the post-dispersal phase, the allocation of time in agriculture was highest for area-restricted movement (40%), followed by travelling (33%) and resting (27%). Resting and area-restricted movement in deciduous forests had a similar time budget, accounting for 70% of the total time allocation. In scrub forests, resting behaviour was dominant (50%), followed by area-restricted movement (30%). For plantations, most of the time (51%) was allocated to area-restricted movement, while the least time (19%) was spent travelling. Resting and area-restricted movement had similar time allocations in grasslands, while travelling had the lowest proportion.

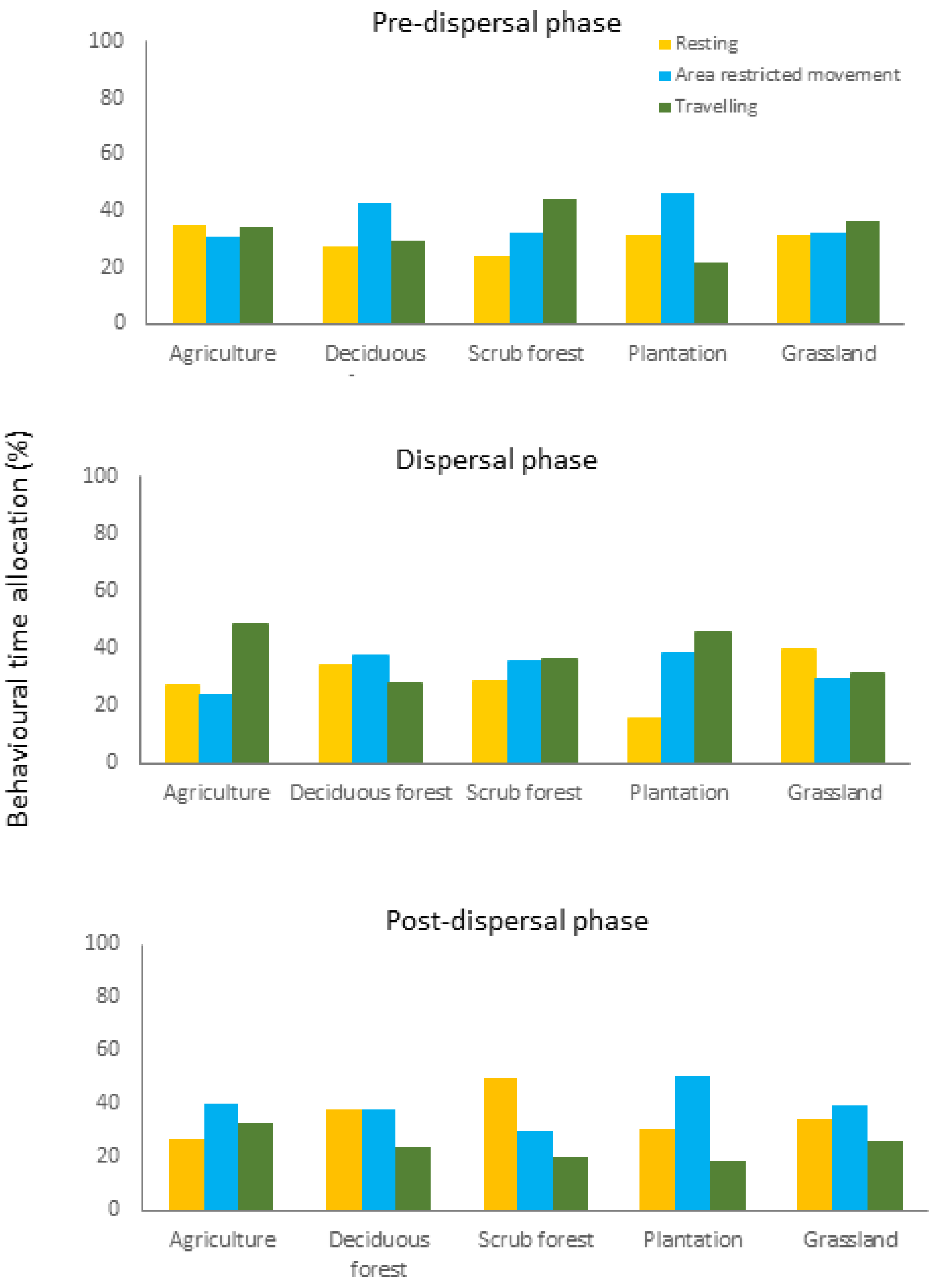


Figure 6.18: Behavioural (3-state) time allocation of tigers in different land use types during the pre-dispersal, dispersal, and post-dispersal phase in the Eastern Vidarbha Landscape of Maharashtra, India

6.4 Discussion

The study used Hidden Markov Models (HMM) to analyse the behavioural patterns of tigers based on their step lengths and turning angles of movement paths during the pre-dispersal, dispersal, and post-dispersal phases. The finding showed that tiger movement could be divided into three distinct behavioural states: resting, area-restricted movement (ARM), and travelling. Moreover, the fitted HMMs offered valuable insights into how environmental and anthropogenic factors influenced tiger behaviour. Conventional and generalised HMMs were used to model the effect of time of day, temperature, habitat, and road distance on movement characteristics within behavioural states and state-switching behaviour. This study provides a novel approach to understanding movement behaviour, making it the first application of the HMM to describe tiger behaviour. Similar behavioural studies on other terrestrial carnivores, such as the Persian leopard *Panthera pardus saxicolor* (Farhadinia et al., 2020), Florida panther *Puma concolor coryi* (van de Kerk et al., 2014, Li & Bolker 2017), black bears *Ursus americanus* (Karelus et al., 2019) and wolves *Canis lupus* (Kosović & Fertalj, 2014) has been modelled using 3-state movement behaviour.

A 3-state HMM was applied to different life stages of tigers, incorporating different predictor variables to analyse the stationary state probabilities and transition probabilities at fixed intervals of 2-h. These findings provide new insights into the effects of life stages and their different movement patterns. Furthermore, tigers exhibited distinct responses to stationary probabilities, transition probabilities, and time budgets across the three dispersal phases. Most of the time was spent in area-restricted movement during pre-dispersal, followed by travelling and resting. This phase corresponds to when sub-adult tigers are in their natal area and the period of independence from their mothers. Individuals actively explore new areas and expand their movements beyond their mother's territory. Consequently, their time activity budget reflects a greater emphasis on area-restricted movement and travel with relatively less time to rest.

Dispersing individuals had twice the movement in area-restricted movement and travelling state compared to tigers in their natal areas. While traversing a human-dominated landscape, tigers exhibited faster and more directed movements. Dispersal primarily occurs outside PAs, which are a matrix of forest and agricultural landscapes. These patches are fragmented owing to human settlements, agriculture, and the presence of roads. Thus, the need for increased movement arises during travel, as tigers must navigate the landscape and minimise the risk of reaching suitable habitats during dispersal. Moreover, movement outside PAs is energetically costlier. In such circumstances, tigers allocate their activity budget equally among resting, ARS, and travelling. Thus, by incorporating a highly mobile strategy, dispersing tigers can minimise risk by travelling greater distances in a fragmented landscape while satisfying their foraging requirements through resting and area-restricted movement. In addition, direct and rapid movements through a specific area may indicate low motivation to stay in a habitat perceived as suboptimal (Doherty and Driscoll, 2018). These factors likely contribute to the behavioural adaptations of tigers during dispersal in landscapes shaped by human influence. In addition, dispersing tigers had longer step lengths in area-restricted movement and travelling in non-forest areas, owing to their movement in a human-dominated landscape.

During the post-dispersal phase, tigers establish a stable or temporary home range in which they actively defend and maintain their territories. During this phase, the primary activities of tigers consist of resting and territorial movements, which encompass both area-restricted movement and travel. As a result, there is a minimal distinction between area-restricted movement and travelling states. The time activity budget of tigers is predominantly allocated to territorial movement (60%), followed by the resting state (40%). The activity budget reflects the need for resident tigers to maintain their home range and defend access to mates irrespective of foraging or thermoregulatory requirements. Further, territorial movement plays a vital role in the behaviour and ecology of tigers, as it directly influences their ability to acquire essential resources and contributes to population dynamics.

Effect of variables on stationary state probability

Stationary state probability refers to the likelihood that an animal is in a specific behavioural state under fixed covariate conditions (Leos-Barajas et al., 2017; Clay et al., 2020). Consequently, the stationary probabilities of tigers responded differently to diel time (time of day), temperature, and habitat across the dispersal phases. During the pre-dispersal phase, tigers exhibit adaptive behaviour by altering their stationary probabilities. They were more active and moved faster during dawn and dusk, which is consistent with the nocturnal and crepuscular behaviour of the species (Karanth & Sunquist, 2000; Linkie & Ridout, 2011; Wang et al., 2015). They shifted their behaviour to a more exploratory or foraging state in the morning and changed to resting during the night. Tigers in this phase are in an exploratory movement as they search for new territories and habitats, often venturing beyond their mother's territory with extended movement bouts. Furthermore, the results provide evidence that tigers modulate their behaviour in response to temperature variations, suggesting the involvement of thermoregulatory strategies in diel activity patterns and temporal shifts in movement behaviour. These findings indicate that increased temperature affects behavioural responses, with individuals more likely to switch states and prefer to travel than rest. Additionally, the probability of area-restricted movement peaked between 25-35 degrees and decreased with an increase in temperature.

Similarly, the time of day and habitat significantly affected the stationary state probability and movement during dispersal. Individual variations were observed, indicating that the differences in the likelihood of travel while resting and area-restricted movement remained consistent across the three mixture groups. When moving through a human-dominated landscape, individuals showed a higher probability of travelling during dusk and late evening and later switched to a resting state at midnight. During the day, dispersing tigers exhibited primarily exploratory behaviour, with a peak between 10-12 h having a higher step length in non-forested habitats. Tigers, while traversing fragmented areas, face risks and increase human activities during the day, resulting in changes in movement parameters and behavioural states. The tigers showed a higher probability of movement confined to a smaller area between the fragmented patches and shifted to faster movement at night. Previous studies have indicated that similar behaviour was observed in the Persian leopard *Pardus saxicolor*, black bear *Ursus americanus*, and Florida panther *Puma concolor coryi*, suggesting that they likely patrol their territories during the darkest hours of the night (Karelus et al., 2019; Farhadinia et al., 2020; van de Kerk et al., 2015; Li & Bolker, 2017). However, one male tiger exhibited a lower probability of travel because its movement was primarily confined to agricultural areas, indicating a higher likelihood of area-restricted movement.

During the post-dispersal phase, tigers exhibited variations in behaviour and movement that were influenced by habitat. They had longer step lengths while foraging in forests, and travelled faster in non-forested areas. This adaptability can be attributed to landscape structure, availability of vegetation cover, and habitat patchiness in a human-dominated landscape. The results also indicated that tigers in forest habitats had a higher probability of area-restricted movement (mixture 1) and resting (mixture 2), suggesting that individuals spend more time actively exploring or resting in specific forest areas. In non-forest habitats, they exhibited a higher persistence of travelling (mixture 1) or resting (mixture 2), indicating that individuals either spent more energy by moving faster between patches or potentially conserved energy for subsequent activities. Habitat degradation reduces high-quality foraging areas, affecting the utilisation of non-forest habitats for travel or rest. For example, Florida panthers primarily rested during the day and transitioned from an intermediate state to an exploring state when travelling between patches in more open areas (van de Kerk et al., 2015). However, one female tiger showed a higher probability of travelling in the forest, potentially related to prey search or territorial defense. In contrast, tigress showed a high probability of area-restricted movement in non-forest habitats, such as agricultural fields, indicating restricted foraging or temporary refuge-seeking. The findings also show tigers behavioural response to time of day. The area-restricted movement and resting dominated, as their primary activity was maintaining and defining their home ranges. The resting state was most prevalent late in the morning and gradually shifted to area-restricted movement, with high activity levels observed at dusk. On the other hand, the area-restricted movement remains active primarily during daylight hours, peaking between 10-15 h, potentially reflecting periods of increased movement in foraging behaviour. Moreover, individuals exhibited a low probability of travel; however, there was a peak in the evening, suggesting that they moved faster during this time.

Effect of variables on transition probability

The transition probability matrix provides valuable information on the probabilities of transitioning between different states in tiger behaviour, thereby revealing their state-switching behaviour. The findings of the study identified the high behavioural plasticity of tigers in response to time of day and ambient temperature fluctuations. Moreover, including time of day as a covariate effectively captured the temporal patterns in tiger behaviour. The probability of transitioning from resting to travelling was higher in the early morning and late evening, indicating increased activity levels during the pre-dispersal phase. Additionally, the transition to the foraging state peaked between 10-12 h, suggesting moderate activity. Furthermore, tigers were more likely to transition from a foraging to a travelling state in the evening. These findings are consistent with those of previous studies on tigers, which were more active during crepuscular and nocturnal periods. This behaviour can be attributed to the increased activity of their prey species during these times (Karanth & Sunquist, 2000; Linkie & Ridout, 2011; Wang et al., 2016). It is also reasonable that the foraging state reflects other dynamics in tiger behaviour, such as moderate activity within core areas during the daytime. They are more likely to shift to large-scale movements for patrolling and defending territories during dawn and dusks. Furthermore, the persistence of the travelling state remained high during dawn and dusk, indicating that once tigers were in this state, there was a strong probability that they remained in that behavioural state. This phenomenon may reflect an "all-or-nothing" strategy observed in other animals, such as seals committing to a specific behaviour once initiated, regardless of changing environmental conditions (Krebs et al., 2010). I also found that ambient temperature increased transition rates from foraging to fast movements for tigers. This finding further implies that higher temperatures may promote the continuation of travelling behaviour rather than switching to other states, such as resting or area-restricted movement.

During dispersal, tigers exhibited variations in behavioural transition to the time of day. These findings highlight the temporal dynamics of state-switching behaviour in tigers, revealing specific periods associated with distinct state transitions. When tigers traverse human-dominated landscapes, their movement is affected by fragmented habitat patches. These habitat patches are present within a matrix of agricultural landscapes and human settlements; thus, their encounters with humans are high. Reduced habitat availability and increased human disturbance lead to a high probability of tigers remaining in the same behavioural states. For example, when tigers are resting or foraging, there is a high likelihood of remaining in the same state, whereas the probability of transitioning to a travelling state becomes high during twilight and nighttime. The shift to foraging and resting states during the day allows tigers to access the habitat required to minimise their energy expenditure in a human-dominated landscape. Moreover, increased nocturnal behaviour and faster movement reduce the risk of encountering humans and facilitate dispersal in fragmented landscapes. For example, African lions *Panthera leo* increase their travel speed near bomas, which is likely to reduce their chances of encountering and being detected by humans (Nisi et al., 2022). Similarly, tigers increase their movement speed outside protected areas (Habib et al., 2021), particularly in regions with high forest fragmentation.

The transition probability during the post-dispersal phase was significantly influenced by time of day and habitat. Tigers exhibited varied responses to forest and non-forest habitats, with individual behaviour influenced by specific local contexts. For example, established individuals are more likely to remain in the same resting state in non-forest habitats. This behaviour may be attributed to the landscape composition and human disturbances that tigers encounter in human-dominated landscapes. Tigers tend to adopt a less mobile state to minimise interactions with humans and anthropogenic disturbances. However, their transition from resting to foraging increased when travelling through forested areas with less human interference. Tigers also exhibited variability in transitioning to a travelling state within forested areas. To the time of day, resting was predominant during the day, with a higher probability of foraging peaking in the afternoon and travelling in the early morning. Established individuals with a defined home range invested more in resting and territorial movements (area-restricted movement and travelling) to access, patrol, and defend their territories. They exhibited crepuscular movement and demonstrated higher nocturnal activity with increased travel during the evening. Tiger home ranges encompass various land uses, including forests and agricultural areas. Consequently, their movements within the home range include multi-use landscapes, increasing the travel probability when individuals move through non-forest habitats. Furthermore, tigers had the highest probability of being in the travelling state while traversing non-forest habitats and transitioned to area-restricted movement when moving through forested areas.

In conclusion, this study provides novel insights into tiger behaviour and the influence of environmental and anthropogenic factors on tiger movement patterns. These findings have important implications for the conservation and management of tigers, especially in human-dominated landscapes, where habitat fragmentation and human disturbances pose significant challenges. By understanding the behavioural adaptations of tigers during different phases of their life, conservation efforts can be aimed to ensure their long-term survival and coexistence with human activities. Additionally, this study highlights the effectiveness of HMM as a valuable tool for analysing and understanding the behaviour of endangered species, opening possibilities for future research on other terrestrial carnivores.

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Supplementary files

Table S6.1: Details of data used for HMM analysis during the pre-dispersal (9420 location), dispersal (5400 location) and post-dispersal phase (8980 location) in the Eastern Vidarbha Landscape of Maharashtra, India

ID	Date start	Date end	No. of days
Pre-dispersal phase			
Brh female	21-10-2016	03-11-2016	15
E1	05-03-2019	30-05-2019	87
E3	29-04-2019	24-07-2019	86
Fazlu	11-06-2018	11-11-2018	154
Kolsa female	07-03-2017	08-06-2017	94
Kolsa male	10-03-2017	08-06-2017	91
T09	13-04-2016	18-05-2016	36
T10	12-04-2016	20-05-2016	39
Tipu	08-03-2019	10-07-2019	125
Walker	01-03-2019	03-06-2019	95
Dispersal phase			
Fazlu	20-11-2018	08-12-2018	19
Kolsa female	09-01-2018	12-03-2018	63
T09	10-08-2016	08-12-2016	121
T10	27-07-2016	09-09-2016	45
Tipu	10-07-2019	10-08-2019	32
Walker	21-06-2019	29-11-2019	162
Post-dispersal phase			
E3	01-09-2019	25-01-2020	147
Kaalu	07-06-2019	27-09-2019	112
Kolsa female	14-03-2018	12-01-2019	305
T09	15-01-2017	10-06-2017	147
T10	06-12-2016	18-04-2017	134
Tipu	09-08-2019	31-10-2019	84
Walker	01-12-2019	27-03-2020	118

Table S6.2: Heterogeneity mixture table for individual tigers during the pre-dispersal, dispersal, and post-dispersal phase

Individual ID	**Mix1**	**Mix2**	**Mix3**
Pre-dispersal phase			
Brh female		+	
E1		+	
E3		+	
Fazlu	+		
Kolsa female			+
Kolsa male			+
T09	+		
T10		+	
Tipu	+		
Walker	+		
Dispersal phase			
Fazlu	+		
Kolsa female	+		
T09	+		
T10		+	
Tipu			+
Walker		+	
Post-Dispersal phase			
E3		+	
Tipu		+	
T10	+		
Kaalu		+	
Kolsa female			+
T09	+		
Walker		+	

Figure S6.1: Pseudo-residual plots of final HMM of tiger during the pre-dispersal phase

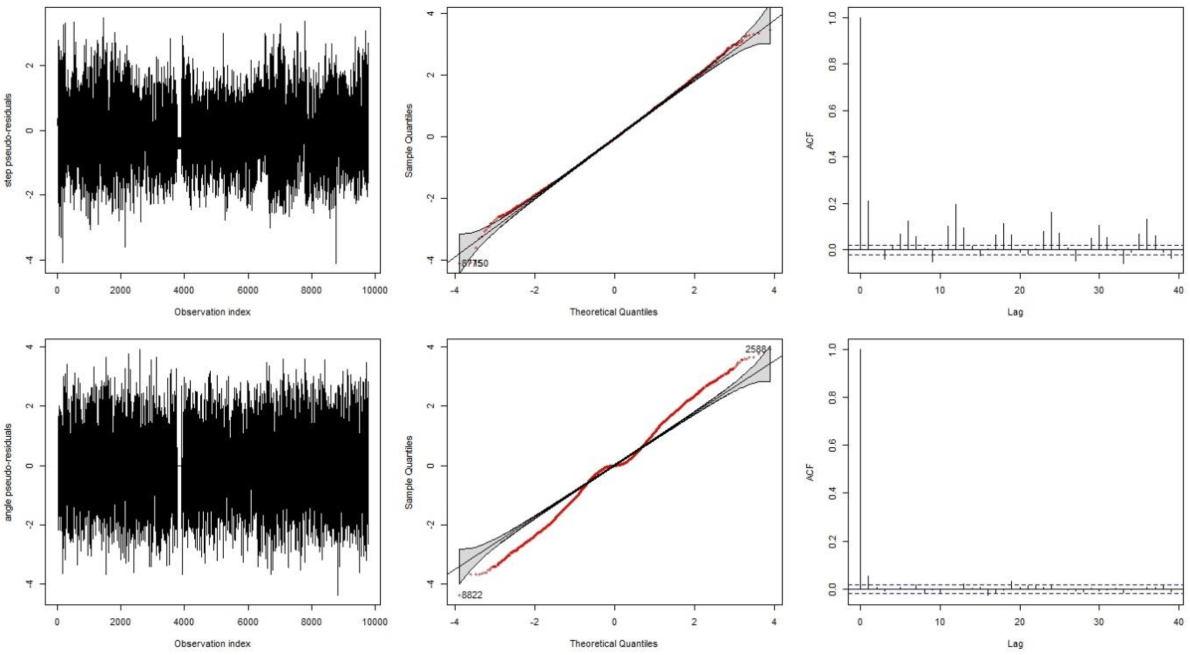

Figure S6.2: Pseudo-residual plots of final HMM of tiger during the dispersal phase

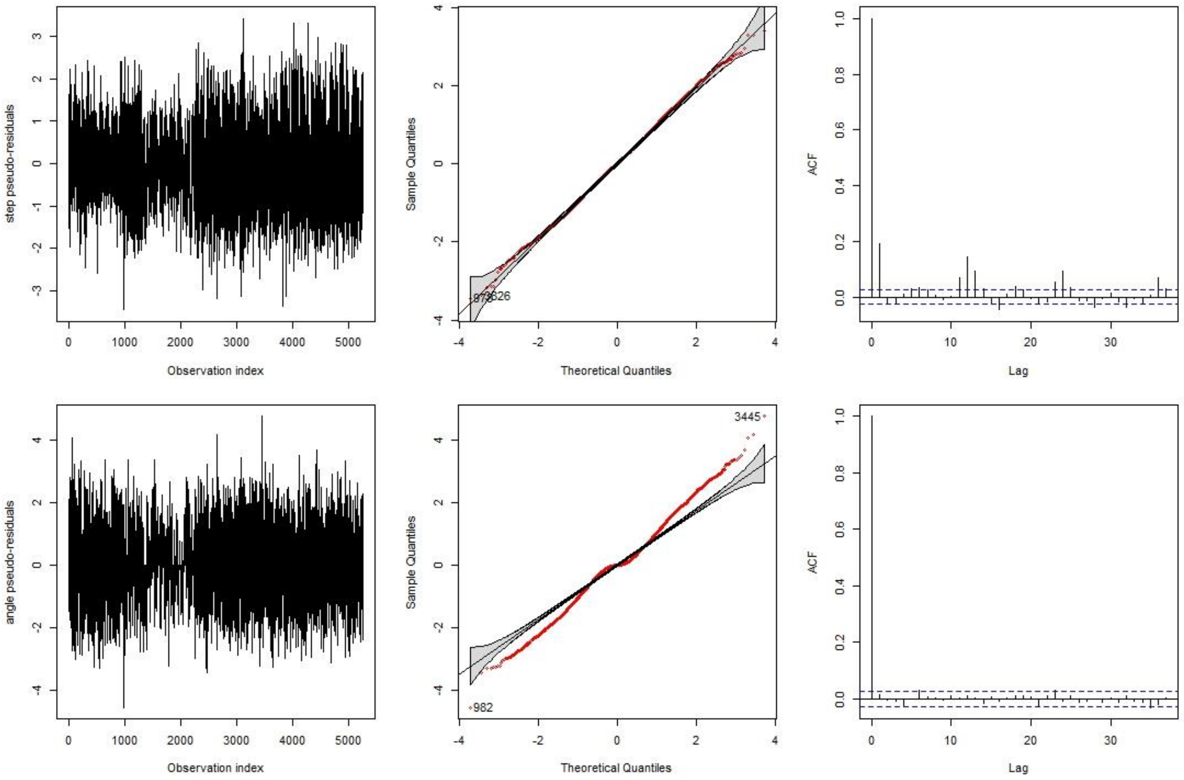

Figure S6.3: Pseudo-residual plots of final HMM of tiger during the post-dispersal phase

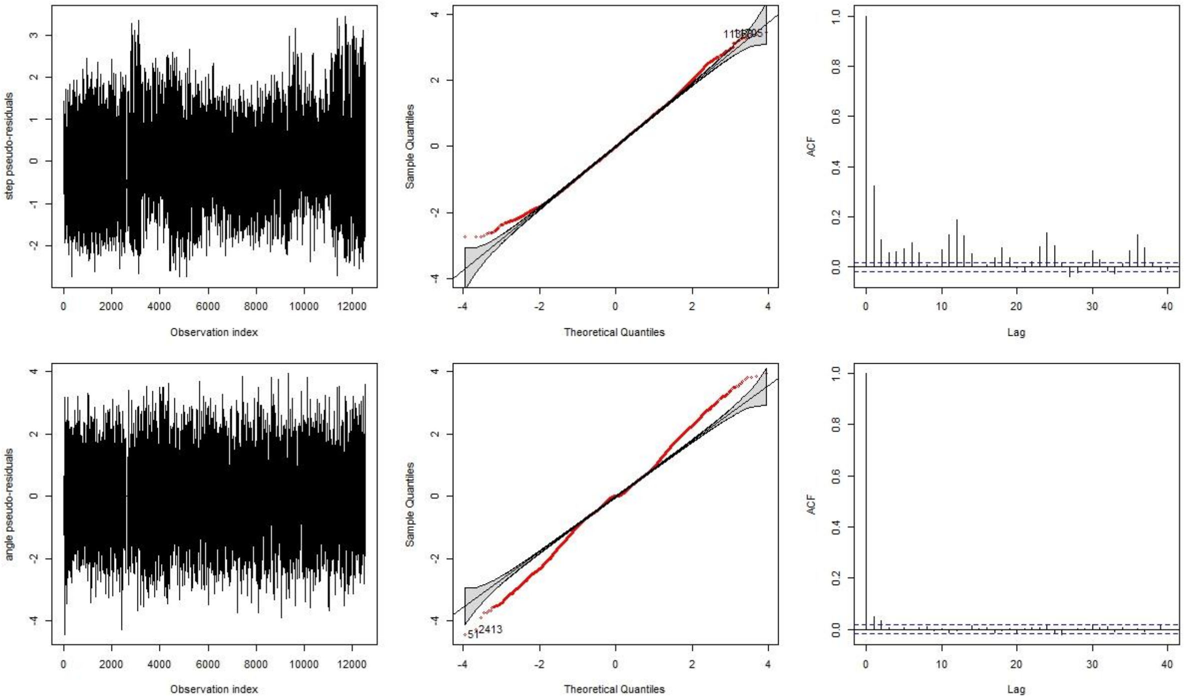

Table S6.3: Details of HMM models considered examining covariate effects on transition probabilities and movement parameters with varying numbers of mixtures

Model name	**Covariates**
Additive models	
Model 1	temp
Model 2	time of day
Model 3	dist.road
Model 4	habitat
Mix model 1	temperature + time of day
Mix model 2	temperature + dist.road
Mix model 3	time of day + dist.road
Mix model 4	temperature + habitat
Mix model 5	time of day + habitat
Mix model 6	dist.road + habitat
Full model	Temperature + time of day + dist.road + habitat
Interaction models	
Interaction 1	temp * time of the day
Interaction 2	temp * habitat
Interaction 3	time of the day * habitat
Interaction 4	temp * time of the day * habitat
Interaction 5	temp * time of the day + habitat
Interaction 6	temp * time of the day + dist.road + habitat
Interaction 7	temp * time of the day + dist.road + habitat
Interaction 8	temp * time of the day * habitat + dist.road
Interaction 9	temp * dist.road
Interaction 10	time of the day * dist.road

CHAPTER 7

TO EVALUATE RESOURCE SELECTION PATTERNS USING RADIO-TELEMETRY ACROSS THE LANDSCAPE

Chapter 7

To evaluate resource selection patterns using radio-telemetry across the landscape

7.1 Introduction

Habitat selection and animal movement are fundamental ecological processes that determine species distribution, abundance, and interactions within their environment (Elith & Leathwick, 2009). This process can directly influence individual fitness and population dynamics, leading to an understanding of space use patterns (Boyce et al., 2002). Animals select habitats that offer forage and refuge from predation or facilitate movement (Avgar et al., 2013; Dickie et al., 2017). By contrast, animals may avoid habitats that impede or impose a risk of predation (Droghini & Boutin, 2018; Prokopenko et al., 2016). Furthermore, this mechanism is influenced by competition between and within the species (Nielsen et al., 2010). Habitat selection has been extensively studied to understand how animals respond to foraging resources (Bastille-Rousseau et al., 2020), environmental risks (e.g. predators, roads; Fortin et al., 2005; Prokopenko et al., 2017), and other landscape features (e.g. slope, terrain; Fortin et al., 2005; Ellington et al., 2020). Understanding the mechanisms underlying habitat selection, animal movement, and the influence of environmental and anthropogenic factors is crucial for unravelling ecological dynamics, conserving biodiversity, and managing human impacts on ecosystems.

The "behaviour-specific habitat selection" concept implies that animals select habitats that meet their specific behavioural requirements. Because each behavioural state has distinct resource needs, how an animal selects habitats in the landscape may vary significantly. Since behaviour is not often considered in habitat selection models, it can lead to incorrect conclusions about resource use (Roever et al., 2014). Thus, the resources required for various behavioural states, such as foraging, resting, and travelling, are likely to be distinct and possibly opposing. Additionally, the optimal habitat characteristics for specific behaviours, such as travelling or resting, may differ from those preferred during foraging. Conservation planning efforts have largely ignored animal behavioural states and habitat selection (Wilson et al., 2012). This is primarily due to the limitations of long-term behavioural observation without observer presence influencing the behaviour (Mahoney & Young, 2017). However, recent advancements in modern GPS and telemetry have enabled researchers to understand animal movements on a much finer temporal scale (Cagnacci et al., 2010). Consequently, it is possible to study animal behaviour coupled with habitat selection. For example, high-temporal GPS data can reveal explicit movement patterns from which statistical techniques can deduce different behavioural states (Morales and Ellner, 2002; Patterson et al., 2009).

Behavioural studies have shown to be an important aspect of habitat selection across various species such as elk *Cervus elaphus* (Fryxell et al., 2008), killer whales *Orcinas orca* (Ashe, Noren & Williams, 2010), Bluefin tuna *Thunnus maccoyii* (Pedersen et al., 2011), lions *Panthera leo* (Elliot et al., 2014), and elephants *Loxodonta africana* (Roever et al., 2013). More recently, studies have evaluated a more complex relationship between behaviour-specific habitat selection, animal movement, and factors influencing selection. These environmental and anthropogenic factors are multifaceted, and factors such as climate, topography, food availability, and vegetation structure define habitat selection and its associated behaviour (Hecker et al., 2023; Pay et al., 2022; Thorsen et al., 2022). In contrast, anthropogenic factors can introduce novel resources or disrupt existing habitats, thereby altering the decision-making process for animals. For example, Dickie et al. (2020) found that wolves and bears are attracted to linear features, whereas prey species avoid them. Moreover, to reduce the chance of encounters with humans, large carnivores spatially avoid anthropogenic features (Abrahms et al., 2015; Wilmers et al., 2013) and display temporal shifts in activity and habitat use (Ordiz et al., 2011; Frank et al., 2019; Wilmers et al., 2021; Suraci et al., 2019).

Large carnivores in the Anthropocene have experienced range contractions and are threatened by extinction (Wolf & Ripple, 2017). Human-driven environmental shifts, such as climate change and land use modifications, resulting in increased temperatures and altered precipitation patterns, are driving global changes in biodiversity (Holt, 1990; Wiens et al., 2009; Chen et al., 2011; Schewe & Levermann, 2012). Similarly, land-use changes result in habitat destruction and fragmentation (Daye & Healey, 2015), community homogenisation (Gossner et al., 2016), and loss of species richness (Murphy & Romanuk, 2014). Humans are a major source of mortality for large carnivores, with retaliation from livestock losses (Woodroffe & Frank 2005, Darimont et al., 2015; Oriol-Cotterill et al., 2015b), lethal predator control, poaching, and poorly managed trophy hunting (Treves & Karanth, 2003; Loveridge et al., 2017), leading to population declines (Woodroffe 2000, Ripple et al. 2014).

For example, tigers (*Panthera tigris*) lost approximately 95% of their distribution range. The current population co-occurs with humans in most of their range in mixed-use landscapes within and outside protected areas (Habib et al., 2021). Few large carnivore populations expand their habitat near humans, despite the risks posed by human activity (Boydston et al., 2003; Chapron et al., 2014). This suggests that carnivores may adopt flexible behavioural strategies to minimise the risk of human-induced mortality, enabling their existence in a human-dominated landscape. Some species also differ in movement and habitat selection across dispersal phases and life stages (Barry et al., 2020; Elliot et al., 2014). Therefore, it is critical to determine the response of dispersing individuals to environmental and anthropogenic factors, and whether their responses differ from those of non-dispersing individuals. These responses can be a conjunction of behavioural state and habitat selection, providing insights into the behavioural plasticity of species.

The diverse behaviour of species requires different habitat characteristics, which are spatially segregated, particularly when inhabiting a heterogeneous landscape (Roever et al., 2010). Conservation efforts must consider species-specific behavioural requirements, movement patterns, and the impacts of human activities on habitats. By identifying these key factors, we can develop targeted strategies to mitigate negative impacts, restore connectivity, conserve crucial habitats, and promote sustainable land-use practices. Therefore, understanding the behavioural mechanisms that facilitate the coexistence of species in diverse habitats is important for conservation efforts. In this chapter, I examine behaviour-specific habitat selection by tigers during three phases: pre-dispersal, dispersal, and post-dispersal. This chapter further explores multi-scale habitat selection, and the primary question was to understand (a) how resource selection patterns vary between protected and non-protected areas and (b) how environmental and anthropogenic factors influence resource selection.

7.2 Methods

7.2.1 Telemetry data

Tigers were captured, collared, and monitored from 2016 to 2022 in the Eastern Vidarbha Landscape. Individuals were fitted with GPS collars (GPS Plus, Vectronic Aerospace GmbH) with different programming schedules based on the dispersal phase of the tigers. All GPS locations were resampled to one location every two hours (± 10 min tolerance) and used only for individuals with regular time-interval data or a subset of the data. All GPS locations were resampled to one location every 2-h (± 10 min tolerance) by the function *'track_resample'* in the package *'amt'* (Signer et al., 2019) in R software. For individuals with irregular GPS fixes, I subsampled only those data with regular time intervals of 2-h for further analysis.

7.2.2 Behavioural classification

Hidden Markov models (HMM) were used to identify the 3-state behaviour of tigers during the pre-dispersal, dispersal, and post-dispersal phases (Langrock et al., 2014; Patterson et al., 2008). I classified the behaviour based on the step length and turning angles between consecutive GPS fixes to incorporate movement behaviour into the habitat selection analysis. HMM analyses are state-switching models that assume that animal movement is driven by underlying behavioural modes (Patterson et al., 2017). The model was fitted with three behavioural states: state 1 (resting state with stationary mode), state 2 (area-restricted movement characterised by movement over shorter distances with variable turning angles), and state 3 (travelling state characterised by movements over longer distances with relatively constant turning angles). The behavioural models were fitted with the gamma distribution for the step length and the circular von Mises distribution for the turn angles (Avgar et al., 2016). The Viterbi algorithm was used to assign each step to the most likely behavioural state based on the results of the HMM (Zucchini et al., 2017). The analysis used the package '*momentuHmm'* (McClintock & Michelot, 2018) in the R software (R Core Team, 2022).

7.2.3 Habitat selection and movement analysis

The spatial scale at which habitat selection can be estimated depends on the definition of habitat availability. I evaluated the habitat selection on two scales, i.e., "*landscape and fine-scale level*". The "landscape level" refers to an extensive area much larger than the home range of an individual, such as the entire study area, referred to as second-order habitat selection. On the other hand, habitat selection at the "fine-scale level" occurs when the availability of habitat is determined within smaller areas or shorter distances, for example, considering the animal's ability to move between consecutive hourly locations referred to as fourth-order habitat selection (Johnson, 1980).

Landscape-level habitat selection

Habitat selection was evaluated using a resource selection function (RSF) at the landscape scale, where the extent of availability was defined by the study area (Manly et al., 2007). To define the available space for RSF, I considered the 100% minimum convex polygon encompassing all observed GPS locations of tigers, with a buffer equal to the radius of a circular mean male home range size (r = ~ 18 km). The GPS locations were randomly sampled from this availability space at a ratio of 10:1. RSF was obtained by fitting a generalised linear model with the *glm* function in R (R Core Team, 2022). The GPS locations were treated as the response variable, categorised as 'TRUE' for used locations and 'FALSE' for available locations (Figure 7.1).

Fine-scale habitat selection and movement

I used a two-stage approach to quantify habitat selection at a fine-scale level. First, an integrated step selection analysis (iSSA) was modelled to understand the influence of environmental and anthropogenic covariates at the local scale. Second, I integrated iSSA into behaviour-specific habitat selection and movement parameters, where availability was defined by regular temporal resolution (Avgar et al., 2016). iSSA allows for simultaneous habitat selection and movement parameter estimates (e.g. step length and turn angle) by relaxing the implicit assumption that these are independent (Signer et al., 2019). This method assesses habitat preference in animals by comparing each step used (i.e., movement between two consecutive GPS fixes) to those of randomly placed available steps (i.e., that animal could have taken) within the movement path. The available steps are generated from the gamma distribution fitted to the empirical step length distribution and random turning angles by the von Mises distribution. I generated 10 random steps per used step at a 2-h interval (10:1 available-to-use ratio) based on the recommendations of Thurfjell et al. (2014). I also generated sets of true and random steps considering individuals' behavioural states (resting, area-restricted movement, and travelling) across the dispersal phase of tigers. Moreover, a unique step ID was assigned to each used step and its associated available steps. The covariates were extracted at the start and end points of each step. The covariates extracted at the starting point and interaction with movement parameters, such as step length (or logarithm of step length), were used to infer movement speed. In contrast, covariates extracted at the end of each step were used to infer habitat selection (Avgar et al., 2016).

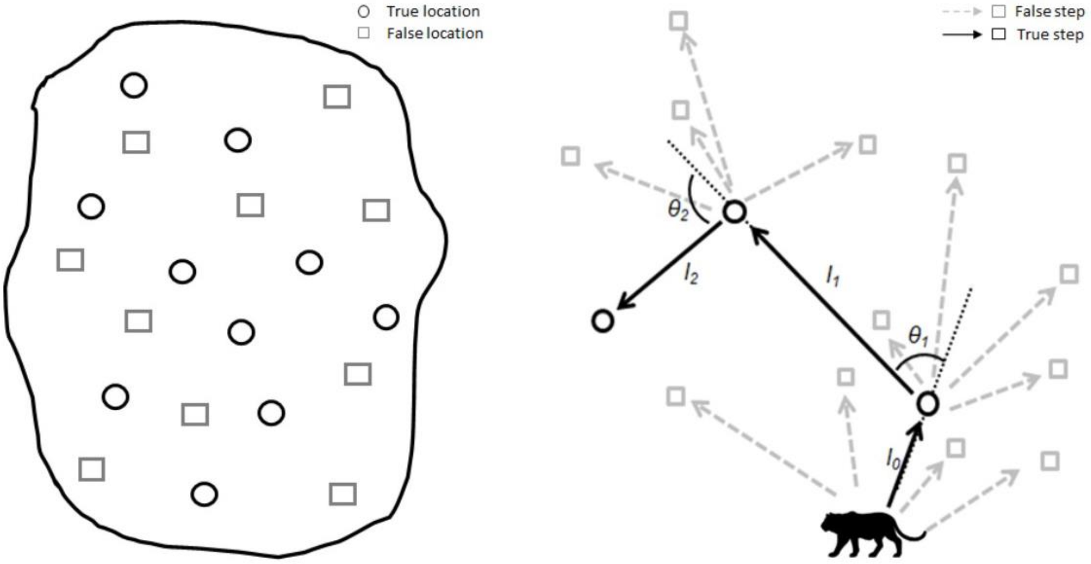

Figure 7.1: Illustration of animal location showing habitat selection at two scales (a) landscape-scale, i.e., second-order habitat selection and (b) fine-scale (step-level habitat selection)

7.2.4 Environmental and anthropogenic covariates

For RSF and iSSF, environmental covariates, human disturbances, forest fragmentation, and anthropogenic disturbances were included. I obtained land use data of 60 m resolution from Bhuvan (NRSA, 2016; http://bhuvan.nrsc.gov.in/). Land use classes included built-up land, agriculture, forest, grassland, and water. To assess vegetation cover, I used the normalised difference vegetation index (NDVI) derived from Landsat 8 from Google Earth Engine. These datasets were obtained between March 2016 and December 2021, with spatial and temporal resolutions of 30 m and 32 days, respectively (Gorelick et al., 2017). The Euclidean distance between each tiger location and nearest drainage was calculated using ArcMap 10.6.1. To quantify anthropogenic disturbances, the Euclidean distance to the nearest road was calculated using the OpenStreetMap geospatial data repository (OpenStreetMap 2020) in Google Earth Engine™ (Gorelick et al., 2017). Road data were further classified into highways, primary roads, and minor roads. Human disturbances included the distance to human settlement, population count, and nightlight intensity. Furthermore, I used forest fragmentation classes mapped using the '*Landscape Metrics' tool in* ArcMap 10.6.1, and divided them into seven classes.

7.2.5 Candidate model and selection

Candidate models for each RSF were developed to understand habitat selection at a landscape scale. Each candidate model included a set of core covariates that comprised important habitat features that play a significant role in tiger habitat selection (Hussain et al., 2022; Karanth & Sunquist, 2000; Sarkar et al., 2017). Moreover, core covariates are expected to influence movement and selection regardless of human and anthropogenic disturbances. Therefore, the core model incorporated covariates, such as land use composition, vegetation cover (NDVI), and distance to drainage. To create competing candidate models, the core model was expanded to include additional covariates representing roads, human disturbance, and forest fragmentation. Furthermore, combination models that incorporated core and anthropogenic covariates were included. The analysis also comprised a full model that included all the covariates (Table 7.1).

For iSSF, the candidate models were similar to those for RSF, except that the iSSA models included movement-related covariates (Table 7.2). The core model includes the cosine of the turn angle (cos_ta), which describes the directionality of an individual's movement (Avgar et al., 2013; Turchin, 1998). It is defined as the circular measure of a linear correlation factor (between -1 and 1), where a negative value indicates moving backward from the previous location, zero indicates a random walk, and a positive value indicates moving forward (Benhamou, 2006). Tigers were expected to move and select habitats differently throughout the day. Therefore, I also included the log step length (log_sl) interaction with the time of day (tod) category to account for temporal movement differences. Additionally, tiger movement (log_sl) relative to drainage or water availability was modelled by including an interaction between the distance to the nearest drainage at the step's start location and the log of the step length (log_sl). The core model also included distance to drainage at the end of the steps for habitat selection. Along with these core covariates, all other variables and models were the same as those used in the RSF models (Table 7.2).

All covariates were scaled, centred, and screened for collinearity using Pearson's correlation coefficient with a threshold for model fitting of |r|> 0.7 threshold for model fitting. Logistic regression was used for random steps/locations available (coded as 0) for each true step/location (coded as 1) as the response variable to the environmental and anthropogenic variables as fixed variables. I used the functions *fit_rsf* and *iSSF* from the package *'amt'* in R (Signer, Fieberg & Avgar, 2019). The best-fit model had the lowest AIC for landscape and fine-scale habitat selection and movement. From the output of RSF and iSSA, the relative selection strength (RSS) was calculated following Avgar et al. (2019). Each parameter value expresses the relative selection strength (RSS) on a log scale (Avgar et al., 2017) for a 1-unit increase in the corresponding covariate, where positive values express selection and negative values express avoidance. For continuous variables, such as distance or NDVI, I calculated the RSS for selecting a given feature over the mean of the covariate.

Table 7.1: Candidate models used to test the habitat selection of tigers influenced by environmental, human disturbances and forest fragmentation at the landscape-level

Model	**Explanatory covariates**
Null	~ 1
Core	~ Built-up + agriculture + forest + grassland + ndvi + dist.drainage
Roads	~ Core + dist.HW + dist.PR + dist.MN
Human disturbance	~ Core + dist.HS + human.population
Forest fragmentation	~ Core + patch + edge + perforated + small.core + medium.core + large.core
Roads and human disturbances	~ Core + dist.HW + dist.PR + dist.MN + dist.HS + human.population
Roads and forest fragmentation	~ Core + dist.HW + dist.PR + dist.MN + patch + edge + perforated + small.core + medium.core + large.core
Human disturbance and forest fragmentation	~ Core + dist.HS + human.population + patch + edge + perforated + small.core + medium.core + large.core
Full	~ Core + dist.HW + dist.PR + dist.MN + dist.HS + human.population + patch + edge + perforated + small.core + medium.core + large.core

"dist" is an abbreviation for "distance-to" and indicates the distance of each location to the environmental or anthropogenic variables (drainage: water body; HW: highway; PR: primary road; MN: minor road and HS: human settlement)

Table 7.2: Candidate models used to test the habitat selection and movement influenced by environmental, human disturbances and forest fragmentation in tigers at the fine-scale level

Model	**Explanatory covariates**
Null	~ 1
Core	~ cos(TA[a]) + log(sl[b])*tod_end + log_sl*dist.drainage_start + built-up + agriculture + forest + grassland + ndvi_end + dist.drainage_end
Roads	~ Core + dist.HW_end + dist.PR_end + dist.MN_end
Human disturbances	~ Core + dist.HS_end + human.population_end
Forest fragmentation	~ Core + patch + edge + perforated + small.core + medium.core + large.core
Roads and human disturbances	~ Core + dist.HW_end + dist.PR_end + dist.MN_end + dist.HS_end + human.population_end
Roads and forest fragmentation	~ Core + dist.HW_end + dist.PR_end + dist.MN_end + patch + edge + perforated + small.core + medium.core + large.core
Human disturbances and forest fragmentation	~ Core + dist.HS_end + human.population_end + patch + edge + perforated + small.core + medium.core + large.core
Full	~ Core + dist.HW_end + dist.PR_end + dist.MN_end + dist.HS_end + human.population_end + patch + edge + perforated + small.core + medium.core + large.core

[a] *Turning angle*

[b] *Step length*

"dist" is an abbreviation for "distance-to" and denotes the distance of each location to the environmental or anthropogenic variables (drainage: water body; HW: highway; PR: primary road; MN: minor road and HS: human settlement)

"_end" and "_start" denote if the covariate was extracted from the start or the end of the animal step

7.3 Result

The dataset included 27,605 GPS locations for habitat selection at the landscape level. For fine-scale habitat selection and movement parameters, 25,767 locations were used at 2-h intervals. Behaviour-specific habitat selection was analysed across different life stages during the pred-dispersal, dispersal, and post-dispersal phases. The tracking duration for individual tigers ranged from two to 23 months in the landscape.

7.3.1 Landscape-level habitat selection

The full model was selected as the best-fit model and had the lowest AIC value compared with the other competing models (Table 7.3). The primary factors influencing tiger habitat selection included environmental covariates, human disturbances, forest fragmentation, and roads in the Eastern Vidarbha Landscape (Table 7.4). At the landscape level, habitat selection was positively affected by the presence of forests, high vegetation cover (NDVI), and increasing distance to drainage (Figure 7.2). Tigers tended to select areas close to primary and minor roads, but avoided highways, human settlements, and areas with high human populations (Figure 7.3).

Table 7.3: Best-fit model for tiger habitat selection at the landscape-level using resource selection function (RSF) in the Eastern Vidarbha Landscape of Maharashtra

Name	df	AIC
Full	17	126759.0
Roads and forest fragmentation	15	127585.8
Roads and human disturbances	12	127757.3
Roads	10	129060.3
Human disturbances and forest fragmentation	14	132421.7
Forest fragmentation	12	132778.4
Human disturbances	9	133207.3
Core	7	133832.6
Null	1	181919.3

Table 7.4: Coefficient for habitat selection for tiger at the landscape-level using resource selection function (RSF)

Parameters	Estimate	Std. Error	z value	Pr(>|z|)
Environmental Covariates				
Forest	1.24	0.06	21.13	0.00
Agriculture	-2.00	0.06	-34.19	0.00
Grassland	-0.86	0.07	-12.73	0.00
Built-up	-1.94	0.17	-11.07	0.00
Vegetation cover (NDVI)	0.16	0.01	19.62	0.00
Distance to drainage	0.22	0.01	31.48	0.00
Roads				
Distance to highway	0.05	0.01	7.15	0.00
Distance to primary road	-0.09	0.01	-12.24	0.00
Distance to minor road	-0.56	0.01	-63.50	0.00
Human disturbances				
Human population	-1.26	0.07	-19.00	0.00
Distance to human settlement	0.07	0.01	10.90	0.00
Forest fragmentation				
Patch	-2.38	0.16	-15.20	0.00
Edge	-0.58	0.03	-20.77	0.00
Perforated	-0.22	0.05	-4.51	0.00
Small core	-0.64	0.06	-10.94	0.00
Medium core	-1.18	0.13	-9.02	0.00

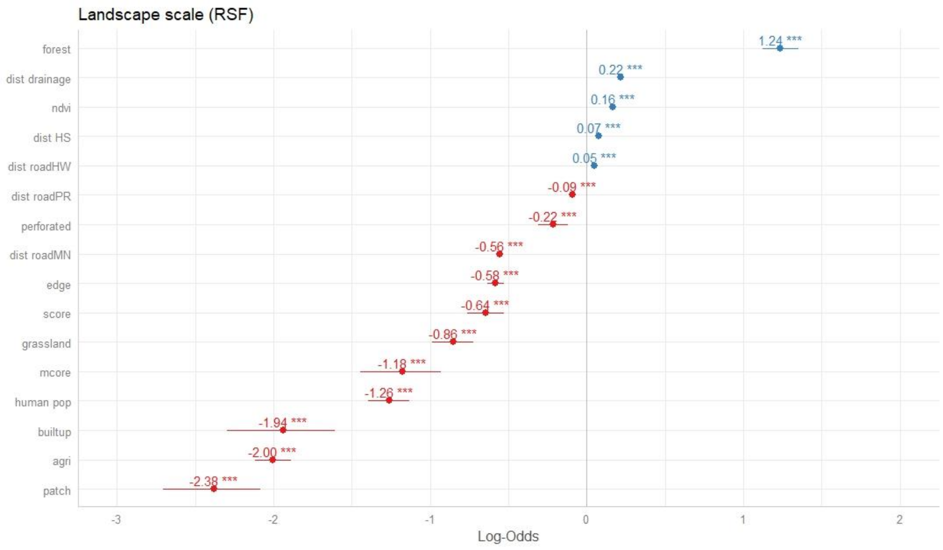

Figure 7.2: Parameter estimates of variables influencing habitat selection of tigers at a landscape level. The grey line represents the zero effect. Significant responses are highlighted by asterisks. The x-axis depicts the estimates, and the y-axis represents the variables. Asterisks indicate significance level: * = 0.05, ** = 0.005, *** = 0.0005

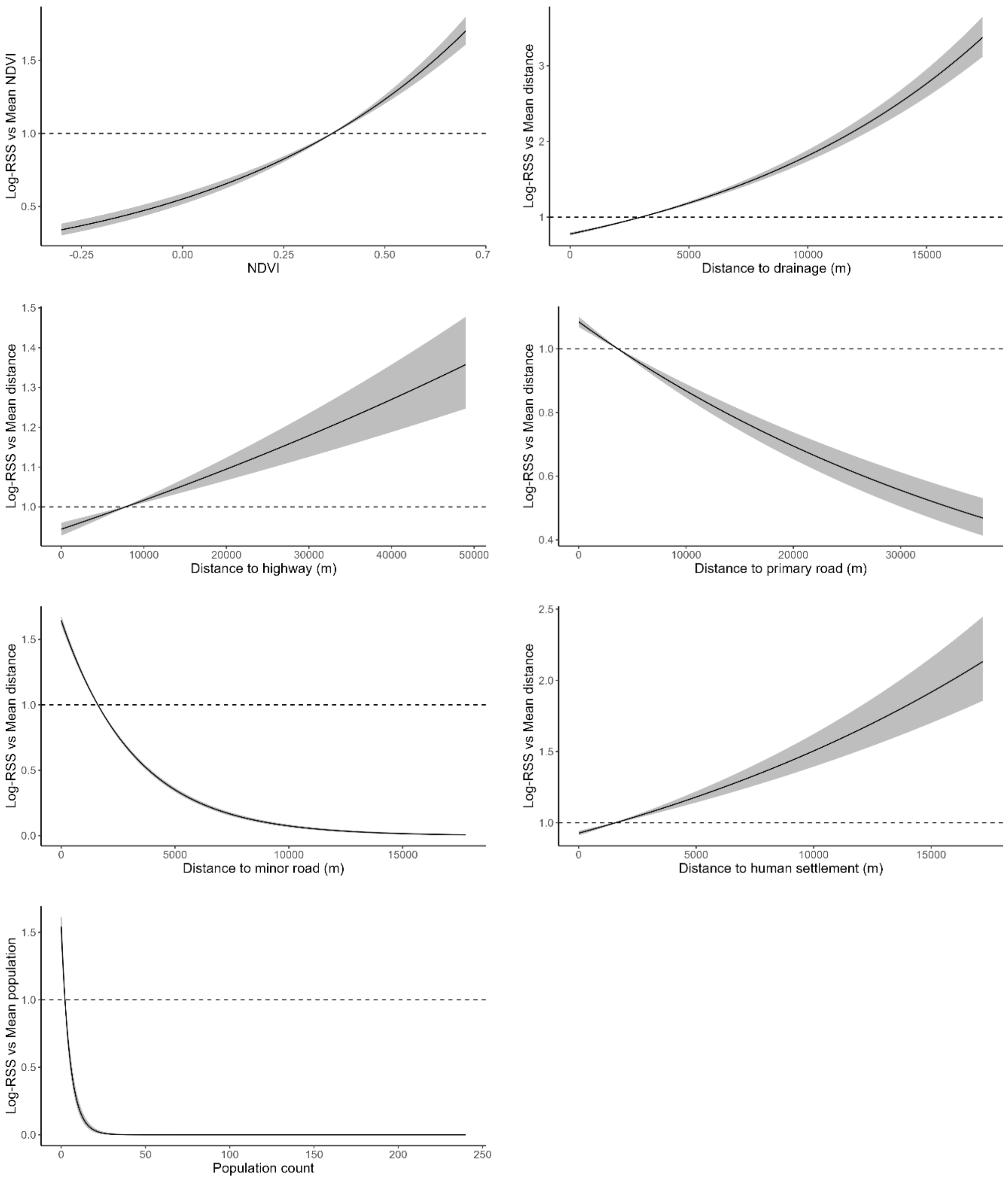

Figure 7.3: Log of relative selection strength (Log-RSS) with 95% confidence interval (shaded area) depicting selection (values > 1) or avoidance (values < 1) at the landscape-level. The range of values of the predictors on the x-axis corresponds to observed ranges. The probability of habitat selection to vegetation cover (NDVI), distance to drainage, distance to roads, human settlement, and population count in the Eastern Vidarbha Landscape

7.3.2 Fine-scale habitat selection and movement

When considering all locations (i.e., across all behaviours) at 2-h intervals, the covariates influencing tigers' habitat selection and movement parameters included human disturbances and forest fragmentation (Table 7.5). The coefficients of the fixed effects contributing to the best-fit model are shown in Figure 7.4. At the local scale, the habitat selection of tigers was positively influenced by the presence of forests, high vegetation cover (NDVI), and small cores (Table 7.6; Figure 7.5). Tigers showed a positive relationship with human population, but the result was insignificant. They selected areas near drainage or streams ($\beta = -0.08$; $p<0.05$). In contrast, tigers avoided areas with high patches of forest fragmentation in the landscape ($\beta = -0.57$; $p<0.05$). Regarding the movement parameters, the coefficient for the turn angle was negative, suggesting territorial movement, although the result was insignificant. Tigers exhibited varying movements based on the time of day, with faster movements at night ($\beta= 0.08$; $p<0.05$). In addition, their movement rate slowed near streams or drainage ($\beta = 0.01$; $p= 0.05$).

Table 7.5: Model selection for tiger’s habitat selection and movement at the fine-scale using integrated step selection analysis (iSSA)

Name	df	AIC
Human disturbances and forest fragmentation	19	146104.3
Forest fragmentation	17	146106.9
Roads and forest fragmentation	20	146109.1
Full	22	146109.4
Human disturbances	14	146143.7
Core	12	146145.0
Roads and human disturbances	17	146148.8
Roads	15	146149.2

Table 7.6: Coefficient for habitat selection and movement for tigers at the fine-scale level using integrated step selection analysis (iSSA)

Parameters	**coef**	**exp(coef)**	**se(coef)**	**z**	**Pr(>|z|)**
Habitat selection					
Forest	0.13	1.14	0.06	2.11	0.03
Agriculture	-0.30	0.74	0.06	-4.66	0.00
Built-up	-0.33	0.72	0.19	-1.75	0.08
NDVI_end	0.06	1.06	0.01	7.20	0.00
Distance to drainage_end	-0.08	0.92	0.04	-1.98	0.04
Forest fragmentation					
Patch	-0.57	0.56	0.17	-3.41	0.00
Small core	0.36	1.44	0.06	5.86	0.00
Movement					
cos_ta	-0.01	0.99	0.01	-0.88	0.38
log_sl*tod_end_night	0.08	1.09	0.01	12.40	0.00
log_sl*drainage_start	0.01	1.01	0.00	1.90	0.05

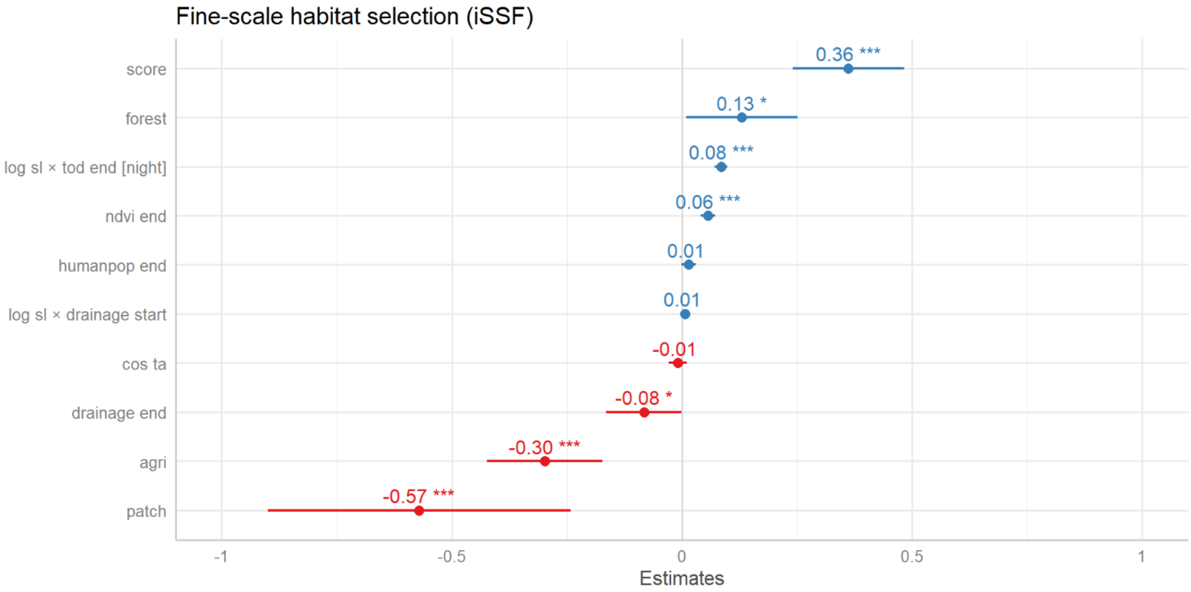

Figure 7.4: Parameter estimates of variables influencing habitat selection and movement of tigers at the fine-scale level. The grey line represents the zero effect. Significant responses are highlighted by asterisks. The x-axis depicts the estimates, and the y-axis represents the variables. Asterisks indicate significance level: * = 0.05, ** = 0.005, *** = 0.0005

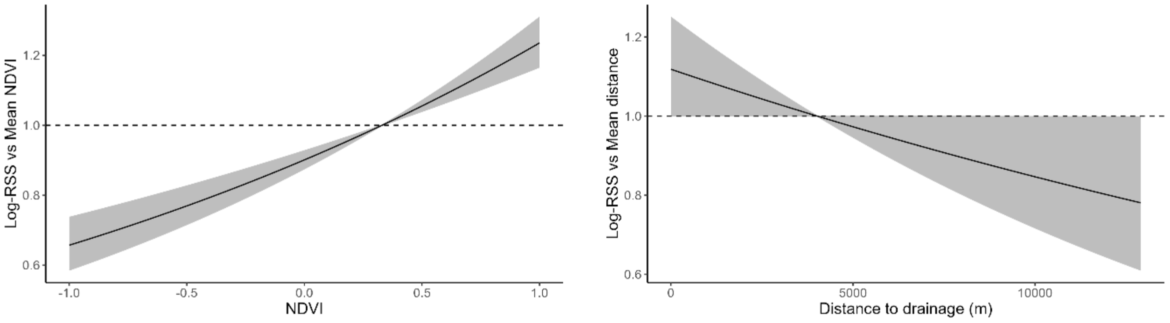

Figure 7.5: Log of relative selection strength (Log-RSS) with 95% confidence interval (shaded area) depicting selection (values > 1) or avoidance (values < 1) at the fine-scale level. The range of values of the predictors on the x-axis corresponds to observed ranges. The probability of habitat selection to vegetation cover (NDVI), distance to drainage, distance to roads, human settlement, and population count in the Eastern Vidarbha Landscape

7.3.4 Behaviour-specific habitat selection

Hidden Markov models (HMMs) are commonly used to identify distinct behavioural states based on animal telemetry data. I applied a 3-state HMM to classify tiger movement into three behavioural states: “*resting*", "*area-restricted movement*", and "*travelling*". Behaviour-dependent habitat selection can be viewed as a standard HMM with a habitat selection observation process. The following description presents the outcomes linking behavioural states across different dispersal phases to habitat and movement parameters.

Pre-dispersal

Forest fragmentation and human disturbances influenced habitat selection across behavioural states during the pre-dispersal phase. The best-fit models selected across the behavioural states are listed in Table 7.7. The turn angle coefficient was negative at the resting sites, indicating no directional persistence (β = -0.18; p<0.001). During the resting state, tigers significantly preferred habitats with forest, grassland, and agriculture, while avoiding edge patches of forested areas (Table 7.8). Tigers in the area-restricted movement selected habitats with dense vegetation cover (NDVI) and tended to remain in areas close to human settlements (Figure 7.6). While travelling, they selected patches of small cores and edges of the forest. The movement rate differed between the time of day, with slower movement observed at night (β= -0.21; p<0.001).

Table 7.7: Model selection for behaviour-specific habitat selection during the pre-dispersal phase using integrated step selection analysis (iSSA) and hidden Markov model (HMM)

Behavioural state	**Model**	**df**	**AIC**
Resting	Forest fragmentation	16	5519.4
Area-restricted movement	Human disturbances	14	14453.4
Travelling	Forest fragmentation	16	9741.9

Table 7.8: Coefficient for behaviour-specific habitat selection and movement of tigers during the pre-dispersal phase

Parameters	**coef**	**exp(coef)**	**se(coef)**	**z**	**Pr(>|z|)**
Resting					
Cos(TA)	-0.48	0.62	0.05	-9.75	0.00
Forest	1.42	4.12	0.73	1.93	0.05
Grassland	1.64	5.13	0.78	2.10	0.03
Agriculture	1.55	4.73	0.75	2.09	0.03
Edge	-0.44	0.65	0.21	-2.07	0.03
Area-restricted movement					
Forest	-0.61	0.54	0.20	-3.12	0.00
Grassland	-0.83	0.44	0.28	-3.00	0.00
Agriculture	-0.57	0.57	0.21	-2.70	0.00
NDVI_end	0.13	1.14	0.04	3.61	0.00
Distance to human settlement_end	-0.07	0.94	0.04	-1.85	0.05
Travelling					
Edge	0.26	1.29	0.10	2.47	0.01
Small core	0.43	1.54	0.23	1.83	0.06
Log_sl*tod_end_night	-0.21	0.81	0.07	-3.03	0.00

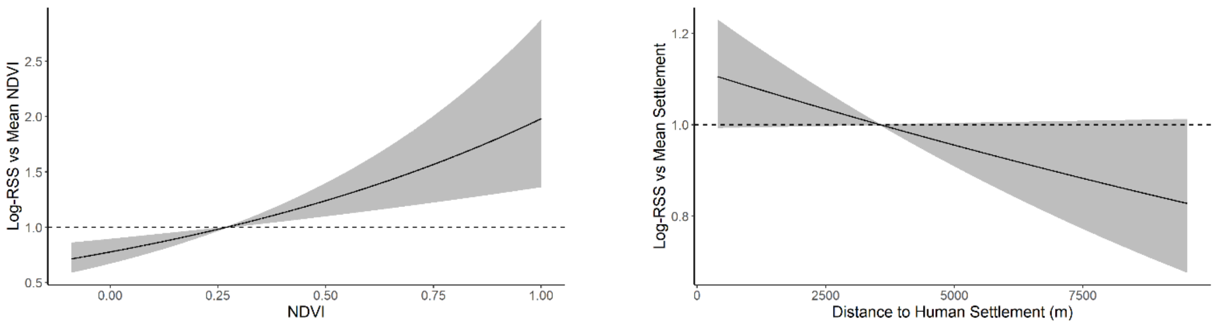

Figure 7.6: Log of relative selection strength (Log-RSS) with 95% confidence interval (shaded area) depicting selection (values > 1) or avoidance (values < 1) during "area-restricted movement" in the pre-dispersal phase

Dispersal

During the dispersal phase, the best model describing behaviour-specific habitat selection included the core model (i.e., land use, NDVI, and distance to drainage) and forest fragmentation (Table 7.9). Tigers exhibited stationary behaviour at resting sites with minimal tortuosity or directional movement (β = -0.94; p <0.001). Land use, NDVI, and the distance to drainage did not significantly affect the selection of resting sites (Table 7.10). Dispersing tigers in area-restricted movement increased their movement rate near the drainage or streams (β = -0.06; p <0.05). In the travelling state, they preferred moving through forested areas (β = 0.56; p <0.05) and selecting habitats with high vegetation cover (Figure 7.7). Moreover, the movement rate of the dispersing tigers was faster at night (β = 0.30; p <0.001) while travelling.

Table 7.9: Model selection for behaviour-specific habitat selection during the dispersal phase using integrated step selection analysis (iSSA) and hidden Markov model (HMM)

Behavioural state	**Model**	**df**	**AIC**
Resting	Core	11	3362.0
Area-restricted movement	Forest fragmentation	18	5558.7
Travelling	Core	12	5600.0

Table 7.10: Coefficient for behaviour-specific habitat selection and movement of tigers during the dispersal phase

Parameters	coef	exp(coef)	se(coef)	z	Pr(>|z|)
Resting					
Cos(TA)	-0.94	0.39	0.06	-15.23	0.00
Area-restricted movement					
log_sl*drainage_start	-0.06	0.94	0.03	-1.97	0.04
Travelling					
Forest	0.56	1.76	0.25	2.25	0.02
NDVI_end	0.09	1.09	0.04	2.32	0.02
log_sl*tod_end_night	0.30	1.35	0.10	2.90	0.00

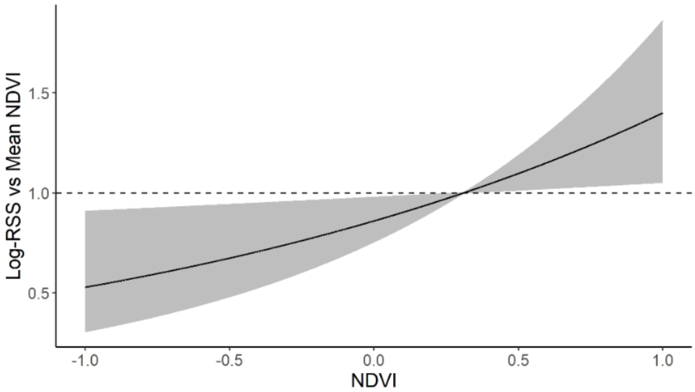

Figure 7.7: Log of relative selection strength (Log-RSS) with 95% confidence interval (shaded area) depicting selection (values > 1) or avoidance (values < 1) during “travelling” in the dispersal phase

Post-dispersal

The set of core covariates was the best model for explaining behaviour-specific habitat selection and movement during the pre-dispersal phase (Table 7.11). This core model comprises habitat features significant for tiger habitat selection, such as land use, vegetation cover, and distance to drainage. Tigers were primarily stationary ($\beta = -0.45$; $p < 0.001$) and selected areas had less grassland and high vegetation cover while resting (Table 7.12; Figure 7.8). During area-restricted movement, forests and grasslands positively influenced habitat selection (Table 7.12). However, there was no significant relationship between habitat selection and covariates during the travelling state.

Table 7.11: Model selection for behaviour-specific habitat selection during the post-dispersal phase using integrated step selection analysis (iSSA) and hidden Markov model (HMM)

Name	Model	df	AIC
Resting	Core	12	11641.8
Area-restricted movement	Core	12	8894.5
Travelling	Core	12	4389.3

Table 7.12: Coefficient for behaviour-specific habitat selection and movement of tigers during the post-dispersal phase

Parameters	coef	exp(coef)	se(coef)	z	Pr(>|z|)
Resting					
Cos(TA)	-0.45	0.63	0.03	-13.44	0.00
Grassland	-0.66	0.52	0.32	-2.08	0.03
NDVI_end	0.05	1.05	0.03	1.98	0.04
Area-restricted movement					
Forest	1.17	3.22	0.42	2.80	0.00
Grassland	1.05	2.86	0.44	2.36	0.01
log_sl*tod_end_night	0.19	1.21	0.04	4.42	0.00

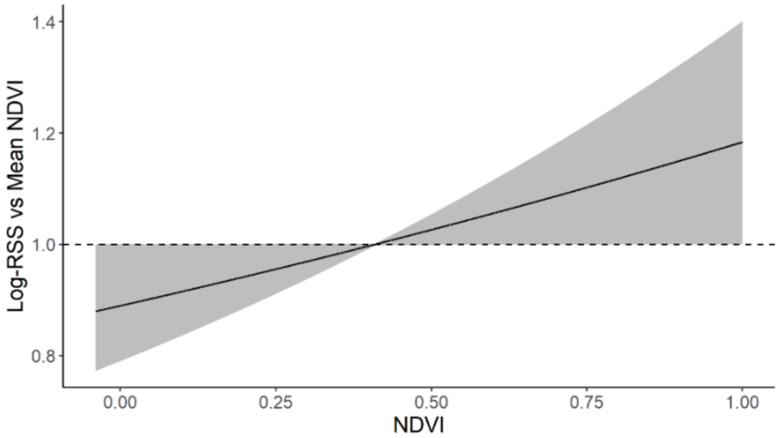

Figure 7.8: Log of relative selection strength (Log-RSS) with 95% confidence interval (shaded area) depicting selection (values > 1) or avoidance (values < 1) during "resting" in the post-dispersal phase

7.4 Discussion

The findings of the study report tiger habitat selection and movement at two scales, i.e., landscape and local scale, which have not been previously described. Moreover, this study conducted in the Eastern Vidarbha Landscape is the first to elucidate behaviour-specific habitat selection across different dispersal phases. The full model incorporating factors such as habitat composition, human disturbances, forest fragmentation, and roads at the landscape level demonstrated a significant influence on tiger habitat selection. However, at the local scale, habitat selection and movement parameters were primarily influenced by habitat composition, human disturbance, and forest fragmentation, with no significant relationships observed with roads.

Forests and vegetation cover influence habitat selection at the landscape and fine-scale levels. Tigers, being large carnivores, tend to prefer forested areas with dense cover for daily activities and movements. Additionally, the activity patterns of tigers are likely influenced by the temporal behaviour of their preferred prey species (Karanth & Sunquist, 2000). For example, the prey species that tigers primarily hunt (Bagchi et al., 2003; Hayward et al., 2012) prefer undisturbed habitats. Dense forest cover is required for tigers to act as ambush predators, helping them avoid early detection by their prey (Wilson & Mittermeier, 2009). Furthermore, vegetation cover facilitates tiger movement, enabling them to navigate more easily in landscapes dominated by human activity. This finding also suggests that tigers avoid areas with agriculture and human settlements, which is consistent with other studies showing a negative association (Smith et al., 1998; Karanth et al., 2004; Carroll & Miquelle, 2006; Naha et al. 2021; Puri et al., 2022). Although tigers are not strongly associated with drainage at the landscape scale, they prefer areas close to drainage at the fine-scale level. A comparison of habitat selection at multiple spatiotemporal scales suggests that the relevance of drainage to tiger habitat selection depends on the scale considered. Similar findings have been observed in studies on lions, where habitat selection differences are dependent on the temporal scale and habitat use decisions depend on the scale considered (Suraci et al., 2019). On a larger scale, tigers may show a negative association with streams or drainage because of the availability of excess water sources within and outside forested areas (Pudyatmoko et al., 2023). However, they tend to select areas near drainage at a finer scale while reducing their movement rate near it. Therefore, it is evident that selecting an appropriate spatiotemporal scale is crucial in habitat selection studies and has a significant influence on the outcome of habitat selection (Boyce 2006; Kittle et al., 2008, Wilmers et al., 2013; Thurfjell et al., 2014).

Anthropogenic disturbances such as roads appear to be important factors for habitat selection only at the landscape level. The impact of roads on movement, whether it facilitates or acts as a barrier, is likely to depend on the traffic volume (Northrup et al., 2012). In the present study, tigers perceived highways as risky habitats and tended to avoid them. Highways with high traffic volumes can act as barriers to animal movement, leading to mortality, displacement, or behavioural avoidance, depending on specific landscape conditions (Anderson, 2002; Carter et al., 2023; Forman et al., 2003; Scrafford et al., 2018; Shepard et al., 2008). This phenomenon has been observed in species such as Asian elephants *Elephas maximus*, gray wolves *Canis lupus*, and black bears *Ursus americanus* (Lesmerises et al., 2013; Wadey et al., 2018; Zeller et al., 2020), where high traffic volumes have been found to increase the risk to animals (Passoni et al., 2021; Prokopenko et al., 2017). The relative selection strength suggests that the effect zone of highways is approximately 10 km for selection or avoidance. Therefore, the ecological impact exceeds linear features and may extend several kilometres in the surrounding landscape. By contrast, tigers preferred to use primary and minor roads while travelling in the landscape. These smaller roads probably have lower levels of human activity and traffic, allowing for the increased permeability of animal movement. Similar patterns of road use have been observed in other species such as brown bears (Dickie et al., 2020; Thorsen et al., 2022).

High population density and proximity to human settlements, which are categorised as human disturbances, also influence tiger habitat selection. At the landscape scale, tigers avoided areas with dense human populations and selected areas away from human settlements. This influence can be assessed using indicators such as global human footprint and habitat fragmentation, which correlate with tiger habitat selection. However, the relationship between tiger habitat selection and human populations or settlements becomes insignificant at a fine scale. Fragmentation poses a significant obstacle to wildlife movement and is a major challenge for large carnivores (Riley et al., 2003; Rytwinski & Fahrig, 2012). Large carnivores such as tigers are particularly vulnerable to habitat fragmentation caused by linear infrastructure. Owing to their extensive home ranges, small population sizes, and low reproductive rates, habitat fragmentation poses a significant challenge to their movement and survival. Furthermore, tigers from the Eastern Vidarbha landscape responded differently to forest fragmentation. They showed a low preference for, or avoidance of, forest habitats with varying levels of fragmentation. However, at a finer scale, they selected forest patches smaller than 1 km^2, referred to as ‘small cores’, and avoided the forest edge. Tigers are habitat specialists, and their specific habitat requirements vary within a landscape. As forest patches become more fragmented and disconnected, movement at the edges of the patches may increase the risk of negative interactions with human activities. Thus, they select ‘small cores’ situated at a relatively greater distance from the forest and non-forest boundary.

These findings highlight the adaptability of tigers in their movement to various habitats. They modified their movement patterns based on the time of day, showing faster movement at night. This temporal variation in movement speed enabled tigers to cover greater distances and navigate through fragmented forest patches in the landscape. Similar patterns have been observed in studies on cougars and lions, where they also demonstrate higher speeds when crossing fragmented areas dominated by human activities to minimise the time spent in multi-use regions (Kertson et al., 2011; Valeix et al., 2012). This strategy reduces disturbances caused by human activities by promoting greater movement during the night in human-dominated landscapes. Tigers displayed similar movement behaviour, with a higher movement rate reported outside protected areas and during the night (Habib et al., 2021).

Behaviour-specific habitat selection and movement

This study combines movement behaviour and habitat selection, and presents the first quantitative assessment of behaviour-specific habitat use by tigers in a human-dominated landscape. Animal behaviour studies often focus on the fine-scale selection of microhabitats or food items, while habitat selection studies assess species-habitat relationships on a larger scale

(Roever et al., 2014). In contrast, behaviour-specific habitat selection offers a deeper understanding of the selection process and enhances the accuracy of the predictive habitat selection estimates. By distinguishing specific behaviours and their associated habitat preferences, researchers can identify the behaviour with the greatest impact on fitness or conservation. Moreover, behaviour-specific habitat selection can lead to improved habitat prioritisation for conservation and management.

The habitat selection of tigers varied depending on the specific behavioural states across the dispersal phases. During pre-dispersal, tigers strongly preferred forest and grassland areas, indicating their tendency to select habitats with minimal human interactions. During this period, sub-adult tigers actively explore new habitats and expand their movement beyond their natal areas. These exploratory forays include movement through multi-use landscapes, including forests and agricultural areas. Consequently, while moving through such a habitat matrix, tigers prefer resting in agricultural fields while avoiding forest edges. When engaged in area-restricted movement, tigers select habitats with dense vegetation cover and prefer areas close to human settlements. Foraging behaviour includes short and tortuous movements indicating stationary activity, thus reducing human interaction risk and alleviating anthropogenic pressures. Cover availability may mediate the ability of carnivores to access feeding opportunities in human-dominated landscapes (Suraci et al., 2019). Similar patterns have been observed in other large carnivores, such as hyenas (Boydston et al., 2003) and brown bears (Ordiz et al., 2011), where these species increased their use of protective cover near humans. Tigers preferred small cores (forest patches < 1 sq.km) and forest edges during the travelling state. This preference reflects the flexibility and adaptability of the species when moving through forested habitats. Additionally, the movement rate of tigers varied depending on the time of day.

The dispersal phase involves the movement of tigers from their natal area to another habitat, where they reproduce and establish a new territory. This phase primarily occurs outside protected areas which are a matrix of forests and anthropogenic landscapes. These patches of habitat are fragmented owing to the presence of human settlements, agriculture, and roads. As tigers move through this landscape, they rest in whichever habitat is available, without showing any preference for habitat variables during dispersal. Dispersers in area-restricted movement exhibited increased movement rates near drainages/streams, suggesting that they use streams as movement corridors. Conventional analyses of habitat selection that do not consider the underlying behavioural states would have failed to capture such behaviour-habitat-specific details. Our findings are consistent with the expectation that dispersing individuals undergo behavioural modifications and highlight the importance of accounting for behavioural states when concluding habitat selection. This consideration is crucial for informing management strategies for conserving tigers in human-dominated landscapes. During travel, tigers prefer to move through forested habitats with dense vegetation. Furthermore, the dispersing tigers exhibited faster movement rates at night while travelling. Their adaptability to anthropogenic factors in a human-dominated landscape may have influenced this behaviour, allowing them to take advantage of forested areas and nocturnal conditions to reduce the potential risks of human presence. Moreover, by employing a highly mobile strategy, dispersing tigers can minimise risks by travelling long distances in a fragmented landscape to reach optimal habitats.

During the post-dispersal phase, habitat selection of tigers was influenced by the presence of forests, grasslands, and vegetation cover across all behavioural states. Tigers preferred resting in areas with dense vegetation and less in open areas because high vegetation provides more cover and shade to rest. During this phase, tigers establish stable or temporary home ranges. Moreover, the primary activities included resting and territorial movements, encompassing area-restricted movement and travel. As a result, there was a minimal distinction between area-restricted and travelling states. Consequently, the patterns of habitat selection in these two behavioural states may be nested within one another and show no difference in habitat selection while travelling. However, tigers were more closely associated with forests and grasslands, where they engaged in area-restricted movements, including hunting and territorial movements within their home range.

In conclusion, this study provides valuable insights into the habitat selection and movement patterns of tigers at the landscape and local scales, particularly focusing on different dispersal phases. This study highlights the significant influence of factors such as habitat composition, human disturbance, forest fragmentation, and roads on tiger habitat selection. Furthermore, the study emphasises the importance of considering behaviour-specific habitat selection and appropriate spatiotemporal scales when studying large carnivores such as tigers. The information derived from studying tiger dispersal is informative and costly, particularly in human-dominated landscapes. However, it also provides crucial insights into carnivore persistence and serves as a guide for management strategies. Additionally, identifying the specific behaviour that is most important for fitness or conservation can be designed to facilitate these goals. For example, if tigers are found to select areas with low human disturbance, conservation efforts can focus on reducing human-wildlife conflict in specific areas. Additionally, behaviour-specific habitat selection offers new perspectives on species-habitat relationships, which can be highly relevant to future conservation and management of the species.

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CHAPTER 8

SYNTHESIS AND MANAGEMENT IMPLICATIONS

Chapter 8

Synthesis and Management Implications

8.1 Synthesis

Animal movement plays an important role in survival, resource acquisition, evading threats, dispersal, and finding mates (Nathan et al., 2008). Furthermore, the ability of animals to navigate through their habitats affects their population dynamics and genetic diversity. Depending on their life stages, animals can exhibit various types of movement, which may vary across spatial and temporal scales. Therefore, the study of animal movement is crucial for ecological research, and offers valuable insights into movement processes and conservation strategies. The Central Indian Landscape serves as a stronghold for tiger populations, with intact and suitable habitats. However, critical tiger-bearing areas within this landscape are located outside protected areas (PAs) and thus experience high human pressure. The degree of anthropogenic pressure varies based on human presence in the human-wildlife matrix, potentially influencing the movement and behaviour of large carnivores such as tigers in the landscape. This thesis aimed to test the hypothesis that the movement and behaviour of tigers in the Eastern Vidarbha Landscape are influenced by a combination of ecological and human-induced factors, which vary across multiple scales within the landscape.

This study focused on tiger movement patterns, space use, behaviour, and habitat selection in the Eastern Vidarbha Landscape of Maharashtra. Tiger movements were categorised into pre-dispersal, dispersal, and post-dispersal phases, with distinct behaviours observed in each stage. Males and females disperse over long distances and are influenced by various ecological and anthropogenic factors, challenging previous assumptions about sex-biased dispersal. Although prior studies have shown a general pattern of sex-biased natal dispersal in tigers (Smith, 1993; Goodrich et al., 2010), behavioural plasticity in sex-biased dispersal challenges previous assumptions. Dispersing tigers exhibited the highest space utilisation, followed by the post- and pre-dispersal phases. Additionally, they require larger areas outside protected areas (Table 5.9, Chapter 5), with males having larger territories. Factors such as forest proportion, patch density, and human population density play critical roles in determining tiger space utilisation (Figure 5.6, Chapter 5). Furthermore, tiger movement within the utilised area is influenced by resource availability, human activity, and habitat characteristics (Figure 5.10, Chapter 5).

While moving through outside protected areas, they showed faster movement and covered longer distances at night, adapting to fragmented habitats. Moreover, reduced human activity at night enables animals to move between distant forest fragments with lower perceived risk associated with human activity and anthropogenic disturbances. Similar altered movements due to habitat fragmentation and human pressure have been observed in other carnivorous species (Poessel et al., 2014; Tigas et al., 2002; Tucker et al., 2018).

Species movement and behaviour have been altered by habitat loss, habitat degradation, and increased human land use (Tucker et al., 2018). In the Eastern Vidarbha Landscape, tigers also modulate their behaviour in response to ecological factors, such as time of day and habitat type, as well as anthropogenic features such as road density. Tiger behaviours were classified into three distinct states: *resting, area-restricted movement, and travelling*. During dispersal, tigers showed increased area-restricted movement and travelling states, along with faster and more directed movement, particularly outside protected areas where habitat patches are fragmented due to human settlements, agriculture, and roads. This increase during travel outside protected areas is energetically more costly, as tigers must navigate fragmented landscapes to reach suitable habitats during dispersal. They confined their movement to smaller areas between fragmented patches and shifted to faster movement at night, similar to the behaviour observed in the Persian leopard *pardus saxicolor*, black bear *Ursus americanus*, and Florida panther *Puma concolor coryi* (Karelus et al., 2019; Farhadinia et al., 2020; van de Kerk et al., 2015; Li & Bolker, 2017). During the pre-dispersal phase, they exhibited exploratory behaviour, emphasising area-restricted movement and travel. Tigers exhibited faster movement during dawn and dusk (Figure 6.4, Chapter 6), which is consistent with the nocturnal and crepuscular behaviour of the species (Karanth & Sunquist, 2000; Linkie & Ridout, 2011; Wang et al., 2015). This phase corresponds to subadult tigers exploring new territories beyond their mothers' range. In contrast, during the post-dispersal phase, individuals tended to remain in resting states in non-forest habitats to minimise interactions with humans while shifting to increased foraging in forested areas with less human interference. During this phase, tigers established stable or temporary home ranges and primarily allocated time to territorial movement (60%) and rest (40%). In forested habitats, tigers had a higher probability of area-restricted movement and resting (Figure 6.14, Chapter 6), indicating more active exploration or resting within specific forest areas. In non-forest habitats, they exhibited a higher persistence of travelling or resting, indicating that individuals either spent more energy by moving faster between patches or potentially conserved energy for subsequent activities.

In human-dominated landscapes, tigers may adapt flexible behavioural strategies to minimise the risk of human-induced mortality, enabling their existence in a human-dominated landscape. Variability in movement and habitat selection across dispersal phases and life stages has also been observed in species (Barry et al., 2020; Elliot et al., 2014). Species responses can be an interplay between behavioural state and habitat preferences, highlighting behavioural plasticity. Consequently, this study evaluated tiger habitat selection and movement patterns at both landscape and fine scales to understand the behavioural adaptability of tigers while selecting resources (Figure 7.1, Chapter 7). At the landscape level, factors such as vegetation cover, distance to water, human population, and road density significantly influenced tiger habitat selection (Figure 7.3; Chapter 7). Tigers tended to avoid areas with dense human populations and select areas distant from human settlements. They showed a preference for primary and minor roads for travel, likely because of reduced human activity, which facilitates animal movement. At a finer scale, tiger habitat selection was influenced by land use, vegetation cover, proximity to drainage, and forest fragmentation (Figure 7.4, Chapter 7). Tigers exhibited a preference for densely vegetated areas for resting and territorial movements, as these areas provide cover and shade. Additionally, they showed a preference for areas near drainage at this scale. Tigers avoided areas with agriculture and human settlements on a fine scale, which is consistent with their negative association with human disturbances. Furthermore, the behaviour-specific habitat selection concept implies that animals select habitats that meet specific behavioural requirements. During the pre-dispersal phase, tigers preferred forest and grassland areas to minimise human interactions, whereas sub-adult tigers actively explored new habitats. When dispersed through fragmented landscapes with high human pressure, tigers exhibited increased movement rates near drainage or streams, suggesting the use of these features as movement corridors during area-restricted behaviour. Dispersing individuals experience behavioural modifications and highlight the importance of accounting for behavioural states when concluding habitat selection. In the post-dispersal phase, habitat selection was influenced by forest, grassland, and vegetation cover across all behavioural states. By considering the intricate relationship between behaviour and habitat preferences, conservation initiatives can be adapted to effectively mitigate human-wildlife conflicts and promote coexistence in shared environments.

The study of animal movement, particularly in species such as tigers, provides crucial insights into their behaviour, habitat requirements, and responses to environmental changes. This study enhances our understanding of tiger ecology in human-dominated landscapes and underscores the importance of integrating behavioural ecology into conservation strategies.

8.2 Management Implications and Recommendations

This study provides new insights into the factors influencing tiger space use, movement, behaviour, and habitat selection in a human-dominated landscape. These findings inform conservation strategies for large carnivores in a human-dominated landscape and underscore the significance of preserving suitable habitats beyond protected areas to support dispersal and ensure the long-term survival of tigers. Conservation efforts can be adapted by considering factors such as habitat composition, human disturbances, forest fragmentation, and roads to safeguard vital habitats, reduce conflict between humans and wildlife, and establish connections between fragmented regions. Moreover, this study highlights the importance of considering behaviour-specific habitat selection and using an appropriate spatiotemporal scale in habitat studies. The specific management implications and recommendations are as follows.

1. Corridor Conservation and Restoration

Ecosystem networks ensure the movement of organisms and the subsequent interactions between species (Opdam et al., 2006; Hagen et al., 2012). These networks also consider various objectives in spatial planning, such as conservation goals and accommodating different land uses as desired by stakeholders (Opdam et al. 2006). Connectivity is a central concept in ecological networks, where a group of areas or ecosystems is interconnected to support and enhance population viability by facilitating movement (Beier, 1998; Opdam et al., 2006). Thus, protecting and restoring suitable habitats for tigers outside protected areas facilitates their dispersal and gene flow. This can involve creating wildlife corridors and promoting habitat connectivity to minimise the impacts of habitat fragmentation. A key strategy is to give precedence to conserving and reviving forested habitats with dense vegetation cover, which is fundamental for the habitat selection of tigers. This can be achieved by implementing habitat restoration projects and reforestation initiatives to enhance the quality of suitable tiger habitat. Another crucial step is to manage existing wildlife corridors to facilitate tiger movement across fragmented landscapes. These corridors play a significant role in connecting isolated habitat pockets, thereby enabling tigers to traverse different habitats. An effective conservation approach must involve collaboration between the local communities and stakeholders. This can lead to the development of land-use plans that prioritise tiger conservation and minimise habitat loss outside protected areas. Furthermore, habitat patches can serve as crucial stepping stones for long-distance dispersal and range expansion, particularly in response to climate-induced changes in habitat suitability (Saura et al., 2014). Enhancing the relationship between corridor design and species movement improves landscape connectivity. For instance, corridors identified through tracking studies have been more effective than those identified through modelling approaches (LaPoint et al., 2013). Subsequently, a telemetry based critical tiger corridor in the Vidarbha Landscape of Maharashtra was identified using the actual tiger movement. This is the first study in India in which actual tiger movement data have been used to identify tiger corridors.

2. Spatial planning and land-use management

The findings of this study emphasise the need to incorporate landscape structure and composition into conservation planning and land use management. This study revealed that factors such as forest cover proportion, habitat patch density, and human population within the tiger's movement range significantly impacted their spatial patterns. Therefore, conservation efforts should aim to maintain and increase forest cover, minimise habitat fragmentation, and limit human encroachment on tiger habitats. Strategic spatial planning plays a vital role in identifying and prioritising areas for conservation and restoration efforts. By utilising such planning approaches, we can maximise the effectiveness of conservation actions, especially outside protected areas. Furthermore, developing effective livestock management practices and reducing pressure on critical tiger habitats is crucial for minimising human-tiger conflicts. This can create a more harmonious coexistence between humans and tigers while conserving large carnivores and their habitats in a human-dominated landscape.

3. Road Planning and Management

Effective road planning and management are critical components of tiger conservation. First, a thorough assessment of the impact of roads on tiger movement is essential to identify potential issues and prioritise mitigation strategies. To ensure the safety of tigers and other wildlife, the construction of wildlife underpasses or overpasses should be considered at specific or critical tiger-crossing zones. These passages enable animals to cross roads without endangering themselves or causing traffic disruptions. Moreover, road planning measures must consider wildlife movement patterns to minimise the barriers that hinder free movement. By aligning road development with natural corridors and avoiding habitat fragmentation, we can facilitate tiger movements in the landscape. Collaboration with transportation authorities is vital for effectively managing roads that pass through tiger habitats. Thus, by incorporating proper road planning and management practices, the influence of roads on the movement of tigers can be minimised.

4. Addressing Habitat Fragmentation

To effectively mitigate habitat fragmentation and support tiger conservation, it is crucial to adopt a multifaceted approach. This includes identifying and safeguarding core areas and stepping stone habitats outside protected areas to facilitate tiger dispersal. Moreover, engaging with landowners and stakeholders is vital for promoting habitat connectivity and establishing land-use practices that are wildlife friendly. Monitoring these habitat patches and their effects on tiger populations is essential to inform adaptive conservation strategies. By combining these efforts, comprehensive measures that prioritise tiger conservation and encourage sustainable development practices can be implemented.

Understanding species movement allows managers to identify flexible management strategies in space and time. Thus, knowledge of the movement patterns of a species is a fundamental requirement for effectively implementing management practices, enabling managers to create scenarios that strike a balance between conservation priorities and alternative land use practices (O'Neal et al., 2008; Shillinger et al., 2008; Game et al., 2009; Redpath et al., 2013). By implementing these management implications and recommendations, stakeholders can contribute to long-term survival and conservation of tigers in human-dominated landscapes. These measures aim to preserve and restore suitable habitats, mitigate human-wildlife conflicts, address the challenges posed by roads and habitat fragmentation, and promote collaborative efforts to conserve and manage tiger populations.

PUBLICATIONS AND CONFERENCES

Received: 25 January 2022 | Revised: 24 August 2022 | Accepted: 26 August 2022

DOI: 10.1002/ece3.9307

Ecology and Evolution Open Access WILEY

NATURE NOTES

Long-distance dispersal by a male sub-adult tiger in a human-dominated landscape

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Abstract

Conservation of wide-ranging species and their movement is a major challenge in an increasingly fragmented world. Long-distance movement, such as dispersal, is a key factor for the persistence of population, enabling the movement of animals within and between populations. Here, we describe one of the longest dispersal journeys by a sub-adult male tiger (*Panthera tigris*) through GPS telemetry in Central India. We analyzed movement metrics, directionality, and space use during three behavioral stages of dispersal. We also used the clustering method to identify resting and kill sites ($n = 89$). T1-C1 dispersed a straight-line distance of 315 km over 225 days, moving an average of 8.38 km/day and covering a cumulative displacement of ~3000 km. Movement rate during post-dispersal was faster (mean = 0.47 km/h) than during dispersal (mean = 0.38 km/h) and pre-dispersal (mean = 0.13 km/h), respectively. The overall movement rate during the night (0.44 km/h) was significantly faster than during the day (0.21 km/h). Likewise, during dispersal, the movement was faster (mean = 0.52 km/h) at night than day (0.24 km/h). The average size of clusters, signifying resting and kill sites, was 1.68 ha and primarily away from human habitation (mean = 1.89 km). The individual crossed roads faster (mean = 2.00 km/h) than it traveled during other times. During the post-dispersal phase, T1-C1 had a space use of 319.48 km^2 (95% dBBMM) in the Dnyanganga Wildlife Sanctuary. The dispersal event highlights the long-distance and multiscale movement behavior in a heterogeneous landscape. Moreover, small forest patches play a key role in maintaining large carnivore connectivity while dispersing through a human-dominated landscape. Our study underlines how documenting the long-distance movement and integrating it with modern technology can improve conservation management decisions.

KEYWORDS
carnivore, displacement, habitat fragmentation, natal area, telemetry

1 | INTRODUCTION

Habitat loss and increased human land use are primary threats to many wildlife species, altering their movement and behavior (Tucker et al., 2018). Animal movement is further reduced by habitat fragmentation, degrading habitat quality and linear features such as roads (Andersen et al., 2017; Crooks et al., 2017; Fahrig, 2003; Jønsson et al., 2016; Shepard et al., 2008). Mammalian carnivores tend to have large home ranges and long dispersal distances, making them vulnerable to landscapes that have been fragmented by anthropogenic changes (Crooks et al., 2011; Dobson et al., 2006; Ripple et al., 2014). Long-distance dispersal is central to several ecological processes (Levin et al., 2003; Nathan, 2003), including gene flow (Trakhtenbrot et al., 2005), colonization of new areas, range shift, and functional connectivity between populations (Clobert et al., 2012; Noss et al., 1996; Weaver et al., 1996). The long-term population persistence in fragmented landscapes may depend on individuals traversing through a human-dominated landscape to reach suitable habitats (Watts et al., 2015).

In India, protected areas (PA) designated as tiger reserves cover 2.21% of the geographical region, and 35% of the total tiger population resides outside these PAs (Habib, Ghaskadbi, et al., 2021). The tiger populations are mostly confined to small protected areas because the habitat outside those areas is highly fragmented, which affects their movement within and outside protected areas (Habib, Nigam, et al., 2021; Thatte et al., 2018). Consequently, it is challenging for tigers to move through a fragmented and human-dominated landscape. Moreover, the long-term survival of the tiger population in a fragmented landscape depends on successful dispersal from one area to another, thus maintaining the connectivity between subpopulations and isolated populations.

Dispersal involves three successive behavioral stages: departure, transience, and settlement (Clobert et al., 2009). Accordingly, the dispersal behavior of sub-adult tigers can be classified into three distinct behavioral phases, that is, pre-dispersal, dispersal, and post-dispersal. The pre-dispersal phase is identified by the movement of individuals within their natal area. The dispersal phase involves movement from its area of birth to another habitat, where it reproduces and establishes a new territory (Howard, 2015; Waser & Jones, 1983). Post-dispersal phase is identified by movement in an area having a stable and defined home range over time. The movement behavior during dispersal in a highly interspersed mosaic of forested areas, agriculture fields, and human settlements is rarely documented. Studies on tiger dispersal are limited, and few have described long-distance dispersal primarily based on camera trap data and VHF/GPS telemetry (Sarkar et al., 2021; Singh et al., 2021; Smith, 1993; Wang et al., 2015). Moreover, genetic studies have shown gene flow over long distances (Anuradha Reddy et al., 2016; Gour et al., 2013; Joshi et al., 2013).

The advancement of GPS technology made it possible to gain new insights into tiger dispersal and how animals perceive and navigate through a landscape. Additionally, long-distance dispersal routes might help identify land use and landscape features that provide connectivity between non-contiguous populations (Graves et al., 2007). This study reports the longest dispersal distance recorded by a sub-adult male tiger from the Vidarbha region of Maharashtra, India. We documented movement and space use from the pre-dispersal to the post-dispersal phase and described the chronological event during dispersal. We analyzed the movement data from the GPS collar with environmental covariates (land use and vegetation cover) depicting the landscape through which the individual moved. Our study also quantified the characteristics of clusters (resting/kill) and the effect of linear features, that is, roads, on movement. We conclude by discussing the long-distance dispersal in a human-dominated landscape and its implications for conservation and management.

2 | MATERIAL AND METHODS

2.1 | Study area

The study was carried out within and outside of protected areas of Eastern Vidarbha Landscape (EVL), Maharashtra, India. This region is a part of the Central Indian Tiger Landscape, dominated by teak (*Tectona grandis*) and bamboo (*Dendrocalamus strictus*). The region encompasses an area of approximately 97,320 km^2, and forest cover accounts for 27.5% of the total area (Habib, Nigam, et al., 2021). The landscape is a mosaic of agricultural lands, human settlements and wildlife areas (Habib et al., 2017). Large carnivores in the region include tiger (*Panthera tigris*), which co-occurs with other species like leopard (*Panthera pardus*), sloth bear (*Melursus ursinus*), gaur (*Bos gaurus*), and several other ungulate species.

2.2 | Field methods

We captured and collared sub-adult male tiger T1-C1 on February 25, 2019. The individual was immobilized using a combination of Medetomidine hydrochloride, Ketamine hydrochloride, and Xylazine. The dosages were based on visual observation of body weight (150 kg) and age. The drug was remotely injected using an air-pressurized Dan-Inject projector (Model IM). The radio-collaring was part of a more extensive study in which sub-adult tigers were collared to understand the dispersal patterns, space use, and movement in a human-dominated landscape. Tigers were classified as sub-adult following (Sadhu et al., 2017). Animals were fitted with Iridium GPS radio-collars (Vectronics, Germany) and had a high spatial accuracy of location (±5 m). The collar was programmed to record locations every 1–3 h depending on the dispersal behavior of the individual. During the pre-dispersal phase, when the tiger was within its natal area, we received location every 3-h interval. During dispersal, when it moved out of its natal area, we programmed to receive intensive location every 1-h interval. During the post-dispersal phase, locations were received every 3-h time interval.

2.3 | Analysis

We calculated movement metrics (movement speed and turning angle) within each of three phases: pre-dispersal, dispersal, and post-dispersal. We identified these three phases by calculating the net squared displacement (NSD) in ArcGIS 10.6.1 with ArcMET tool (Wall, 2014). NSD is movement metrics that helps to understand movement behaviors over time (Bunnefeld et al., 2011). Inflection points and increase in the NSD over time help identify movement modes such as migration, dispersal, nomadism, and range residency (Börger & Fryxell, 2012). We identified dispersal movement and age from the peak in the NSD graph, which indicates the commencement of dispersal from its natal area.

We calculated daily distance traveled (sum of displacement in 1 day) and daily displacement (linear distance between the start and end locations for each 24-h period) during all three phases. We considered a 24-h period from the first location of dawn and the first location of the following dawn. We also estimated the mean movement speed (km/h) across the three dispersal phases. To calculate the movement speed, we scaled the step length (Euclidean distance between successive locations) divided by the time the individual took to complete the distance due to the varying interfix intervals (Leblond et al., 2016). The movement parameters were calculated using adehabitatLT (Calenge, 2015) and the animal movement tool (Signer et al., 2019) in the R programming software (R Core Team, 2020). We used the Kruskal–Wallis test to compare the mean movement speed during the pre-dispersal, dispersal, and post-dispersal phases as data were not normally distributed. Next, we used the Mann–Whitney *U* test to compare day and night movement speeds. To estimate the space use in each of the three phases, we applied the dynamic Brownian Bridge Movement Model (dBBMM) to estimate the utilization distribution in the package move (Kranstauber et al., 2012). The dBBMM requires a time-stamped series of animal locations and the estimated telemetry error associated with each location. The dBBMM allows the variance of the Brownian motion ($\sigma 2m$) to vary along the movement path for user-defined subsets of *n* locations. We then included these values in a Brownian bridge movement model to estimate 95% utilization distributions (UDs). We considered the 95% utilization distribution as space use in three dispersal phases.

To understand the directionality or orientation of the animal, we calculated the turning angles across the three phases. We estimated the circular mean, from the von Mises distribution of tuning angles (Mardia & Jupp, 1999). The mean turning angle is between $-\pi$ and π and defines the degree of linearity in an animal movement. A mean turning angle of zero implies a strong persistence in direction, whereas a mean turning angle of $-\pi$ or π suggests that movement is undirected. We used the package circular (Lund et al., 2017) to calculate the circular mean and test for directionality. All calculations and statistical analysis were carried out in program R 4.0.4 (R Core Team, 2020).

We identified resting and kill clusters formed during dispersal using the GPSeqClus package (Clapp et al., 2021). The algorithm uses time-series location data to sequentially aggregate locations to build clusters based on three user-defined criteria: search radius, temporal window, and minimum number of locations. We used the average step length per hour of T1-C1 as the search diameter for cluster identification. The maximum temporal window for cluster identification was 3 days, and we considered eight locations as minimum cluster locations. Resting and kill sites were validated from field observation. We calculated average cluster size, time spent, number of visits, and distance to the nearest forest edge and human settlement. To estimate habitat composition, we created a buffer of mean cluster radius around every cluster's median location and extracted the percentage of land cover in ArcGIS (10.6.1). The land use data of 60 m resolution were acquired from Bhuvan's open-source website (NRSA, 2016; http://bhuvan.nrsc.gov.in/). We also used normalized difference vegetation index (NDVI) to indicate vegetation cover of the resting clusters and kill sites. NDVI datasets from Landsat 8 were obtained from Google Earth Engine™ (GEE) between June 2019 and January 2020 at a spatial and temporal resolution of 30 m and 32 days, respectively (Gorelick et al., 2017). From the start date of each cluster, the nearest available mean NDVI was generated. NDVI value of one indicates a high density with green leaves, and a negative value indicates no vegetation.

3 | RESULTS

T1-C1 was tracked for 396 days and recorded 6240 GPS locations between February 2019 and March 2020. We describe the movement, exploration, and space use during the pre-dispersal, dispersal, and post-dispersal period. We report the chronological events that occurred during the dispersal. The space use during the pre-dispersal phase in the Tipeshwar Wildlife Sanctuary covered an area of 18.72 km^2 (95% dBBMM). The average daily distance covered was 2.76 km (range: 0.10–8.52 km), linear displacement of 1.33 km/day, and traversed maximum displacement of 5.46 km in a day (Figure 1a,b). The dispersal event spanned 225 days from June 21, 2019, to January 31, 2020, within a human-dominated landscape. T1-C1 traversed 2000 km by moving an average daily distance of 8.38 km (range: 0.05–31.75 km) and linear displacement of 6.19 km/day and covering a maximum daily displacement of 32.53 km. During dispersal, the utilization area was 1077.98 km^2 (95% dBBMM). The post-dispersal phase was identified by stable and territorial movement in the Dnyanganga Wildlife Sanctuary and covered an area of 319.48 km^2 (95% dBBMM). During this phase, it traveled an average daily distance of 9.29 km (range: 0.25–23.31 km) and linear displacement of 6.91 km/day (range: 0.003–26.31 km). The straight-line displacement between the natal area and the furthest location was approximately 315 km.

3.1 | Movement speed

The mean movement speed exhibited by T1-C1 was highest during post-dispersal (0.47 km/h; range: 0–3.26 km/h). During the

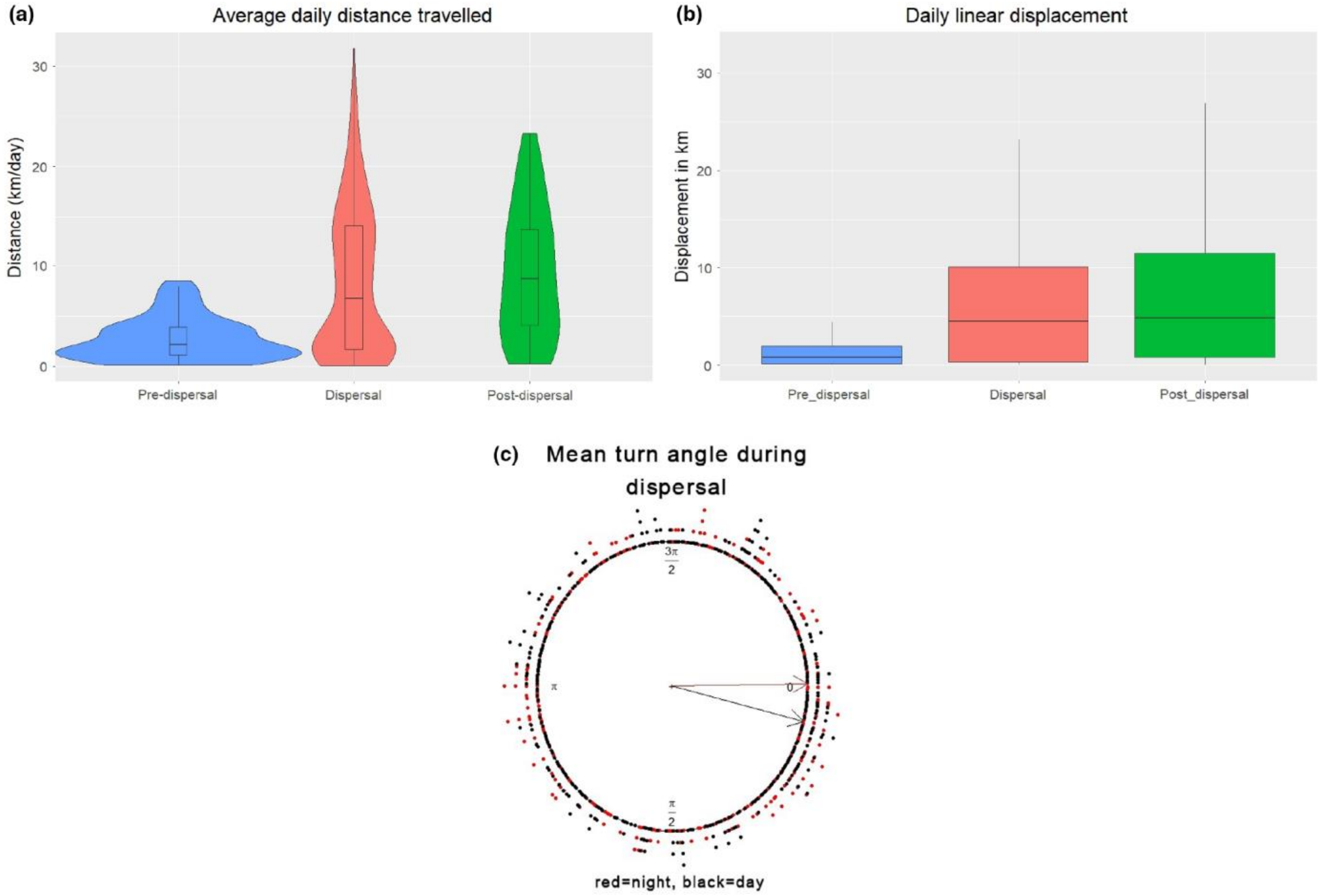

FIGURE 1 Movement of a sub-adult tiger (*Panthera tigris*) T1-C1 during pre-dispersal, dispersal, and post-dispersal phase in the Vidarbha Landscape of Maharashtra, India (a) average daily distance traveled, (b) daily linear displacement, and (c) mean turn angle during dispersal (red = night, black = day).

TABLE 1 Mean movement speed of a sub-adult tiger (*Panthera tigris*) T1-C1 during pre-dispersal, dispersal, and post-dispersal phase from the Vidarbha Landscape of Maharashtra, India.

	Movement (km/h)		
Phase	Overall (min–max)	Day (min–max)	Night (min–max)
Pre-dispersal	0.13 (0–2.56)	0.11 (0–2.56)	0.15 (0–2.29)
Dispersal	0.38 (0–3.50)	0.24 (0–2.36)	0.52 (0–3.50)
Post-dispersal	0.47 (0–3.26)	0.27 (0–2.15)	0.65 (0–3.26)

dispersal and pre-dispersal period, the average movement speed was 0.38 km/h (range: 0–3.50 km/h) and 0.13 km/h (range: 0–2.5 km/h), respectively (Table 1). During the pre-dispersal phase, there was no significant difference in the mean movement speed during the day (0.11 km/h; range: 0–2.56 km/h) and at night (0.15 km/h; range: 0–2.29 km/h). While dispersing, the average movement rate varied significantly between day (0.24 km/h, range: 0–2.36 km/h; $p < .001$) and night (0.52 km/h, range: 0–3.50 km/h). Similarly, mean hourly displacement at night (0.65 km/h; range: 0–3.26 km/h) was also more than day (0.27 km/h; range; 0–2.15 km/h) during the post-dispersal period ($p < .001$).

3.2 | Directionality

During the pre-dispersal phase, the movement of T1-C1 was undirected (mean turning angle = −2.88) suggesting uniform distribution of turning angle. During the dispersal, the mean turning angle was 0.11, indicating strong persistence in direction and linear movement. Moreover, the directional persistence or tendency to move in a straight line was more at night (mean turning angle = −0.01) than during the day (mean turning angle = 0.24; Figure 1c). During post-dispersal, the wide range in the mean turning angle ($\text{mean}_{\text{day}} = -0.60$; $\text{mean}_{\text{night}} = 0.24$) indicates a mix of tortuous and forward movement in the landscape.

3.3 | Chronological dispersal event

The dispersal event of T1-C1 occurred between two protected areas, Tipeshwar and Dnyanganga Wildlife Sanctuary, separated by a linear distance of 240 km. The movement during dispersal occurred in a landscape with a mosaic of tropical dry deciduous forest, open scrub, agricultural fields, and human habitation. T1-C1 began dispersing from the natal site, that is, Tipeshwar Wildlife Sanctuary, on June 21, 2019, at the age of 30 months. The density of tigers at the Tipeshwar WLS was reported 6.18 individuals/100 km^2 (Habib et al., 2020). T1-C1 initial movement was confined to a small plantation in a nursery adjacent to the park. During this period, there were two resting clusters, one within the plantation and the other 800 m away. After 12 days, the tiger started moving in the southern direction crossing the Painganga river into the state of Telangana. The forest patches that are located southward act as a wildlife corridor and connect to nearby protected places like the Painganga Wildlife Sanctuary and, further south, Kawal Tiger Reserve.

T1-C1 continued southward movement through the corridor, crossing a primary road (n = 1) and minor roads (n = 20). The southward trajectory was maintained until 12 July, covering a linear distance of 200 km from its natal area. However, T1-C1, on encountering a small village and an adjacent 4-lane national highway, turned and continued moving north along the same corridor path (Figure 2). This northward movement continued until 22 September and moved west along which the corridor extends. This westward trajectory movement continued for another 100 km, and then the tiger turned around and retraced his steps in the east direction. However, after traveling for a straight-line distance of 50 km, the tiger changed direction and moved toward the south during October 10–12, 2019.

The trajectory of T1-C1 after 12 October was west and northwestern direction moving through a mosaic of fragmented forest patches and primarily dominated by agricultural fields until it reached another forested area. It took him 25 days to get to this area after moving through a landscape with high human population, roads and railway lines. Until 27 November, the tiger explored the forested landscape with wild prey and domestic cattle kills and finally moved north to enter the Dnyanganga Wildlife Sanctuary. T1-C1 entered the sanctuary on 29 November, where he later established his area. However, before establishing a stable area in the sanctuary, he moved further 90 km west and southwest of the sanctuary, including the forested landscape of the Ajanta caves. After more than a month of exploring the landscape, T1-C1 movement was confined to the Dnyanganga Sanctuary and adjoining fragments of forest patches outside the PA and eventually had a defined core area within the sanctuary. We monitored the individual through camera trapping in the sanctuary for 10 months after the collar was removed. There was no report of the presence of tigers other than T1-C1 when it entered the sanctuary. However, co-predator like leopards was present in the area and adjoining forest patches.

Overall, the cumulative distance traveled by T1-C1 was 3000 km. During the dispersal phase, it traveled 2000 km and covered eight districts of Maharashtra and two states of India between June 2019 and January 2020. While traversing through a mosaic of forested and agricultural landscapes, we identified 89 clusters (forest = 73; outside forest = 16), of which 12 were known kill sites (Figure 3). The average size of the cluster was 1.68 ha (range: 0.001–10.74 ha; n = 89) in a human-altered landscape. The mean cluster size inside forest (1.91 ha; range: 0.01–10.74 ha) was significantly larger than in non-forested areas (0.62 ha; range: 0.001–3.30 ha; $p < .05$). The average cluster duration was less in the forest (38.41 h; range: 7–122 h) than in areas outside (46.31 h; range: 7–176 h). Moreover, T1-C1 spent more time in clusters with larger sizes (forest: 6–8 ha and outside forest: 2–4 ha); in both forest and non-forest areas (Table 2). The average cluster distance inside the forest was 2 km (range: 0.3–5.0 km) from human settlements, while in non-forested areas, it was 1.4 km (range: 0.52–2.5 km). The average NDVI value of clusters was 0.23 and ranged from 0.12 to 0.38. Overall, clusters had the highest proportion of forest (83.4%), followed by agriculture (11.4%), grassland (4.6%) and water (0.5%), respectively.

While dispersing through a human-dominated landscape, T1-C1 crossed linear features such as railway lines (n = 7), interstate highways (n = 34), and primary roads (n = 67) before reaching the Dnyanganga Sanctuary. The individual crossed primary roads more at night (n = 51) than day (n = 16). Similarly, it crossed highways at night (n = 29) more often than day (n = 5) while dispersing in a human-dominated landscape. The movement rate significantly increased when crossing roads (mean = 2.00 km/h) than traveling in non-road areas (mean = 0.30 km/h; $p < .05$). Subsequently, the trajectory path of T1-C1 showed territorial movement behavior confined to the sanctuary and adjoining forested landscape. Therefore, after tracking for more than a year, the GPS radio-collar was removed using a drop-off mechanism.

4 | DISCUSSION

We recorded one of the longest dispersals of a male tiger, traveling a maximum linear distance of 315 km in a human-dominated landscape. The dispersal journey was remarkable for its length, duration, and movement through a highly interspersed mosaic of forested areas and agricultural fields. Evidence of such long-distance dispersal in tigers has been recorded previously in a few studies through radiotelemetry (VHF and GPS), intensively monitored populations (camera traps) and genetic studies across various landscapes in the Indian subcontinent (Gour et al., 2013; Reddy et al., 2012; Sarkar et al., 2016, 2021; Singh et al., 2021; Smith, 1993). Such movement occurs in both sexes, with males moving longer distances from few kilometers to hundreds of kilometers (Table 3) and can be influenced by various factors. In general, male dispersal is related to intrasexual competition for mates, inbreeding avoidance, and resource competition (Dobson, 1982; Greenwood, 1980; Perrin & Vladimir, 1999; Pusey & Wolf, 1996). Information from long-distance dispersal thus provides knowledge and helps identify functional corridors, which are crucial to designing conservation policies for large-ranging species like tigers.

The dispersal journey of T1-C1 involved three distinct movement phases and traveled a cumulative distance of ~3000 km from its natal area to the site where it localized after dispersal. The dispersal route of a large-ranging carnivore like tigers highlights the multiscale nature of the individual movement and the ability to navigate a heterogeneous landscape. The dispersal event started during the monsoon and lasted until winter. During the period of monsoon, vegetation cover, availability of water, and productivity in

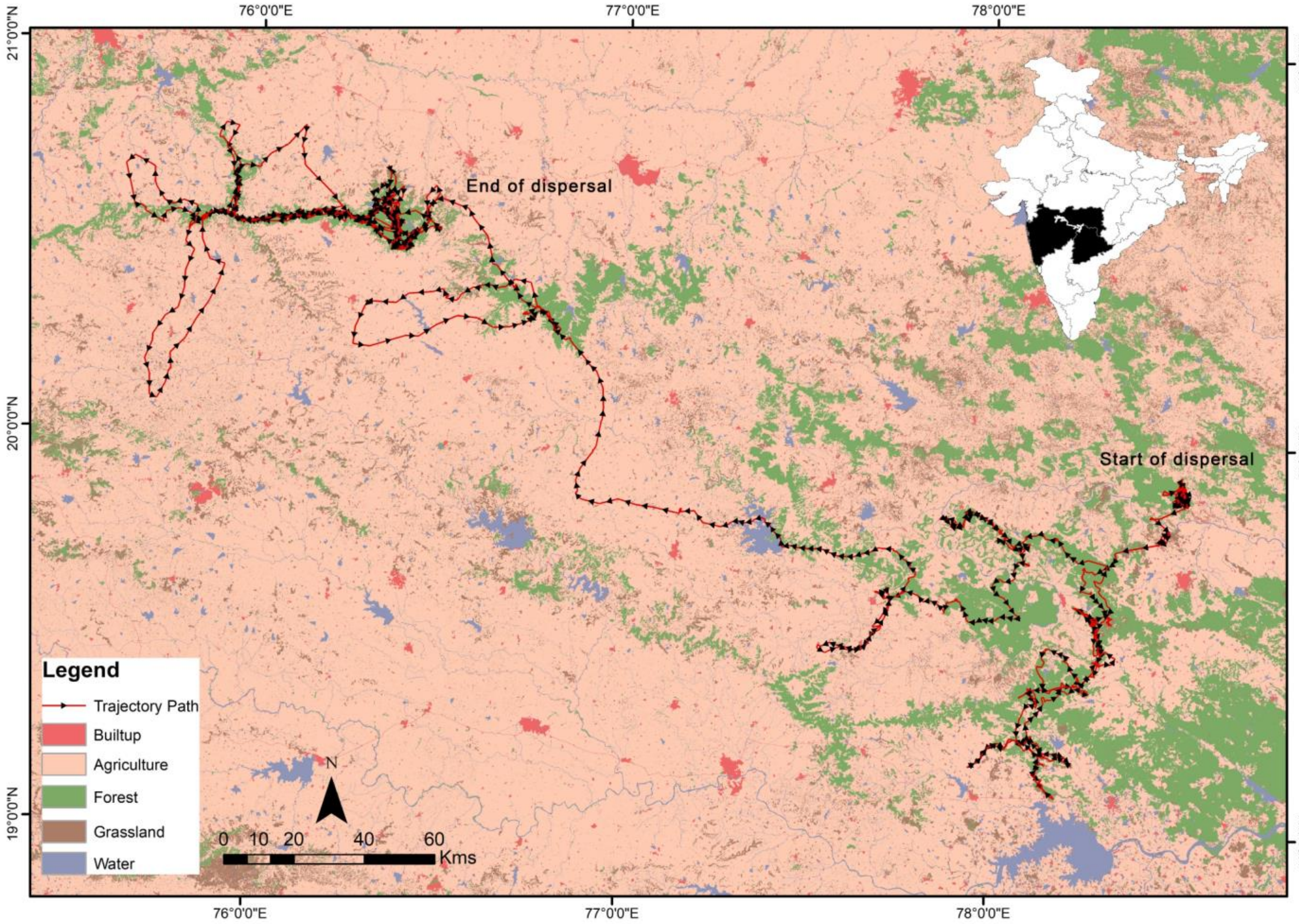

FIGURE 2 Dispersal movement of a sub-adult tiger (*Panthera tigris*) T1-C1 from Tipeshwar to Dnyanganga Wildlife Sanctuary traveling through a human-dominated landscape.

dry deciduous habitat increases, making dispersal more permeable through a human-dominated landscape. Moreover, the agricultural fields with growing crops act as a cover for dispersal. Additionally, the availability of livestock increases as they are left to graze in the forested areas and form easy prey for dispersing tigers.

During post-dispersal, we found that the daily distance traveled and displacement was higher than in the dispersal and pre-dispersal phases. We also found a wide range in turning angles, suggesting the movement to be more tortuous and forward movement. This is probably because of the environmental features and mosaic of habitats within the landscape that influences movement. T1-C1 space use included multiple core areas (17.29 km^2) within the Dnyanganga Sanctuary and encompassed a larger fragmented area, including forest and agricultural fields outside the PA. Thus, it adapted a high territorial movement to cover a more extensive territory while criss-crossing agriculture fields and forested areas in a human-dominated landscape. Similarly, studies on cougars and lions exhibited higher speeds while traversing through fragmented human-dominated areas to reduce time spent in multiple-use areas (Kertson et al., 2011; Valeix et al., 2012). Moreover, temporal changes in movement speed allow the individual to cover longer distances and more fragmented forest patches occurring both inside and outside the sanctuary. Thus, it minimizes the anthropogenic disturbances by moving more at night (0.65 km/h) than during the day in a human-dominated landscape. Similar movement behavior was reported in tigers that exhibited higher speeds outside PA and at night (Habib, Ghaskadbi, et al., 2021).

The movement was more linear with strong directional persistence during dispersal with a maximum mean movement speed of 3.50 km/h during the night. Altered movement patterns due to habitat fragmentation and human pressure have been observed in many carnivore species worldwide (Poessel et al., 2014; Tigas et al., 2002; Tucker et al., 2018). His movement was more confined and restricted within small forest patches and sheltered in these patches during the day (mean turn angle = 0.24). While at night, it traveled extensively from one forest patch to another interspersed in the landscape with high directional persistence (mean turn angle = −0.01). This variability in movement behavior can be attributed to behavioral plasticity while moving through a human-dominated landscape, thus minimizing human encounters and reducing anthropogenic pressure. Moreover, change in land use and increase fragmentation limits the movement of dispersing tigers. To negotiate movement in such a human-dominated area, animals move faster at night with more directionality (Habib, Ghaskadbi, et al., 2021; Ordiz et al., 2017).

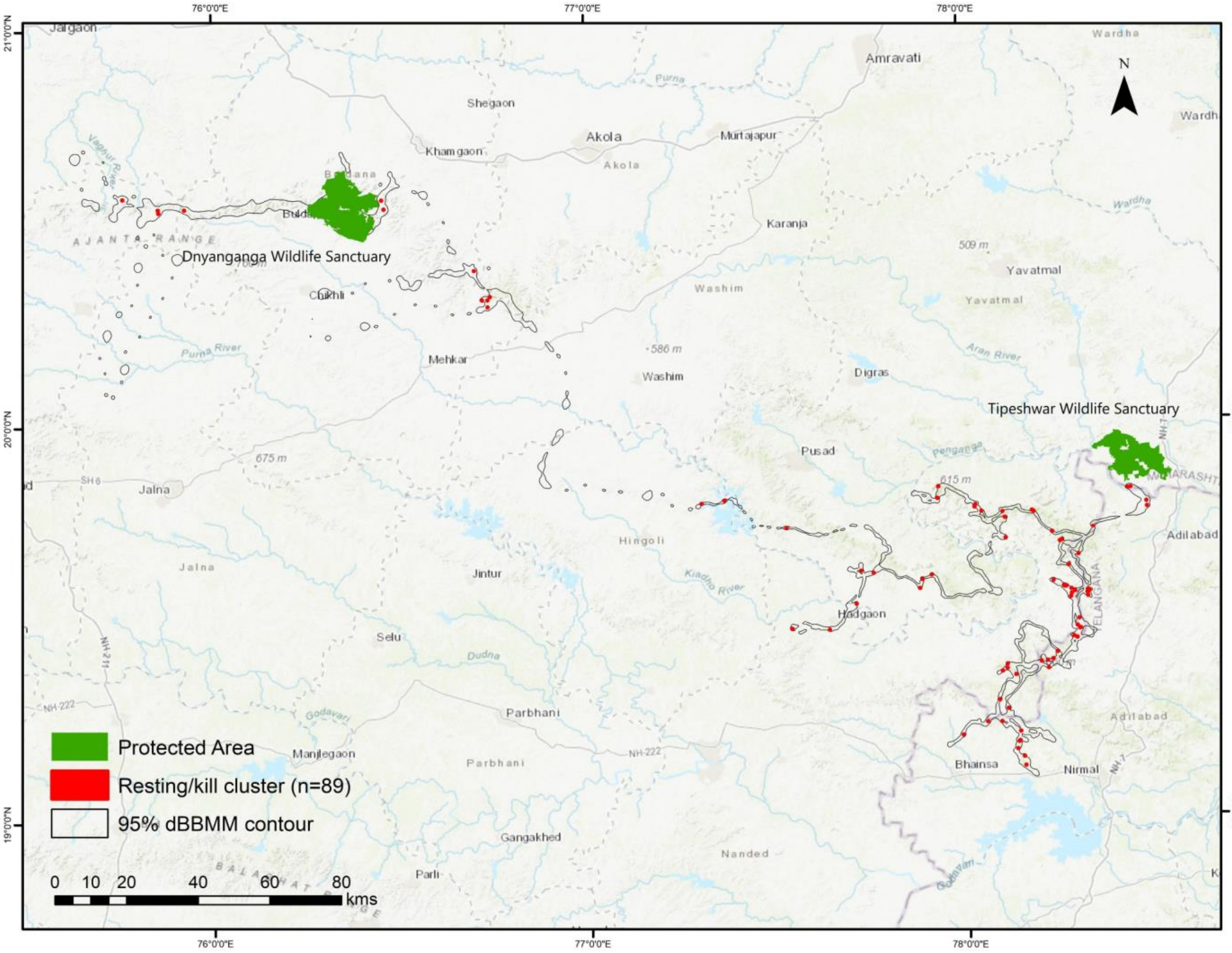

FIGURE 3 Resting clusters and kill sites of a sub-adult tiger (*Panthera tigris*) T1-C1 during dispersal in a human-dominated landscape. The dispersal direction is from Tipeshwar to Dnyanganga Wildlife Sanctuary.

TABLE 2 Cluster characteristics (cluster size, number of clusters, time duration, and distance to human settlements) of a sub-adult tiger (*Panthera tigris*) T1-C1 while dispersing through a human-dominated landscape in the Vidarbha Landscape of Maharashtra, India

System	Cluster size (ha)	Number of clusters	Mean time spent (h) ± SD	Number of visits	Mean NDVI ± SD	Distance to forest edge (m) ± SD	Distance to human settlement (m) ± SD
Forest	0–2	43	32.98 ± 25.66	2	0.23 ± 0.05	433.07 ± 357.19	1898.78 ± 1159.15
	2–4	22	47.36 ± 28.18	2	0.24 ± 0.05	438.46 ± 311.19	2207.30 ± 778.83
	4–6	4	20.75 ± 12.61	2	0.21 ± 0.07	606.77 ± 444.59	1302.89 ± 687.84
	6–8	3	68.00 ± 52.12	4	0.20 ± 0.04	223.30 ± 257.54	2150.23 ± 394.60
	>8	1	57.00	3	0.26	1279.93	3337.51
Non-forest	0–2	14	42.43 ± 57.35	2	0.20 ± 0.05	1245.77 ± 1607.74	1345.46 ± 737.41
	2–4	2	73.50 ± 94.05	3	0.17 ± 0.02	1238.92 ± 4.74	1441.57 ± 600.36

The clusters formed along the dispersal path highlighted the characteristics of resting places or short-term refugia and also acted as kill sites, where it persisted mainly on domestic cattle. Our result shows that T1-C1 spent less time per event in larger clusters inside the forest and more time in smaller clusters outside forested areas. The differential cluster size and time spent in non-forest areas with respect to forested areas can be attributed to the mosaic habitat and anthropogenic disturbances. The habitat patches in a human-dominated landscape are at varying distances from each other and interspersed with agricultural fields. Due to the fragmented habitat outside forested areas, small clusters were observed between forest fragments as probable resting sites. Such clusters were away from human settlements, primarily in moderate-to-high vegetation cover. However, the time spent in these small clusters was higher as the animal would be compelled

TABLE 3 Details of dispersal studies on tigers in the Indian subcontinent and distance traveled by males from their natal area during dispersal

Author	Place	Method	Euclidean dispersal distance (km)	Cumulative distance covered (km)
Smith (1993)	Royal Chitwan National Park, Nepal	VHF collar	71	–
Sarkar et al. (2016)	Panna Tiger Reserve	VHF/GPS/Satellite collar	250	440
Murthy (2017)	Bandhavgarh Tiger Reserve	Camera trapping	280	–
Sadhu et al. (2017)	Ranthambhore Tiger Reserve	Camera trapping	220	–
Singh et al. (2021)	Ranthambhore Tiger Reserve	Camera trapping	148.4	–
Current study (T1-C1)	Vidarbha Landscape	GPS collar	315	~3000

to rest in these refuge patches during the daytime when human activity is maximum. As human activity reduces at night, the animal can move between forest fragments situated far away from each other. Whereas, in forested areas, the habitat is contiguous, making movement more conducive during day and night. Thus, the animal spent less time resting in larger clusters, perceiving a low risk attributed to human activity and anthropogenic disturbances.

In addition to the landscape heterogeneity, linear features such as roads affect the rate of movement while crossing roads compared to when traveling in non-road areas. Moreover, T1-C1 avoided high-traffic roads by crossing roads at night as animal perceives roads and human activity as risk (Frid & Dill, 2002; Northrup et al., 2012; Thurfjell et al., 2015). Thus, linear features such as roads can act as barriers to animal movement either through mortality, displacement, or behavioral avoidance, depending on the landscape (Anderson, 2002; Forman et al., 2003; Scrafford et al., 2018; Shepard et al., 2008). Consequently, habitat mosaic and landscape structure greatly influence dispersal patterns by facilitating or restricting movement (Holderegger & Wagner, 2008).

4.1 | Conservation implications

The study highlights the importance of documenting long-distance dispersal by GPS telemetry, otherwise difficult to record at such a fine temporal scale. The dispersal event of T1-C1 has interesting conservation implications as it moved through a human-dominated landscape. While dispersing, the animal crossed numerous barriers such as rivers, national highways, major roads, and railway lines. The journey through a mosaic of land use revealed the significance of fragmented areas or refuge islands and dispersal corridors. The dispersal route provided the possible functional connectivity between the primary tiger habitat in Maharashtra and Telangana. However, the growing human population and further expansion of urban areas could compromise connectivity and influence movement. Because the tiger population relies upon dispersal between patches of primary habitat and adjoining landscape, land management and government agencies must consider enhancing connectivity and restoration of fragmented patches for the population's long-term survival. The study also highlights the importance of small forest fragments in a landscape, which are essential in maintaining connectivity. Thus, successful animal dispersal indicates functional connectivity among habitats and can be used as an indicator for wildlife recovery.

AUTHOR CONTRIBUTIONS

BH and PN conceived ideas and designed methodology; ZH carried out fieldwork, analyzed the data, and led the writing of the manuscript. PG helped in field data collection. RG and PP helped in capture and local field support. All the authors contributed critically to the draft and gave final approval for publication.

ACKNOWLEDGMENTS

We are thankful to the Ministry of Environment, Forest and Climate Change (MOEFCC) and Maharashtra Forest Department (MFD) for the permission to collar animals and conduct research. MFD is duly acknowledged for the funding provided to carry out the research project. We are also thankful to the Field Directors, DFOs, RFOs, forest guards, and watchers for their constant support, advice, and input during the fieldwork in the Vidarbha landscape. We are also grateful to our field assistants (Irfan, Mangesh, Noor, Rama, and Roshan) for providing constant support and necessary help throughout the study. I am thankful to Dr. Hussain Reshamwala and Mr. Shaheer Khan for their critical thought in the analysis. We thank the Director, Dean, and Research Co-ordinator of the Wildlife Institute of India and Chief Wildlife Warden, Govt. of Maharashtra, for supporting the study.

FUNDING INFORMATION

Funding was provided by Maharashtra Forest Department, Government of Maharashtra.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The dispersal data of the endangered species contain location data outside protected areas, which are prone to poaching and human prosecution. Moreover, the movement corridor and forested areas are used by other tigers and will make other dispersing individuals prone to many risks including poaching. Because of conservation reason, our request may be considered not to share the location data.

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How to cite this article: Hussain, Z., Ghaskadbi, P., Panchbhai, P., Govekar, R., Nigam, P., & Habib, B. (2022). Long-distance dispersal by a male sub-adult tiger in a human-dominated landscape. *Ecology and Evolution*, *12*, e9307. https://doi.org/10.1002/ece3.9307

Received: 25 July 2020 | Revised: 16 November 2020 | Accepted: 4 December 2020

DOI: 10.1002/ece3.7156

ORIGINAL RESEARCH

Ecology and Evolution Open Access WILEY

Not a cakewalk: Insights into movement of large carnivores in human-dominated landscapes in India

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Funding information
Funding was provided by Maharashtra Forest Department and Department of Science and Technology, Govt. of India.

Abstract

Large carnivores play an important role in the functioning of ecosystems, yet their conservation remains a massive challenge across the world. Owing to wide-ranging habits, they encounter various anthropogenic pressures, affecting their movement in different landscape. Therefore, studying how large carnivores adapt their movement to dynamic landscape conditions is vital for management and conservation policy.

A total of 26 individuals across 4 species of large carnivores of different sex and age classes (*14 Panthera tigris, 3 Panthera pardus, 5 Cuon alpinus, and 4 Canis lupus pallipes*) were GPS collared and monitored from 2014–19. We quantified movement parameters (step length and net squared displacement) of four large carnivores in and outside protected areas in India. We tested the effects of human pressures such as human density, road network, and landuse types on the movement of the species. We also examined the configuration of core areas as a strategy to subsist in a human-dominated landscape using BBMM.

Mean displacement of large carnivores varied from 99.35 m/hr for leopards to 637.7 m/hr for wolves. Tigers outside PAs exhibited higher displacement than tigers inside PAs. Moreover, displacement during day–night was significantly different for tigers inside and outside PAs. Similarly, wolf also showed significant difference between day-night movement. However, no difference in day–night movement was found for leopard and dholes. Anthropogenic factors such as road length and proportion of agriculture within the home range of tigers outside PAs were found to be significantly different. All the habitat variables in the home range showed significant difference between the social canids. The core area size for tiger outside PA and wolf was found greater than PAs.

The study on movement of large carnivore species across landscapes is crucial for conservation planning. Our findings can be a starting point for interlinking animal movement and landscape management of large carnivore conservation in the current Anthropocene.

KEYWORDS

canids, core areas, displacement, felids, movement ecology, radio telemetry

1 | INTRODUCTION

Across the globe, large carnivores are considered as the most charismatic yet vulnerable components of their ecosystems (Miquelle et al., 2005). Positioned at the top of food chains, they influence all trophic levels, thereby shaping the entire community (Ripple et al., 2014). However, throughout their distributional range, large carnivore populations continue to decline rapidly due to anthropogenic pressures such as habitat degradation and fragmentation, depletion of wild prey, persecution, and illicit commercial trade in body parts (Weber & Rabinowitz, 1996).

Owing to their wide range requirements, large carnivores inherently occur at low densities across their distribution (Woodroffe & Ginsberg, 1998). However, the idyllic contiguous landscapes required for the long-term conservation of such species are being increasingly compromised due to competition with humans over space. To survive, large terrestrial predators must negotiate human-modified landscapes adjoining protected areas (PAs) which are under various landuse types. Such peculiar scenarios may lead to perceived or potential human–wildlife conflict posing a risk to the existence of wildlife in the area. Consequently, large carnivore conservation has become the prime focus of various stakeholders from scientists to policymakers (Linnell et al., 2001; Treves, 2009; Weber & Rabinowitz, 1996).

India is known for its rich biodiversity and is home to the highest number of large terrestrial carnivores (average body weight > 15 kg) in the world (Johnsingh, 1986). It also ranks 2nd in the world human population with 1.3 billion people and a density of 450 people per km^2 (UN World Population Report, 2017). Based on the World Bank Report (2015), 60.4% of the total land in India is under agriculture resulting in a habitat matrix of human agricultural landscapes interspersed with PAs. As a result, humans are in direct competition with wildlife over limited resources, particularly, space. India is also home to 25% of world's cattle and holds the highest number of the world's livestock (19th All India Livestock Census, 2012). In conjunction with agriculture, the country's total road length is spread over 5.6 million km, with the highest global density of 1.70 km roads per square kilometer of land (Basic Road Statistics of India, 2016).

In this setting, survival of large carnivores depends on their ability to adapt to the human-modified environment. The movement parameters of species are shaped in response to the dynamic structure of a landscape (Fahrig, 2007) and plays a major role in obtaining resources, evading threats, dispersing and finding mates (Clobert et al., 2009; Swingland & Greenwood, 1983). Consequently, this affects population dynamics through genetic connectivity as well as individual fitness (Morales et al., 2010; Nathan et al., 2008). Extrinsic factors such as habitat quality, resource availability, as well as anthropogenic features (settlement, roads, landuse changes, population density) also influence animal movement. Many studies have shown that anthropogenic features may affect animal movement either way (Andersen et al., 2017; Evans et al., 2019; Kerley et al., 2002; Kozakai et. al., 2013; Trombulak & Frissell, 2000; Webb et al., 2011).

Large carnivores exhibit different movement patterns and space use across landscapes due to their wide-ranging and varied territorial behavior. The rapid rate at which landscapes are changing may compel wide-ranging terrestrial mammals to adapt and change their movement patterns for long-term survival. The PAs in India are small, isolated with compromised functional connectivity (Chundawat et al., 2016; Mondal et al., 2016) and wide-ranging large carnivores need to move through areas with varying degrees of human activity to maintain healthy populations. However, they may be reluctant to cross certain habitat boundaries (Haddad, 1999). The study of movement parameters of such species is imperative to gain insights into fundamental biological processes like dispersal strategies, foraging, social interactions, and general patterns of space use that play a major role in determining community and population structures (Nathan et al., 2008).

The advancement of GPS technology has revolutionized animal tracking studies (Cagnacci et al., 2010; Kays et al., 2015). The fine-scale location data at varied temporal and spatial scales allow more rigor and accuracy in such studies. In this paper, we studied the movement parameters of four large carnivores in the Central Indian Landscape, India. We evaluated the movement patterns of tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*), and wolves *(Canis lupus pallipes)* in different systems, that is, protected area and outside protected area. We examined the effect of landuse, human density, and road length as surrogates of human footprint on the movement of these wide-ranging species across PAs and outside PAs. We hypothesized that 1. species outside PA would travel more (i.e., with longer displacement) than present in PA, 2. species will move faster at night in outside PA, and 3. species movement will be more in the human-dominated landscape because of environmental and anthropogenic factors.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted across various PAs and outside PAs in the state of Maharashtra, India. This includes the Eastern Vidarbha Landscape (EVL) of the Nagpur and Chandrapur Divisions and districts of Pune and Solapur. The study on tigers, dholes, and leopards was conducted in EVL across 2 PAs (Tadoba Andhari Tiger Reserve and Umred Karhandla Wildlife Sanctuary) and outside PA (Brahmapuri Forest Division). EVL encompasses an area of approximately 50,000 km^2 and 40% of forest cover of the total area. It also has 8,540 villages with a human population of >10 million people which makes the landscape matrix of agricultural lands and wildlife areas. (Habib et al., 2017). The habitat in the landscape is primarily tropical dry deciduous forest with teak (*Tectona grandis)* and bamboo *(Dendrocalamus strictus)* as the dominant flora and is home to an estimated number of 312 tigers (range 270–354) (Jhala et al., 2020). The study on wolves was conducted across the grasslands of semi-arid landscapes in two districts of Pune and Solapur in Maharashtra.

This semi-arid region receives less rainfall that makes it suitable for wolves. The summer season is very dry and extremely hot, with temperatures regularly exceeding 45°C. The terrain is gently undulating with mild slopes and flat-topped hillocks with intermittent shallow valleys, which form the major drainage channels. Crop fields, grazing lands, scrublands, grasslands, villages, and open forest (Figure 1) dominate the area.

2.2 | Study species

The Tiger (*Panthera tigris tigris*), Asia's largest obligate terrestrial carnivore is categorized as Endangered under the IUCN Red List of Threatened Species. In India, it is listed in Schedule I of the Indian Wildlife (Protection) Act, 1972, under the highest level of protection. Tigers are wide-ranging, territorial felids, and Tropical

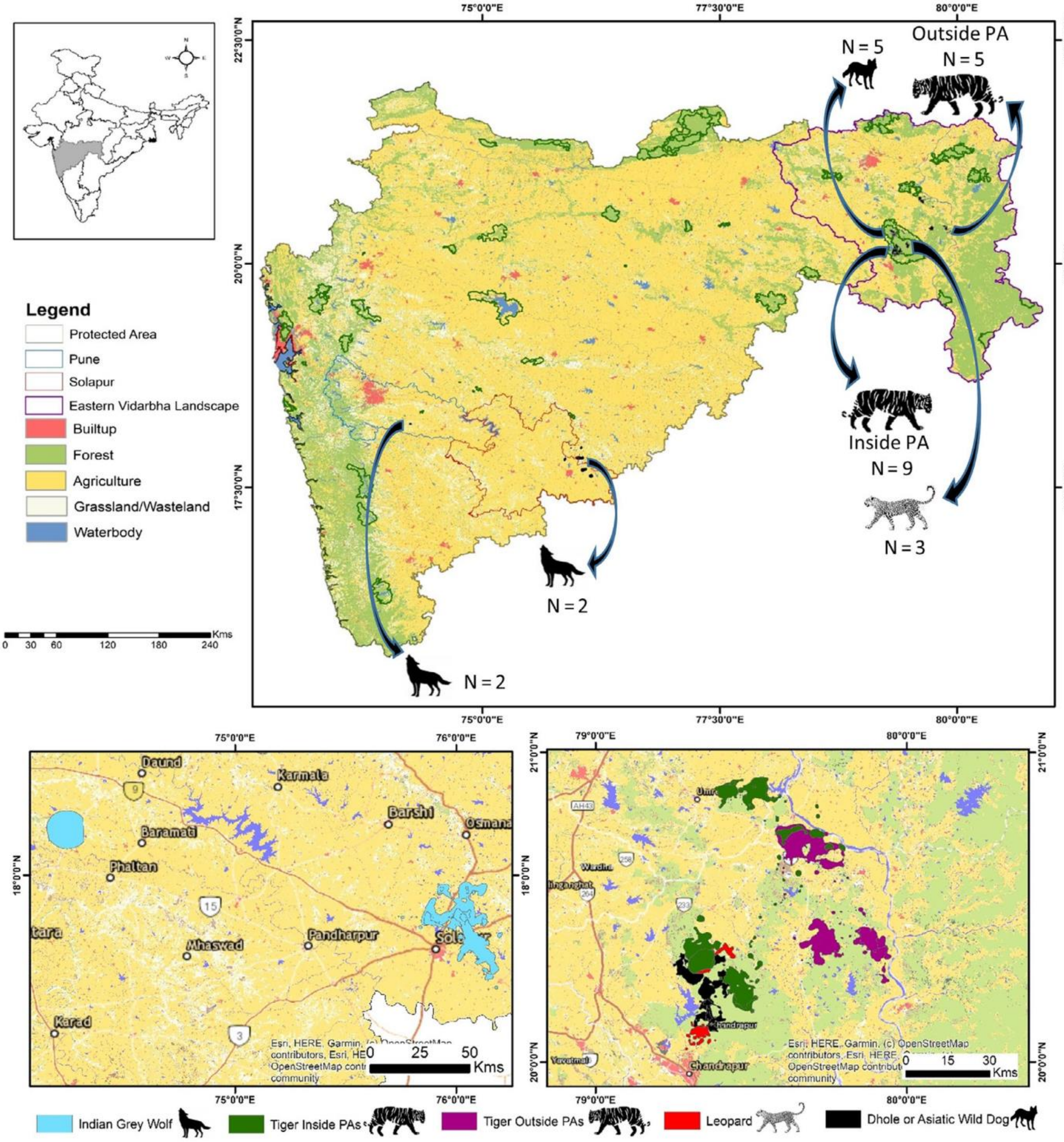

FIGURE 1 Map of study sites (top) with landuse and protected areas, (below left) home ranges of wolves and (below right) home ranges of tigers inside and outside PA, leopard, and dhole in Maharashtra, India

Dry Forest is the largest habitat that supports tiger populations in the Indian subcontinent (Smith et al., 2011; Wikramanayake et al., 1998). Most of the tiger populations are present in PA's but their size in India is too small to maintain viable populations of this species over time. Several studies on tigers were carried out to understand the home ranges patterns and size of home range can be highly variable across their habitat and landscape (Chundawat et al., 1999; Goodrich et al., 2010; Jhala et al., 2010; Naha et al., 2016; Sarkar et al., 2016; Sunquist, 1981). However, information on their movement parameters and the impact of environmental and anthropogenic features is not studied so far in India.

The leopard *(Panthera pardus)* is a highly adaptable, widely distributed felid, and is listed as Vulnerable under the IUCN Red List. In India, the leopard is also listed in Schedule I of the Indian Wildlife (Protection) Act, 1972. Wherever leopards coexist with tigers, lions, and dholes, a high degree of intraguild competition is observed (Hayward & Slotow, 2009; Wang & Macdonald, 2009). Leopards display great behavioral plasticity by shifting feeding preferences, space use, microhabitat use, and activity pattern (Karanth & Sunquist, 2000) which enables them to survive in human-altered landscapes.

The Asiatic wild dog *(Cuon alpinus)* or dhole, is a social canid and is the only extant species of the genus *Cuon*. The monotypic species is listed under the Endangered category of the IUCN Red List and is protected under Schedule II of India's Wildlife (Protection) Act, 1972. Throughout their range, dholes are one of the top predators of tropical forests. In India, dholes share habitat with large carnivores like the tiger and leopard. Previous studies on dholes have focused on the intraguild competition, behavioral ecology, and genetics (Acharya, 2007; Ghaskadbi et al., 2016; Habib, Ghaskadbi, et al., 2018; Hayward et al., 2014; Johnsingh, 1980; Modi et al., 2018) but information on their movement ecology is limited.

The Indian wolf *(Canis lupus pallipes)* is distributed across Central India, up to Rajasthan in the north and Karnataka in the south (Shahi, 1982), and their population is estimated at 2000–3000 individuals (Jhala, 2000). They are categorized as Endangered by the IUCN Red List of Endangered Species. It is protected under Schedule I of the Wildlife (Protection) Act 1972. The Indian wolf is an iconic top predator in the open grasslands and adapted themselves to survive in the human-dominated landscape (Shahi, 1982; Jhala, 1991; Habib, 2007. Studies on *C. l. pallipes* suggest that this species is a part of an ancient clade which has not mixed with the wolf-dog clade, making them unique among other wolves of the world (Sharma et al., 2004; Shrotriya et al., 2012). Few studies have been conducted to estimate home range size but information on their movement is not studied so far in India. The average home range reported using minimum convex polygon method for three packs of Indian wolf ranged from 113.4 to 227.6 km^2 (Jethva, 2003). The study conducted in southern Maharashtra found the average home range of the four packs was 183.58 ± 22.9 km^2, with the average core area (50% MCP) of 9.74 km^2 (Habib, 2007).

2.3 | Capture and radio-collaring

Overall, 26 individuals across 4 species of large carnivores were radio-collared (Figure 1) and monitored from years 2014–19. The animals were fitted with GPS collars that were programmed to take fixes at different intervals (Table 1). The GPS data was downloaded from satellite links (Iridium and Globalstar) as well as UHF ground download receiver. The animals were intensively tracked in the field using VHF ground tracking.

We captured 14 tigers (nine from PAs; five outside PA) across different age and sex classes (Table 1). The captured tigers were initially identified for collaring by field-based monitoring and camera trapping. After identification, the individuals were tracked and immobilized using combination of Medetomine hydrochloride, Ketamine hydrochloride, and Xylazine (dosages based on the body weight, age, and sex). Dosage was injected remotely using an air-pressurized Dan-Inject projector (Model IM) from an open-top vehicle, and the immobilized animal was approached. Collared tigers were monitored intensively between 2014–19 to study their movement and ranging patterns. We followed the same protocol for capturing dholes and used the drug combination of Tiletamine and Zolazepam (Zoletil 100, Virbac) (Van Heerden et al., 1991). The drug mixture was delivered from a vehicle remotely using a Dan-Inject projector (Model JMSP.25). We captured 5 dholes across age and sex classes including three adult males, one subadult male, and one adult female. The dholes were intensively monitored from 2017–18 to study their ranging pattern. Furthermore, 3 leopards (two females and one male) were captured using baited cage and monitored from 2014–15. Baited cage was allured by a live goat (to lure the animal toward the trap) kept in a separate chamber inside the cage, and when the animal approaches the prey, a mechanical trapping system gets activated to slide down the rear door to trap the animal. The trapped animals were immobilized using a drug mixture of Ketamine and Xylazine. Between 2017 and 2018, 4 wolves consisting of two males and two females were collared in the semi-arid landscape of Maharashtra. Wolves were captured using soft-catch leghold traps. Traps ($n = 25$) were set up in a circle, placed ~20 cm away from each other, and wolf gland lure No. 100 (Stanley Hawbaker and Sons, Fort London, Pennsylvania) was used as an attractant to trap wolves (Habib, 2007). Traps were monitored continuously and trapped wolves were captured using double-threaded nylon hockey net (Habib & Kumar, 2007) and immobilized using a Ketamine–Xylazine drug mixture. The average time for capturing of an individual wolf was 41.06 ± 21.54 hr.

2.4 | Understanding movement parameters

We assessed the movement patterns of 4 large mammals using two movement parameters, such as mean displacement (step length) and net squared displacement (NSD). Displacement is defined as the straight-line distance between two consecutive GPS locations of an animal trajectory. Varying interfix intervals across species were made uniform by

TABLE 1 Species-wise detail of each individual's characteristics, number of locations used, habitats, and type of collars used to study the movement of 4 large carnivores in India

Species	Individual ID	Sex	Age	Habitat/ System	GPS location acquired	Monitoring days	Monitoring period	Collar type
Wolf	W1	Female	Subadult	Outside PA	6,748	615	25.12.17 to 01.09.19	Iridium, UHF/VHF/Activity
Wolf	W2	Male	Subadult	Outside PA	2,148	217	28.12.17 to 01.08.18	Iridium, UHF/VHF/Activity
Wolf	W3	Female	Adult	Outside PA	6,049	604	22.01.18 to 16.09.19	Iridium, UHF/VHF/Activity
Wolf	W4	Male	Adult	Outside PA	VHF Collar	604	22.01.18 to 16.09.19	VHF/Proximity Collar
Tiger	T07	Female	Adult	PA	1,871	520	17.10.14 to 20.03.16	Iridium, VHF/Activity
Tiger	Umred F	Female	Subadult	PA	2,109	308	12.03.18 to 13.01.19	Iridium, VHF/Activity
Tiger	T17	Female	Subadult	PA	1,687	267	07.03.17 to 28.11.17	Iridium, VHF/Activity
Tiger	T42	Male	Adult	PA	1,301	166	19.10.14 to 02.04.15	Iridium, VHF/Activity
Tiger	T09	Male	Subadult	PA	837	148	18.03.16 to 12.08.16	Iridium, VHF/Activity
Tiger	T10	Male	Subadult	PA	712	113	18.03.16 to 08.07.16	Iridium, VHF/Activity
Tiger	T7-C1	Male	Subadult	PA	3,324	358	10.06.18 to 02.06.19	Iridium, VHF/Activity
Tiger	T7-C2	Male	Subadult	PA	1,532	183	09.06.18 to 08.12.19	Iridium, VHF/Activity
Tiger	T103	Male	Subadult	PA	2,135	375	09.03.18 to 18.03.18	Iridium, VHF/Activity
Tiger	T01	Male	Adult	Outside PA	1,097	217	15.09.15 to 19.04.16	Iridium, VHF/Activity
Tiger	T9 brh	Male	Subadult	Outside PA	4,870	549	12.08.16 to 17.02.18	Iridium, VHF/Activity
Tiger	T10 brh	Male	Subadult	Outside PA	2,440	284	09.07.16 to 18.04.17	Iridium, VHF/Activity
Tiger	E3	Female	Subadult	Outside PA	3,747	329	02.01.19 to 26.11.19	Iridium, VHF/Activity
Tiger	Brh M	Male	Subadult	Outside PA	833	155	03.06.16 to 04.11.16	Iridium, VHF/Activity
Leopard	L25	Female	Adult	PA	48	38	03.08–13 to 09.09.13	GPS Global Star/VHF
Leopard	L26	Female	Adult	PA	297	462	03.08.13 to 07.11.14	GPS Global Star/VHF
Leopard	L41	Male	Adult	PA	96	415	23.04.15 to 10.06.16	GPS Global Star/VHF
Dhole	D1	Male	Adult	PA	1,799	77	29.07.17 to 13.10.17	GPS Plus UHF 1C Activity/ VHF
Dhole	D2	Male	Adult	PA	1,407	177	25.10.17 to 19.04.18	GPS Plus UHF 1C Activity/ VHF
Dhole	D3	Female	Adult	PA	1,007	58	20.02.18 to 18.04.18	GPS Plus UHF 1C Activity/ VHF
Dhole	D4	Male	Subadult	PA	441	20	14.02.18 to 05.03.18	GPS Plus UHF 1C Activity/ VHF
Dhole	D5	Male	Adult	PA	111	16	24.05.18 to 08.06.18	GPS Plus UHF 1C Activity/ VHF

postprocessing all data into an hourly data format for further analysis (Abrahms et al., 2017; Leblond et al., 2016). Mean displacement during day and night was also compared across individuals and landscapes by classifying location using animal movement tool (amt).

We also calculated NSD, which is the squared distance between the original location and each successive location (Papworth et al., 2012). A graph of NSD versus time gives a curve starting at the point of origin of a movement trajectory gradually reaching maximum NSD. NSD can remain constant or begin to drop as the animal returns to the point of origin where NSD = 0. Based on NSD, we calculated the time required for an animal to reach maximum displacement and return to the point of origin within the home range. The point of origin was selected randomly within the home range (approximately in the center of the home range) of the individual at a random time, calculated the revisit time, and considered it as one cycle. The time required to complete one such cycle was calculated. All movement parameters and analyses were carried out using *adehabitatLT* (Calenge, 2011) and animal movement tool (Signer et al., 2019) in program R 3.6.3 (R Core Team, 2020).

2.5 | Understanding effect of anthropogenic factors on movement

Anthropogenic factors such as human population density, landuse, and road network have an adverse effect on animal movement through fragmented and disturbed habitats (Tucker et al., 2018). We estimated the human population density, landuse proportion, and road network within the home range of large carnivores. Home range was estimated using the Brownian Bridge Movement Model, BBMM (Bullard, 1999). BBMM is a widely used method that estimates the path of an animal's movement probabilistically from data recorded at brief intervals. BBMM quantifies the utilization distribution of an animal-based on movement paths, accounts for temporal autocorrelation, and high data volumes (Fischer et al., 2013). The model approximates the movement path between two subsequent locations by applying a conditional random walk. We calculated utilization distribution for each individual at 50% and 95% isopleths to define the core area and home range, respectively, using the ArcMET extension tool (Wall, 2014) in ArcGIS 10.2 (Fischer et al., 2013; Laver & Kelly, 2008).

We used the human population density map (1 km resolution) available on the open-source website (Stevens et al., 2015; http://www.worldpop.org.uk/). The landuse data of 1:25,000 scale was acquired from Bhuvan's open-source website (NRSA, 2016; http://bhuvan.nrsc.gov.in/). The landuse maps were generated using "Resourcesat AWiFS" satellite imagery and classified Maharashtra into 13 landuse classes. We reclassified the original 13 classes into five major classes for analysis (Table 2). The road network data was obtained using Open Street Maps (Openstreetmap, 2015). We used primary and secondary roads for our assessment because of their significant impact on the movement of animals owing to higher traffic volumes (Saxena et al., 2020).

TABLE 2 Bhuvan's NRSA LULC original landuse classes and reclassified classes used for evaluation of the proportion of landuse within the home range

S. No.	Original class	Reclassified class
1	Builtup	Builtup
2	Kharif Crop	Agriculture
3	Rabi Crop	
4	Zaid Crop	
5	Double/Triple Crop	
6	Current Fallow	
7	Plantation	Forest
8	Evergreen Forest	
9	Deciduous Forest	
10	Degraded/Scrub Forest	
11	Wasteland	Grassland/Wasteland
12	Waterbody Max	Waterbody
13	Waterbody Min	

The effect of landuse, human population density, and road network on the hourly displacement was quantified in a regression framework. Each individual across species was considered as a single data point in the analysis. We used the percentage of each landuse class, average human population density, and road length in each animals' home range as a predictor variable. We also compared the landuse and anthropogenic variables within the home range for the same species in different landscapes (tiger inside and outside PAs), social canids between wolf and dhole using *t* test. All the statistical analyses were carried out in R 3.6.3 (R Core Team, 2020).

2.6 | Core area of large carnivores in heterogeneous landscape

Within home ranges, core areas are defined as exclusive areas of intensive use and likely contain features such as preferred foraging areas, dens, and resting sites (Ewer, 1968), facilitating many species to coexist. We computed the number, size, and perimeter of core areas across 4 large carnivore species. All home range metrics were calculated using the ArcMet tool (ArcGIS). For tigers, we compared the size and number of core areas of individuals of different sexes in varying levels of human disturbance. We also compared the core areas of wolf and dhole–two social canids of comparable body size but contrasting habitats. The significance of the results across species and habitats was tested using paired *t* test along with effect size (Zar, 1984).

3 | RESULTS

A total of 48,646 fixes across 26 individuals of 4 large carnivore species were analyzed (Table 1). We examined the fundamental

TABLE 3 Displacement of 4 large carnivores across different habitat types in India

Species	Habitat/system	Behavioral trait	Mean Displacement (m/hr)	Mean displacement during day (m/hr)	Mean displacement during night (m/hr)
Tiger PA	Dry Deciduous Forest (PA)	Solitary	196.23 ± 49.93	174.62 ± 48.6	218 ± 53.58
Tiger Outside PA	Dry Deciduous Forest and Agriculture Interface	Solitary	312.20 ± 136.76	241.11 ± 75.33	377.30 ± 196.85
Leopard	Dry Deciduous Forest (PA)	Solitary	99.34 ± 27.9	101.51 ± 52.48	91.34 ± 11.68
Dhole	Dry Deciduous Forest (PA)	Social	259.92 ± 49.68	337.92 ± 133.97	191.62 ± 66.97
Wolf	Human-Dominated Grassland-Agriculture Mosaic	Social	637.70 ± 87.8	471.09 ± 165.62	819.33 ± 154.22

movement parameters, the impact of human footprint, and configuration of core areas of tiger, leopard, wolf, and dhole across a gradient of human disturbance.

3.1 | Movement parameters of large carnivores

Inside PA, the average hourly displacement of tiger and leopard was 196.23 ± 49.93 m/hr and 99.34 ± 27.9 m/hr, respectively, whereas dhole moved an average of 259.92 ± 49.68 m/hr. Outside PA, the mean tiger displacement was 312.20 ± 136.76, and wolf moved an average of 637.70 ± 87.80 m/hr (Table 3).

Mean hourly displacement of tigers was found to be higher outside PA (312.20 ± 136.76 m/hr) than PA (196.23 ± 49.93 m/hr) however, they were significantly not different ($p = .06$; Glass's $\Delta = 2.37$). For tigers inside and outside PAs, mean hourly displacement varied significantly between day (174.62 ± 48.6 m/hr; $p = .0007$; Glass's $\Delta = 0.89$) and night (218.0 ± 53.58 m/hr; $p = .03$; Glass's $\Delta = 1.8$) with higher displacement during night across the landscape. Among sexes, mean displacement per hour of tigers varied with males having larger displacement (252.54 ± 117.59 m/hr) than females (200.42 ± 43.87 m/hr). Moreover, both the sexes showed longer displacement during night than day. Leopards showed the least variation in mean displacement through day and night (101.51 ± 52.48 m/hr and 91.34 ± 11.68 m/hr) respectively. The dhole which inhabits forested areas showed higher displacement during daytime (337.92 ± 133.97 m/hr) as compared to night (191.62 ± 66.97 m/hr), and the difference was found significant ($p = .03$; Glass's Δ=1.09). The wolves showed higher mean displacement during night (819.33 ± 154.22 m/hr) as compared to day (471.09 ± 165.62 m/hr), and significant difference was found ($p = .05$; Glass's Δ=2.1).

Based on NSD, all species across the landscape exhibited a confined movement pattern. The tiger outside PA took 141.4 ± 44.77 hr to complete one cycle (point of origin—maximum displacement—point of origin), whereas tiger inside PA (208.4 ± 167.7 hr) took 32.14% higher time than outside PA. For leopards, the time to complete each cycle was found to be maximum (1,258.50 ± 485.59 hr). Dholes and wolves took similar time to complete one cycle to cover their home ranges (204.915 ± 83.71 hr and 229.76 ± 111.6 hr respectively) (Table 4).

3.2 | Effect of anthropogenic factors on movement of large carnivores

The hourly displacement of the large carnivores varied from 99.35m/h for leopards to 637.7m/h. When we modeled the hourly displacement with the landuse classes, human density, and road length in the home range of the individual, most of the variance is explained by two landuse classes ($F_{2,22} = 4.582$, $p = .021$; agriculture, $r = .52$, $p = .009$ and wasteland/grassland, $r = .49$, $p = .013$). Both variables showed positive association with hourly displacement (Table 5). For tigers, forest area within the home range was not significantly different between PAs and outside PAs (p forest = .06) whereas, agriculture and road length were found to be significantly different (p agriculture = .03, p roads = .02). For the social canids, wolf, and dhole all the habitat variables in the home range were found to be significantly different (p human density < .001, p roads = .005,

TABLE 4 Based on NSD, time required for species to complete one cycle from point of origin to maximum displacement and back as a proxy for time taken to cover one home range circuit

Species	Number of individuals (n)	Number of cycles	Range to complete one cycle (h)	Time to complete one cycle (h)
Tiger (PA)	9	99	15–1,159	208.4 ± 167.7
Tiger (Outside PA)	5	42	21–620	141.4 ± 44.77
Leopard	3	8	216–3,168	1,258.50 ± 485.59
Dhole	5	28	27–708	204.915 ± 83.71
Wolf	4	17	60–480	229.76 ± 111.6

TABLE 5 Description of model parameters used to evaluate the effect of overall hourly displacement of all individuals and regression results of individual models

Model parameters	Degrees of freedom	AIC	Adjusted R^2
Human population density in HR + agriculture area in HR + wasteland/grassland in HR	4	58.982	0.401
Human population density in HR + agriculture area in HR + wasteland/grassland in HR + road length in HR	5	59.703	0.407
Human population density in HR + agriculture area in HR + wasteland/grassland in HR + road length in HR + waterbody in HR	6	61.603	0.381
Human population density in HR + agriculture area in HR + wasteland/grassland in HR + road length in HR + waterbody in HR + Forest area in HR	7	63.551	0.348
Human population density in HR + agriculture area in HR + wasteland/grassland in HR + builtup area in HR + Forest area in HR + waterbody in HR + road length in HR	9	321.071	0.376

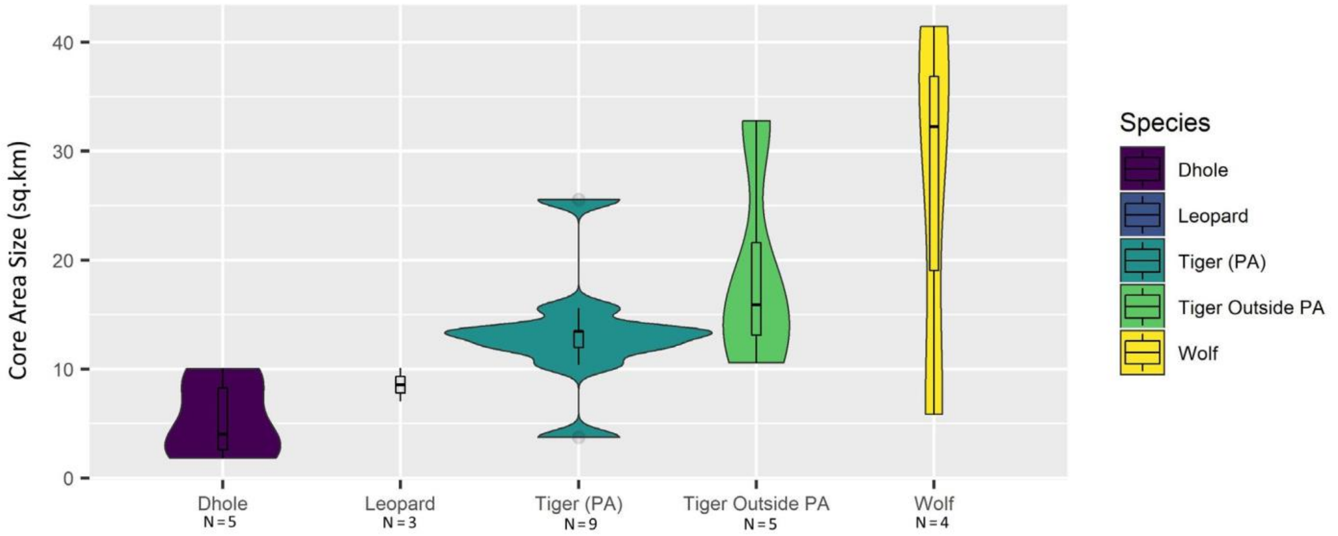

FIGURE 2 Violin plot indicating the distribution of the range of the core area size, median (black center line), and spread of the data (black rectangle) for four large carnivores in India

p agriculture = .04, *p* forest < .001, *p* wasteland/grassland = .008, *p* waterbody = .005).

3.3 | Core area of large carnivores in heterogeneous landscape

All carnivores showed multiple areas of intensive use or cores in their home ranges. The mean number of core areas per individual was not significantly different among species (Table 6). The range of the core area sizes was greater for species outside PAs (tiger: 0.68–29.31 km^2 and wolf: 0.55–25.84 km^2) in human-altered landscapes. For dhole (1.37–7.04 km^2) and leopard (0.65–15.67 km^2), the spread was found lowest inside PA (Figure 2).

The number of core areas of tigers inside and outside PAs was significantly different ($p = .03$; Glass's $\Delta = 1.41$), whereas the difference in size of core areas was not significant ($p = .43$; Glass's $\Delta = 0.07$). Although the median value of core area size was higher for tigers inside PAs (4.0 km^2) in comparison to the tigers outside PAs (1.53 km^2), the range of core area size was greater for tigers outside PAs (0.55–25.84 km^2) than inside (0.65–15.67km^2) (Table 6). The two social canids, dhole and wolf, have a comparable body size, but the size of core areas was completely different. The number of core areas for both canids did not differ significantly ($p = .46$; Glass's $\Delta = 0.07$), but core area sizes were significantly different ($p = .004$; Glass's $\Delta = 5.7$). Core areas of dholes were smaller with narrow ranges (0.6–5.05 km^2), whereas wolves exhibited a wide range of core sizes (0.68–29.31 km^2) similar to tigers outside PAs.

TABLE 6 Mean number, size, and perimeter of core areas of four large carnivores and tigers across sex and between inside and outside protected area in India

Species	Mean no. of core areas	Mean core area size (km^2)	Mean core area perimeter (km)	Total perimeter (km)
Tiger PA	2 ± 1.80	5.99 ± 5.50	14.97 ± 10.56	29.9
Tiger outside PA	3.25 ± 1.70	5.6 ± 7.77	12.53 ± 10.04	40.7
Dhole	2.2 ± 1.7	2.21 ± 1.6	8.17 ± 4.48	18.0
Wolf	2.33 ± 1.52	11.37 ± 9.96	15.08 ± 8.33	35.1
Leopard	2 ± 1.41	3.85 ± 2.74	11.92 ± 7.23	23.8
Tiger outside PA (Male)	3.33 ± 2.08	5.94 ± 8.72	13.02 ± 11.03	43.4
Tiger PA (Male)	3.25 ± 2.21	4.62 ± 5.14	12.05 ± 10.53	39.2
Tiger Outside PA (Female)	3	4.46 ± 4.16	10.93 ± 7.25	32.8
Tiger PA (Female)	1 ± 0	11.23 ± 5.79	19.63 ± 6.57	19.6

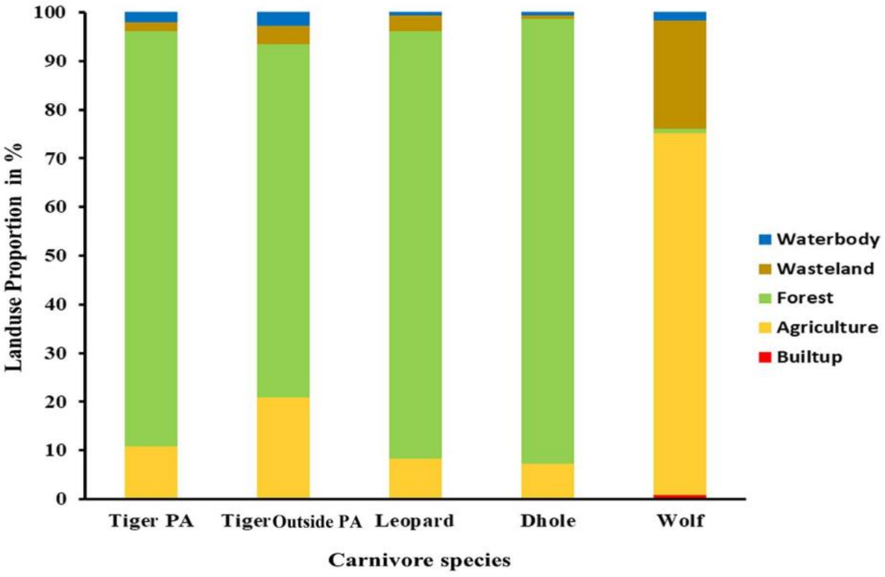

FIGURE 3 Landuse proportion within the home range of four large carnivores in India. Data from Bhuvan's LULC (http://bhuvan.nrsc.gov.in/) was used to classify home ranges

4 | DISCUSSION

4.1 | Movement of large carnivores across human-dominated landscapes

Large carnivore species living outside PAs exhibited greater mean displacement (25.29%) than the species inside PAs with a single exception of the dhole. Dholes moved with higher speeds (i.e., with longer step lengths) among the 3 large carnivores sharing a similar habitat inside PAs. Predominantly occurring in a human-dominated landscape, wolves showed the highest movement among all 4 carnivores, whereas the leopards in natural areas showed the least. We also found tigers outside PAs moved at higher speeds than inside PAs. Our result on wolves and tigers outside PAs ties well with previous studies on similar species in human-dominated landscapes like cougars (*Puma concolor*) and lions (*Panthera leo persica*) that exhibited higher speeds while traversing through fragmented areas to reduce time spent in multiple-use areas (Kertson et al., 2011; Valeix et al., 2012).

Across sexes, both male and female tigers traveled more during night than day. Male tigers traveled faster than female tigers owing to larger home ranges and longer distance to cover in habitat matrix. As males exhibit multiple core areas in human-altered landscapes, the movement rate to travel between core areas was high. The leopard movement was found lowest 99.34 ± 27.9 among all carnivores within the PAs with less difference between day and night movements. This may be because leopards survive in the presence of large predators like tigers and pack-living dholes that make up for their size in numbers. Intense intraguild competition has driven leopards to the boundaries of protected areas where they are faced with increased human pressures (Azlan & Sharma, 2006; Carter et al., 2015; Odden et al., 2010; Seidensticker et al., 1990). Moreover, leopards also took the highest time (1,258.50 ± 485.59 hr) to return from the point of maximum displacement to the point of origin within the home range. Under such circumstances, leopards travel from one core area to another and spend more time in such core areas. This strategy may enable them to coexist with large carnivores and humans. Interestingly, tigers outside PAs took comparatively lesser time (141.4 ± 44.77 hr) to cover their home range than tigers inside PAs (208.4 ± 167.7 hr) even though their home ranges were twice the size. This may be because the tigers in human-disturbed areas move faster owing to the presence of habitat matrix between core areas, which enables them to cover larger areas in a shorter time.

4.2 | Effects of human footprint on movement of large carnivores

As human activities increase, the collateral loss of habitat and biodiversity is accompanied by a change in the movement of animals through fragmented landscapes (Tucker et al., 2018). Landscape structure affects movement parameters because different cover types in the landscape offer different levels of risk and benefit. Landuse types across home ranges of large carnivore species were not significantly different with the single exception of wolves, which live primarily in grasslands and human-altered landscapes (Figure 3). Historically, wolves adapted to live in human-dominated landscapes as they evolved near humans (Anderson, 2018). Moreover, our results indicate that the wolves move faster in human-dominated landscapes may be to negotiate human pressures and avoid them as much as possible within their large home ranges.

The displacement of tigers outside PA was 62.85% higher than inside PA, though it did not differ significantly. Parameters supposed to influence the hourly displacement such as population density, landuse proportion, and road length was significantly different ($p = .01$) within and outside protected area. The forest outside PAs is fragmented with high human density and road network, which may explain the larger home ranges of tigers outside PAs (Habib, Nigam, et al., 2018). To negotiate this fragmented landscape, tigers outside PAs also move at higher speeds than inside PAs.

We also compared the movement parameters of two social carnivores; wolf present in a human-dominated landscape and dhole inhibiting protected area and found that the hourly displacement of wolf was 62.90% higher than dholes. The parameters influencing the hourly displacement such as population density, landuse proportion, and road length were also significantly different ($p = .04$) between the home ranges. Ecologically, as the percent of agriculture in an individual's home range increases, the individual has to move more to exploit resources in the human-dominated landscape. Moreover, area of grassland is positively related, as large carnivores like wolf are known to prefer grassland habitat and showed highest hourly displacement.

We examined the proportion of human population and road length inside the home ranges of the 4 large carnivores in our study areas. As expected, home range of wolves consisted of relatively high human density followed by leopard and tigers outside PAs. Within PAs, dholes showed higher human population pressure (0.51 human/100 km^2) than tigers (0.29 human/100 km^2) in their home ranges (Figure 4). This may be because dholes establish intensive use areas near PA fringes as a strategy to avoid large predators and competition (Ghaskadbi & Habib, 2019). Across our study sites, the home range of wolves had the maximum network of roads (56.6 km), followed by tigers outside PAs (25.7 km). The home range of dholes showed the least length of roads (5.5 km) (Figure 5). All carnivores had primary roads passing through their home ranges, but the disturbance caused by them need not be the same. This is because the roads inside PAs are nonfunctional and only used for limited tourist activity and management.

We also compared the landuse class within tiger home ranges, which suggested that the proportion of forest cover was not significantly different, whereas agriculture outside and inside PAs differed significantly. It is worth discussing that home ranges of tigers outside PAs were primarily forest areas (72.72%). Tigers outside PA uses fragmented landscape and form multiple core areas primarily dominated by forest areas to avoid humans and meet their basic ecological requirements.

4.3 | Core area of large carnivores in heterogeneous landscape

Core areas of animals have been studied to address a wide range of research queries (Hooten et al., 2008) such as social information transmission (Darden et al., 2008), interspecific competition (Neale

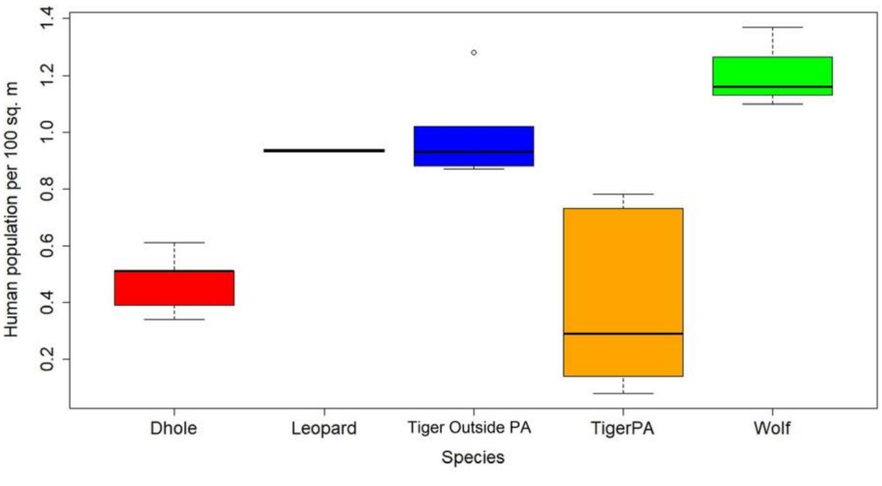

FIGURE 4 Human population density within the home range of four large carnivores in India

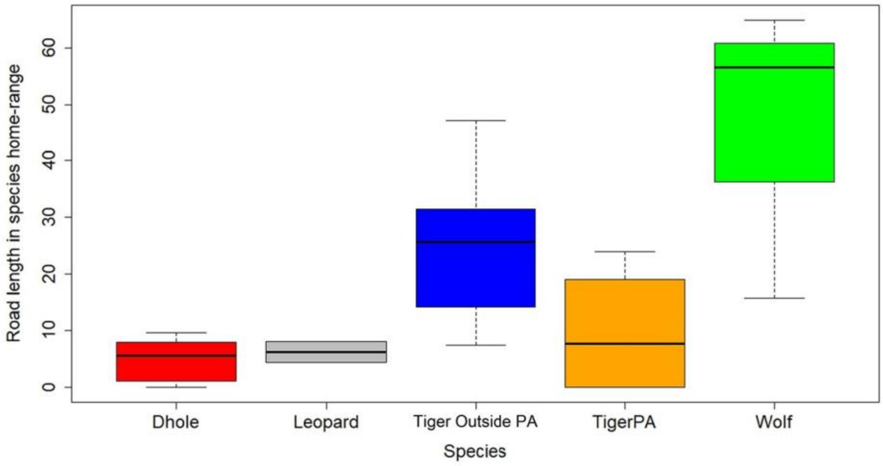

FIGURE 5 Road length (km) within the home range of four large carnivores in India

& Sacks, 2001), trophic cascades (Prange & Gehrt, 2007), habitat selection (Chamberlain et al., 2003), reproductive success (Thompson et al., 2007) and territorial defense (Darden & Dabelsteen, 2008). Our study reports multiple areas of intensive use or cores for all the 4 carnivores across the landscape (Table 6). The number and size of core areas across species did not show a significant difference, but the ranges were different. For species surviving in human-altered landscapes like the wolf and tigers outside PAs, the range of core area size was the greatest, whereas it was the least for the dholes.

For tigers outside PA, we found core areas with a larger perimeter than tiger inside PAs. This may be because of the high level of fragmentation and human pressure. The core area with larger perimeter for tiger and wolf outside PA indicates higher chances of exposure to human-induced effect leading to an increase in human–animal interaction. The female tiger in PA had only one core area, whereas female tigers outside PA had multiple core areas with larger perimeter (Table 6). This result explains the possibility that female tigers outside PAs are more prone to conflict due to their higher energy demand and greater perimeter owing to more chance of interaction with humans.

5 | CONSERVATION IMPLICATIONS

Across the globe, large carnivore conservation is a challenge owing to the habitat loss and fragmentation of natural areas with rapidly growing human populations. In India, the conservation of large carnivores is interlaced with various political, socioeconomic, and emotional issues, which further complicates this challenge. Increasingly, wildlife is compelled to coexist with humans in highly modified landscapes, highlighting the need for planned and coordinated interdisciplinary efforts. Integrating movement ecology in landscape management and policymaking is a desirable approach as it provides insights into how animals are affected by human footprint and the implications on their ecology and conservation. With great advances being made across the world in the field of movement ecology, India is only beginning to take the initial steps into the field.

The novel findings of the large-scale study on the movement ecology of 4 large carnivores of India will have major implications on their conservation and management in the country. They may even guide developing countries with high human and carnivore densities in conservation planning and management and serve as cautionary learning for countries where the densities of populations may increase in the future. If large carnivores are to coexist with humans, there needs to be an understanding of how animals move inside PAs and the adaptations they exhibit outside PAs to survive in the matrix in between. The use and extent of corridors need to be informed by real-time knowledge of animal motion and navigation capacities if we are to safeguard the sensitive connections between the PAs. The authors are aware of the limitations of this study compared to long-term and large-scale radio-collaring studies across the globe. However, our study can be a suitable starting point for further comparative studies to understand the extent to which large carnivores can negotiate landscapes and adapt to survive.

ACKNOWLEDGMENTS

We are thankful to the Ministry of Environment, Forest and Climate Change (MOEFCC) and Maharashtra Forest Department (MFD) for the permissions to collar animals and conduct research. National Tiger Conservation Authority (NTCA), Department of Science and Technology (DST), Govt. of India, and MFD are duly acknowledged for funding provided to carry out the research. We are also grateful to the Field Directors, DFOs, RFOs, forest guards, watchers, and especially our field assistants for providing necessary help on the field throughout the study. We thank the Director, Dean, and Research Coordinator of the Wildlife Institute of India and Chief Wildlife Warden, Govt. of Maharashtra for supporting the study. Finally, we thank our families, friends, and colleagues for bearing with our long absences and quirks as we tracked radio-collared animals in remote areas.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTION

Bilal Habib: Conceptualization (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Resources (lead); Software (lead); Supervision (lead); Validation (lead); Visualization (lead); Writing-review & editing (lead). **Pallavi Ghaskadbi:** Data curation (equal); Formal analysis (equal); Methodology (equal); Writing-original draft (equal); Writing-review & editing (equal). **Shaheer Khan:** Data curation (equal); Formal analysis (equal); Methodology (equal); Writing-original draft (equal); Writing-review & editing (equal). **Zehidul Hussain:** Data curation (equal); Formal analysis (equal); Methodology (equal); Writing-original draft (equal); Writing-review & editing (equal). **Parag Nigam:** Data curation (equal); Investigation (equal); Methodology (equal); Resources (equal); Validation (equal); Writing-review & editing (equal).

ETHICAL APPROVAL

All the four species were captured following standard and approved protocols after due permission from the Ministry of Environment, Forests and Climate Change, Government of India, and Maharashtra Forest Department. The species-specific permit details are as follows: Tigers and Leopards: MOEF&CC – F. No. 1-36/2014-WL-I/05.09.2014; F. No. 1-22/2015/WL/09.10.2015; MFD – SPP-144/13.10.2014; SPP-04/01.01.2016, Wolf: MOEF&CC – F. No. 1-69/2017-WL/16.05.2017; MFD – SPP-15/01.06.2017, Dhole - MFD – SPP-12/05.11.2016.

DATA AVAILABILITY STATEMENT

Because of conservation reasons, the authors are unable to share the location data for the carnivore species.

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How to cite this article: Habib B, Ghaskadbi P, Khan S, Hussain Z, Nigam P. Not a cakewalk: Insights into movement of large carnivores in human-dominated landscapes in India. *Ecol Evol*. 2021;11:1653–1666. https://doi.org/10.1002/ece3.7156

BRITISH
ECOLOGICAL
SOCIETY

BES Annual Meeting

16 – 19 December 2018

Birmingham, UK

This certificate confirms that:

Zehidul Hussain

Attended the above Annual Meeting in Birmingham and gave an oral presentation titled:

Movement ecology of tiger in the Eastern Vidarbha Landscape, Maharashtra, India.

Georgina Glaser

Events Assistant
British Ecological Society

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ICC-2019

Certificate of Participation

Zehidul Hussain

participated and presented paper/~~poster paper~~ in International Conservation Conference held at Aligarh Muslim University, Aligarh, U.P., India during 21st to 23rd October 2019. The title of the presentation was

Understanding Space Use .... in Eastern Vidarbha Landscape, Maharashtra, India

DR. AFIFULLAH KHAN
Conference Director

Orus Ilyas
DR. ORUS ILYAS
Conference Co-ordinator

Organized by
Department of Wildlife Sciences, AMU
and
Wildlife Institute of India, Dehradun

Certificate of Attendance and Presentation

This is to certify that

Zehidul Hussain
Wildlife Institute of India

Attended and Presented the Following Topics at the

IALE-NA 2020 Annual Meeting
May 11-14, 2020
Virtual Remote Conference

Title: The Risky Journey: Movement of Dispersing Tigers in a Human-Dominated Landscape in India

Authors: Zehidul Hussain, Wildlife Institute of India; Pallavi Ghaskadbi, Wildlife Institute of India; Parag Nigam, Wildlife Institute of India; Bilal Habib, Wildlife Institute of India

Certified by: Leslie Pelch, Delaney Meeting and Event Management, for:

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This is to certify that

Zehidul Hussain

has attended the Student Conference on Conservation Science, 29-31 March 2022,

at the University of Cambridge, Downing Street, Cambridge, UK.

Administrator...

Date: 28 March 2022

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