ECOLOGICAL IMPACTS OF ROADS ON MAMMALS AND INTEGRITY OF THE CENTRAL INDIAN TIGER LANDSCAPE

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

(Wildlife Science)

By
Akanksha Saxena

Research Centre

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

2023

DECLARATION

I hereby declare that the thesis titled "**Ecological Impacts of Roads on Mammals and Integrity of the Central Indian Tiger Landscape**" submitted by myself, Ms. Akanksha Saxena (Enrolment No. 16PHD423), to Forest Research Institute 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. Asha Rajvanshi, Wildlife Institute of India, Dehradun and has not formed the basis for an award of any other degree or diploma. 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 Deemed to be University, and has plagiarism to acceptable limits.

Dehradun, the February 20, 2023

Akanksha Saxena

Countersigned:

Dr. Bilal Habib
[Supervisor]

भारतीय वन्यजीव संस्थान
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2. Your Enrolment number is: - **16PHD423**
   (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: **"Ecological Impacts of roads on mammals and integrity of the Central Indian Tiger Landscape."**
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. Asha Rajvanshi**

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Format of progress report

Copy to the following for information and necessary action:-

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Table of contents

Acknowledgment

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I dedicate this work to my father, late Capt. Ashok Saxena, a lover of roads, who famously said ‘there is nothing that my girls cannot do’.

Executive Summary

Road networks are increasing at an alarming pace worldwide, but most rapidly in developing countries like India. The drivers of road building in such countries include the need to make the benefits of development accessible to citizens in the remotest corners. However, road building in ecologically rich and sensitive regions can have severe repercussions for the wildlife in these regions. Road construction leads to destruction of habitats and physically disconnects previously contiguous landscapes. Traffic on roads directly cause wild animal mortality, cause changes in behaviour of wildlife by altering patterns of space use, and in the long-term can cause populations to diminish through either loss due to mortality, or by isolation of neighbouring populations by creating a barrier to their movement. With the increasing pace of road building in ecologically sensitive habitats in developing regions of the world, there is an urgent need to provide science-based solutions to mitigate the impacts of roads on wildlife. This would require understanding responses of wildlife to road-related disturbances of varying intensities.

Through this study, I aimed to understand the responses of a large mammal community to road-related disturbance through different methods, and form a basis for identifying and prioritising road stretches for mitigation of impacts on the large mammal community. The study was based in the central Indian tiger landscape which has one of the greatest potentials for long-term tiger conservation in the country, and at the same time is also facing incremental rates of road infrastructure development. The focal study species included the tiger, its co-predators and primary prey.

I first used camera trap data to assess the responses of the mammal community in the vicinity of a high-speed national highway (NH 44) in the landscape. Camera traps were set-up in the habitat adjacent to three road types (2-lane, 4-lane and 4-lane with mitigation measures) to assess the response of the mammal community to road-related disturbance. By using species richness as well as functional trait diversity to examine if roads cause the exclusion of roadside habitat use by species with certain functional traits (body mass, mobility, reproductive rate and taxonomic), I found that presently there is little evidence of environmental filtering of traits near roadsides. This could be because the study area is part of a protected area (Pench Tiger Reserve), and this could help buffer the impacts of roads to a great extent. Through generalised linear mixed models, I assessed the influence of road and environmental characteristics on capture rates of 8 mammals in the roadside habitat. I found that the disturbance on the highway was found to cause avoidance of the roadside habitat by specialist disturbance-averse species. A significant finding was the comparatively low use of roadside habitat by carnivores, which has direct implications for indirect habitat loss and loss of connectivity, although avoidance also indicates lesser vulnerability to roadkill. Examining the activity patterns of the study species by calculating activity overlaps and significance of similarity with control (natural) activity, I found alterations in temporal activity patterns near the highway which is characteristic of wildlife response to human disturbance. Overall, the study found that species spatio-temporal responses to roads varied with species behaviour. The importance of protected areas in buffering indirect impacts of roads on wildlife also emerged as an important finding, consequently the impacts of roads on wildlife would be more adverse in forests outside the purview of protection. Finally, the study also revealed the impact of construction of mitigation measures on the large mammalian community in the adjacent habitat through (a) restoration of near-natural spatio-temporal habitat use patterns by species earlier found avoiding the habitat, (b) reduction in use of roadside habitat by species earlier found exploiting roadside habitat, and (c) restoration of near-natural prey-predator activity overlaps

While camera trapping revealed the highest use of roadside habitat by chital, I further attempted to understand the behavioural mechanisms that enabled chital to use roadside habitat in the presence of human and vehicular disturbance. I recorded ~35 hours of chital behavioural data from the roadside (National Highway 44) and inside Pench Tiger Reserve, and compared vigilance, non-vigilance and social behaviour at the two sites through scan and focal behavioural sampling. Based on findings of the previous chapter, I postulated that reduced use of roadside habitat by predators would result in a predator release situation, enabling chital to seek shelter from predation near the highway resulting in decreased vigilance levels. Contrary to expectations, chital were more vigilant on the roadsides, while they spent the same proportion of time foraging as they would in the absence of human disturbance. High frequencies of feeding and vigilance bouts among chital at the roadsides indicated that they are in a state of constant vigilance in response to passing vehicles. Chital also did not exhibit behaviours such as resting, vocalising (rutting calls), and nursing at the roadsides, which could have implications for social interactions and communication among group-living species. The study also revealed differential perceptions of natural and human-caused threats through varied anti-predator behaviour employed by chital towards natural predators (inside the park), moving vehicles (high vigilance), and stationary vehicles and humans on foot (flight). There were no significant differences in average group sizes between sites (park and roadside), but larger groups near roadsides showcased reduced vigilance behaviours. Most significantly, the study revealed that the direct cost borne by chital of remaining vigilant against potential human threat is loss of feeding opportunities, i.e., chital at the roadsides have to continually choose between feeding more and being more vigilant. Thus, chital on the roadsides may be tolerant of apparently non-lethal human disturbance (vehicular traffic), but with sensitisation of direct human approach (humans on foot) which may be the reason behind heightened vigilance responses i.e., flight. The study highlights the ability of chital to adapt to areas used by humans, albeit with fitness and social costs that could have long-term consequences.

Next, I assessed the factors affecting habitat use of four major prey species of the tiger and co-predators in the landscape across different road and forest protection types in the landscape. I collected animal presence data from 10 roadside sites in central India through systematic habitat plot sampling, and assessed the probability of habitat use near different road types using generalised linear mixed models. Similar to the results of the camera trapping exercise along NH 44, I found that protection of roadside habitat determines habitat use by wild ungulates. Conversely, the impacts of road-related disturbance would be higher on roads away from protected areas as these areas would have greater avoidance by certain species like gaur and sambar. Additionally, habitats near roads outside protected areas would also have increased presence of humans that would further impede use of such habitat by ungulates. Again, similar to the results of the camera trapping exercise, presence of wildlife crossing structures seemed to decrease the use of habitat near roads by species like wild pig and chital that were previously found to exploit roadside habitats. I used differences in modelled species presence probabilities between a 'no-roads' scenario and 3 road development scenarios (present, up-gradation without and up-gradation with inclusion of crossing structures) to estimate species-specific road effect zones. I found that road effect zone estimates for the four ungulate species reflected the differences in responses to road and environmental characteristics, and were wider near roads outside protected areas and narrow in the vicinity of protected areas. Finally, I found that road development scenarios involving construction of crossing structures especially in the vicinity of protected areas would benefit most ungulates, thereby reducing their road effect zones.

The absence of real-time animal movement and mortality data makes it difficult for field managers and user agencies to design and locate mitigation measures on roads passing through ecologically sensitive habitats. The problem becomes even more complex when prioritising locations of mitigation measures at the landscape scale. To overcome this, I used a simple rule-based metric to delineate priority road segments in the landscape for mitigation of barrier and

collision risk in an easily reproducible ‘exposure-hazard’ framework. I also adapted a method to estimate traffic volumes for the entire landscape using available traffic data (in PCU) and modelling it in a random forest regression framework. Integrating species presence probabilities (predicted and assumed), road, traffic and environmental characteristics with a published traversability model, I estimated 3725 km of roads vulnerable to medium-high collision likelihood, and 3245 km of roads vulnerable to medium-high barrier likelihood within protected areas, corridors and forests of the central Indian landscape. An important finding from the study was that a majority of the roads in these categories are 2-lane roads- with 90% of 2-lane roads posing medium-high barrier likelihood, and 93.4% of 2-lane roads posing medium-high collision likelihood. This finding makes it imperative to use up-gradation plans (2-lane to 4-lane) in the landscape as an opportunity to include structural mitigation measures for enhancing connectivity and reducing animal mortality in central Indian roads.

The study is the first long-term research on the ecological impacts of roads conducted in an important tiger conservation landscape. It has direct management implications for understanding varied species responses to roads, mitigation requirements at different road types and forest protection types, and for landscape-scale prioritisation of sites for mitigating barrier and collision risk.

List of Tables

List of Figures

List of Appendices

Chapter 1

Introduction

1.1. Background

From foot trails to the complex highway systems of today, roads have played an important role historically in connecting human civilisations by promoting trade and commerce, and in connecting economies. Consequently the importance of road infrastructure in reducing poverty, facilitating trade and commerce and promoting economic progress has catalysed governments in developing countries to accord the highest priority to road building (Rodrigue and Theo, 2020). As a result, the rate of road development is among the highest in tropical developing countries (Ahmed, 2014; Gurara et al., 2018). A large part of this development is expected to occur in remote and highly biodiverse regions of such developing economies (Laurance et al., 2014; Meijer et al., 2018).

These countries are among the richest in terms of biodiversity, and also have high rates of population growth. As such the negative consequences of road development for nature and biodiversity are most dire in these regions. Previously pristine wilderness areas are now being opened up to fulfil the need to connect all remote human settlements to make economic and social benefits available to all. Roads already passing through forested areas are being upgraded and expanded to cater to the increasing traffic flow. While road development is indispensable to the developmental needs of such regions, understanding and mitigating the adverse impacts of road development and road network expansion is necessary to ensure that the goals of environmental and biodiversity conservation and economic development are harmoniously fulfilled.

1.2. Impacts of roads on mammals

Globally, roads are the most ubiquitous forms of human disturbance in natural areas. The construction of roads and the subsequent onset of vehicular traffic pose multiple deleterious effects on nature (Jackson, 2000; Laurance et al., 2009), with vast scientific literature attesting to the same. Road networks fragment previously contiguous landscapes into smaller patches (Ibisch et al., 2016). Road development into previously remote areas catalyses activities such as poaching, habitat degradation, and also accelerates forest conversion (Clements et al., 2014). The physical road structure and constantly moving traffic together create a barrier to movement of animals across these structures (Forman et al., 2003) and reduce the habitat available to wildlife (D'Amico et al., 2015). Road-related mortality of wild animals has been recognised as a major cause of decline in animal populations in human-dominated landscapes (Trombulak and Frissel, 2000). In addition to the risk of local extinction of certain species (Clarke et al., 1998; Lankaster et al., 1991), these impacts affect the movement of wide-ranging carnivores (Habib et al., 2021; Kerley et al., 2002) and herbivores (Blom et al., 2005; Leblond et al., 2013), leading to isolation of populations (Lande, 1988). The effects of roads and their emissions are not limited to their physical extent but pervade up to 15-20% of the surrounding landscape (Forman and Alexander, 1998). Road impacts and associated activities endanger apex carnivores in biodiversity rich developing regions of the world, already facing incremental pressures from high human densities (Quintana et al., 2022). These impacts add up and affect the connectivity of natural landscapes, compromising their ability to support viable wildlife populations.

Roads affect wildlife in mainly three ways:

a. causing mortality due to collision with vehicles,
b. reducing the amount of suitable habitat available: through habitat loss and degradation, proliferation of invasive species,
c. creating smaller unviable sub-populations: by forming barriers to dispersal and gene flow

Through multiple pathways, an interplay between species, road and landscape characteristics can lead to these impacts – for example while large area requirements of carnivores makes them more likely to encounter roads, attraction to roadside habitats makes some herbivores and scavengers more vulnerable to roadkill (Barthelmess and Brooks, 2010; Cook and Blumstein, 2013; Roy, 2003). Additionally, these impacts can be direct with results such as road-related mortality, and indirect with results evident in the long-term (Fig. 1.1).

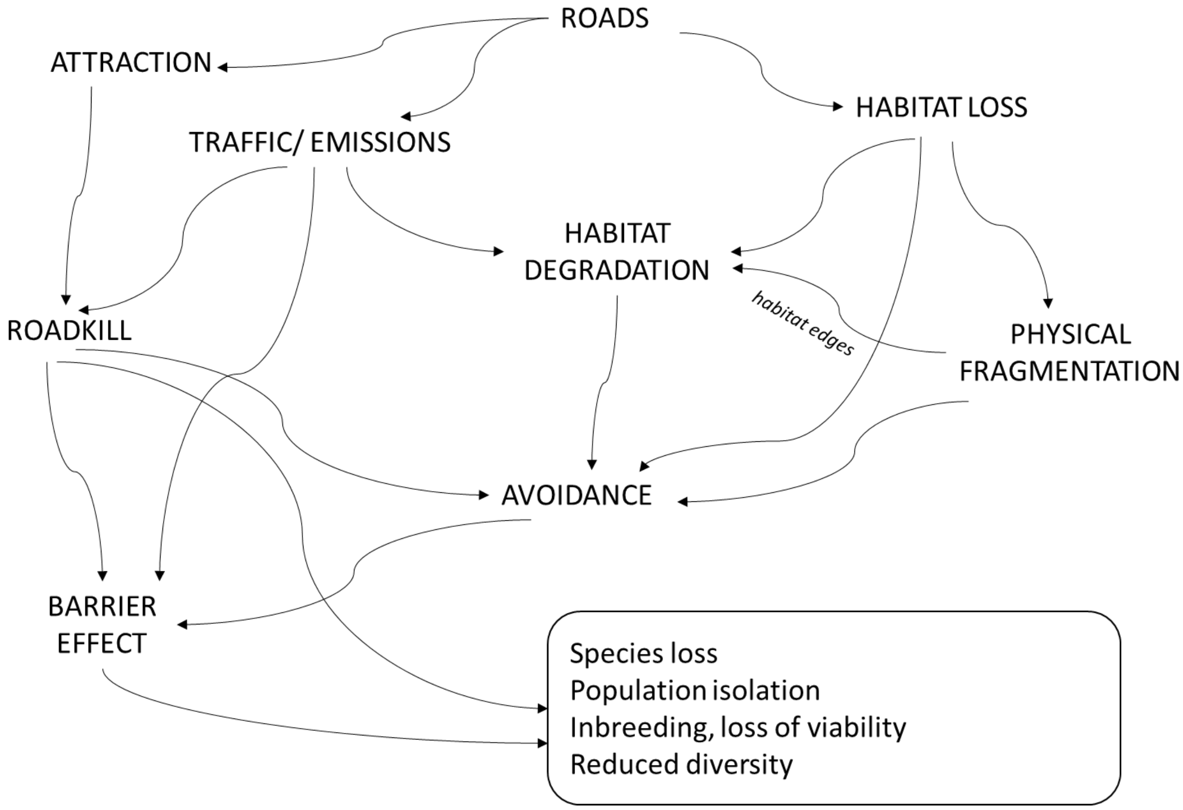

Figure 1.1. Web of road-related impacts, animal responses and long-term consequences

Road-related impacts affect all animal taxa differently (Rytwinski and Fahrig, 2013). For example, while reptiles and amphibians are most vulnerable to roadkill, scavengers profit by feeding on roadkill. However mammals are most vulnerable to road-related impacts because of several characteristics (Bright, 1993; Rytwinski and Fahrig, 2011) such as low population densities, low dispersal rates, large movement ranges, habitat specialisation, low reproductive rates and large body size.

Habitat loss & fragmentation

Roads cause a break in previously contiguous habitats, resulting in physical loss of habitat. These breaks in habitat are characterised by little or no vegetation cover, invasive vegetation and greater anthropogenic disturbances. This alters the quality of habitat and also leads to avoidance of disturbed areas by wildlife.

Roads also cause functional separation or barrier to natural flows and movement between natural areas on opposite sides of a road (Forman, 2005), leading to habitat fragmentation. Moreover when suitable habitat declines in a landscape (as a result of habitat loss), effects of population isolation because of fragmentation and reduction in habitat patch size get magnified (Andren, 1994).

Fragmentation effects in human-modified landscapes are a function of habitat patch size, animal body size (Crooks, 2002) and dispersal ability (Hand et al., 2014). Ibisch et al. (2016) reported that out of the 600,000 or so remaining roadless patches in the world, more than half are less than 1 sq. km in size and only 7% are larger than 100 km^2. These statistics spell doom for the conservation of wide-ranging dispersing wild animals (carnivores, large herbivores) that are most likely to encounter roads and associated traffic.

Wildlife species inhabiting grasslands and forests have been found to be most at risk from habitat loss and fragmentation (Hand et al., 2014), with the greatest ecological impacts occurring when roads or road networks intersect large habitat patches and wide corridors (Forman, 2005). Fragmentation effects are the greatest near natural landscapes as compared with agricultural or suburban landscapes (Forman, 2005), possibly because of the high local abundance of wildlife near natural landscapes, more so within or in the vicinity of protected areas (Grilo et al., 2011).

Habitat degradation

Roads also open up forested areas to new development and cause habitat degradation by creating suitable conditions for invasive species to flourish. Natural pristine and intact areas near roads significantly altered by road emissions (traffic noise, gaseous, solid, liquid) can be rendered unusable by wildlife, and can have greater ecological impacts than habitat loss and fragmentation (Forman, 2005). Chemical and nutrient pollution through liquid and gaseous emissions are also likely to get biomagnified in food chains (Laurance et al., 2009). Additionally there is ample evidence of human activities proliferating in previously pristine areas facilitated by the construction of roads (Blake et al., 2008; Laurance et al., 2001), that lead to biodiversity decline.

Changes in spatio-temporal habitat use patterns & behaviour

Because of human-induced disturbances, animals evolve behavioural responses by changing their activity periods or by avoiding altogether areas that may cause interaction with humans (Bonnot et al., 2013; Burson et al., 2000; Griffiths and van Schaik, 1993). Such shifts in activity patterns to avoid human activity, such as high traffic volume hours, is a common strategy among mammals (Baigas et al., 2017; Mccown et al., 2009; Ngoprasert et al., 2007; Riley et al., 2003). This type of avoidance results in indirect loss of habitat for mammals (Polfus et al., 2011).

Spatial avoidance of habitats in the vicinity of roads has been found to be influenced by multiple factors including road and species characteristics. In Spain, red deer and wild boar showed spatial avoidance of road surfaces, i.e. the avoidance of the clearing in vegetation due to linear infrastructure (D’Amico et al., 2015). While avoidance can also be a function of greater availability of suitable habitat away from roads (Rost and Bailey, 1979), carnivores that naturally thrive along edge habitats also show less preference for habitats road edges (Dijak and Thompson, 2000). Areas with high density of linear infrastructure including roads were avoided by Asian elephants by changing their seasonal migrations routes (Joshi and Singh, 2007). Grizzly bears preferred using roads with low traffic volumes, and selected against publicly used forestry roads (Kasworm and Manley, 1990; Wielgus et al., 2002).

Home range selection by mammals is also influenced by the presence and density of roads. While forest-dwelling caribou (Leblond et al., 2013), black bears (Brody and Pelton, 1989) and bobcats (Poessel et al., 2014) selected home ranges that were away from highways or away from areas with high road density, Habib et al. (2021) found that large carnivores in human-dominated landscapes included roads in their home ranges in contrast with their conspecifics inside protected areas with lesser road densities. Lyons et al. (2018) found that roads decreased the carrying capacity of grizzly bears by 30% in the landscape. Several other telemetry-based studies have found that avoidance of road-related disturbance leads animals to choose sub-optimal habitats. On the flipside, choosing home ranges with roads in them increases the risk of animal mortality.

Additionally, factors such as interactions with conspecifics, particularly in carnivores, influence the avoidance of habitat in the vicinity of roads ultimately affecting home range selection. For example, roads create artificial home range boundaries in carnivores (Kaczensky et al., 2003). Female home range boundaries were found to be clustered along roads in case of Florida panthers (Schwab and Zandbergen, 2011) and bobcats (Riley et al., 2006), resulting in the ‘cage effect’, leading to social isolation because of lack of genetically effective migration (migration resulting in genetic exchange).

Studies of radio-collared carnivores have showed individually varying utilization of habitat and road crossing behaviour across life stages, sex and land-use patterns (Ascensão et al., 2014; Colchero et al., 2011; Laundre et al., 2001; Mccown et al., 2009; Poessel et al., 2014; Rico et al., 2007; Riley et al., 2006; Valeix et al., 2009). Kit foxes avoided high road density areas during breeding, denning and pupping season (Jones et al., 2017). Adult male grizzly bears and female grizzly bears with cubs selected optimal habitats which left sub-adults with sub-optimal habitats in the vicinity of roads (Gibeau and Herrero, 1998). The sub-adults of the population were thus exposed and vulnerable to habituation to disturbance and mortality risks, thereby removing healthy individuals from the population (Mueller et al., 2004). Such sex and age specific responses may also influence use of crossing structures by wildlife (Ford et al., 2017).

For carnivores the ‘landscape of fear’ hypothesis (Laundre et al., 2010), when applied to human-modified landscapes, suggests that areas where perceived risk is greater would be less likely occupied by wildlife. Stewart et al. (2016) found that the time spent by wolverine individuals at baits decreased with increasing human disturbance. Similar effects were observed by Kerley et al. (2002) in Amur tigers, where 63% of tiger kills were found abandoned as a result of disturbance by humans along roads. High traffic levels influenced the abandoning of foraging by grizzly bears, even as roadsides had more productive vegetation during springtime (Mattson et al., 1987). These responses varied between male and female grizzlies. Female grizzlies, while exploiting roadside habitat to make use of productive vegetation and avoid contact with males, risked the survivorship of cubs and sub-adults leading to higher mortality rates and lower fecundity.

Avoidance of wildlife crossing structures has been observed to be positively correlated with traffic volume and level of human activity (Barrueto et al., 2014; Saxena and Habib, 2022), although some habituation of traffic has been seen in some species. However some studies have also shown habituation of herbivores to human disturbance and traffic (Burson et al., 2000; Schultz and Bailey, 1978). Impalas showed habituation of vehicles and few (19.5%) flight responses in Kruger National Park, but were found to avoid close proximity of paved roads than unpaved roads (Mulero-Pázmány et al., 2016). Sub-adult Canadian Rocky mountain grizzly bears habituated to human-modified areas and roads, but this also made them more vulnerable to roadkill (Gibeau and Herrero, 1998). Habituation of road-related disturbance has been documented more in herbivores, and large carnivores have been shown to be sensitive to all forms of human disturbance.

Heightened levels of vigilance in herbivores inhabiting areas with high human presence, such as on roadsides, may also affect animal health by causing physiological stress (Iglesias-Merchan et al., 2018) and decrease effective foraging (Puig et al., 2021; Tsunoda, 2021). Increased vigilance can also lead to reduction in other vital social activities (St. Clair and Forrest, 2009). Carnivores in the vicinity of human infrastructure have also been found to exhibit decreased variation in behavioural patterns (Stewart et al., 2016)

Barrier effect & loss of connectivity

Avoidance behaviour results in a decrease of road-related mortality but increases the barrier effect of the road (Jaeger et al., 2005). The decision to cross a road by an animal is the result of a trade-off between the risk of mortality and the benefits of resources and shelter from predators/conspecifics (Brody and Pelton, 1989; Gibeau and Herrero, 1998). In mammals, this is a learned behaviour, and would vary with differences in species/taxa cognitive abilities and anti-predator strategies (Jacobson et al., 2016; Kintsch et al., 2015). The areas used for movement and crossing roads are characterised by certain environmental factors such as presence of large forest patches, adequate vegetation cover, riparian areas with drainage structures and road network configuration and type (Baigas et al., 2017; Carvalho et al., 2016; Poessel et al., 2014).

Behavioural aversion to movement across roads is reinforced with mortality of animals attempting to move across roads, but may also vary with species preference of habitats and degree of adaptability (Hennessy et al., 2018). The inability of some animals to cross roads and the active avoidance of others leads to the barrier effect, which in the long-term, can cause local populations to become isolated (Shepard et al., 2008).

Road (width), traffic (volume, heterogeneity, daily pattern) and landscape characteristics (land use patterns) influence the magnitude of the barrier effect of roads (Brody and Pelton, 1989; Chen and Koprowski, 2016; Dyer et al., 2002; Mccown et al., 2009; Rico et al., 2007; Seidler et al., 2014). The cumulative barrier effect is greater in human-dominated areas (agricultural landscapes), where human activity and traffic on roads create impediments to movement as well as habitat degradation and disturbance because of road and anthropogenic activities (Forman, 2005; Paton et al., 2017).

Major roads provide a greater barrier than minor roads to long-ranging carnivores like Florida panther, with more road crossings being recorded across minor roads (Schwab and Zandbergen, 2011). Movement is affected by traffic volume, more for carnivores than herbivores (Alexander et al., 2005; Baigas et al., 2017; Chen and Koprowski, 2016). The barrier effect in some species is more prominent for females than for males- in the Canadian Rocky Mountains, roads presented a barrier to female grizzly bears while allowing partial movement to males (Gibeau and Herrero, 1998). Cullen et al. (2016) found higher densities of jaguars and low population persistence in populations in highly fragmented landscapes that could further reduce by road-related mortality. Elimination of suitable habitat and disruption of migration pathways causes previously connected animal populations to become genetically isolated (Forman and Deblinger, 2000a; Riley et al., 2006) and become vulnerable to local extinction. Genetic differentiation in populations separated for about 50 years because of roads could also attain the same degree of isolation as those populations that are separated spatially by several hundred kilometres (Roy et al., 1994). Kuipers et al. (2021) found that loss of habitat connectivity in highly fragmented regions can be a major contributor (up to 90%) to the possibility of terrestrial species extinction. Ensuring dispersal of species living in fragmented landscapes is thus critical for ensuring long-term persistence.

Long-term impacts of road-related effects

Human activity affects density, diversity and distribution of wildlife in forests (Griffiths and van Schaik, 1993). This may be due to varying animal responses to edge-related disturbance and disturbance due to traffic on roads. For large mammals in Tanzania (Newmark et al., 1996) and India (Gubbi et al., 2012), differential density effects were found for different species in different habitats with respect to road-related disturbance. However, roads also drive activities such as hunting and resource extraction that indirectly reduce mammalian densities in forest areas (Vanthomme et al., 2013). However, the same study found differential responses to roads for some mammals that profited from vegetation along roadsides or because of low hunting pressures on those species. Within protected areas, however, effects of road-related disturbance on species diversity could be less evident (Sangiwa et al., 2019), because of availability of favourable habitat and absence of secondary human activities.

In the long-term, the interplay between road-related impacts and other anthropogenic influences can impact the persistence of local populations (Roger et al., 2010). Anthropogenic causes of animal mortalities that are directly facilitated by roads are sometimes too great to promote natural population growth (Mace et al., 1996), and recolonization of such areas where animal populations have decimated is also compromised because of high road densities (Thiel, 1985).

Because of their large area requirements, carnivores are most affected by linear infrastructure. Roads impede carnivore movement in a landscape, and imperil long-term survival of such species in a fragmented landscape through multiple pathways. For example, 20 vehicle-related Florida panther mortalities in a highly fragmented and small population is more than the natural mortality rate and could put the population at risk of local extinction (Schwab and Zandbergen, 2011). Adverse impacts of population fragmentation in mountain lions, such as high levels of inbreeding, reproductive failure, intraspecific strife and lack of individual dispersion have been reported (Riley et al., 2014). Artificial home range boundaries created by roads affect the reproductive chances of dispersing individuals, leading to genetically ineffective migrations (Riley et al., 2006). Threshold levels of road densities are reached when patch sizes are not sufficient for carnivores to have any territories (Mech et al., 1988), resulting in shrinking of natural ranges, or forcing individuals to include high traffic roads in their home ranges (Habib et al., 2021). For long-ranging and sparsely populated carnivores with low reproductive rates, this situation poses the threat of no-breeding or in-breeding. Such results indicate the need for contiguous roadless habitats for the conservation of apex predators.

Prey response to road-related disturbance: predator-release or predation risk?

Prey have evolved anti-predator behaviour to avoid threatening stimuli. It has therefore been proposed that prey respond to human disturbance the same way as they would to a predator, i.e., according to the ‘risk-disturbance hypothesis’, disturbance stimuli (of anthropogenic origin) should be analogous to predation risk (Chen and Koprowski, 2016; Frid and Dill, 2002). This response depends on available habitat, distance from refuge, costs of abandoning the resource, size and approach speed of stimuli etc. It is the persistence of threatening stimuli that then causes certain animals to completely avoid or abandon habitats, explaining the avoidance behaviour of herbivores mentioned in the preceding section. The hypothesis also predicts that since herbivores consume lesser plant biomass in the presence of human disturbance, it could indirectly affect plant community structure and have cascading effects at lower trophic levels (Chase, 1998). Moreover, the fitness costs of being vigilant against perceived predation risk in human-dominated areas are also high.

Top predators regulate community structure and function by regulating prey numbers (Ford et al., 2014; Polis and Strong, 1996). However, carnivores in human-modified landscapes are unable to perform their ecological functions of being top-predators and regulating prey populations. Human-related disturbances can affect the density of carnivores through avoidance or reduction in densities (Kuijper et al., 2016). Differential responses to anthropogenic disturbance among prey and predators suggest that increased abundance of herbivores near moderately disturbed sites is a consequence of 'predation release' i.e., a greater abundance of prey in the absence of predators that are more sensitive to anthropogenic disturbance (Berger, 2007; Rogala et al., 2011). The absence of carnivores thus affects the densities and habitat use of herbivores, and this can translate into increase in browsing intensity and overall use of roadside habitat (Laurian et al., 2012), and low recruitment of native vegetation and other fauna (Hebblewhite et al., 2005), leading to cascading effects down the trophic levels.

Road effect zones

Road effects are not limited to the physical extent of the road, but also percolate into the adjacent habitats. This zone has been called the 'road effect zone' (REZ) (Forman et al., 1997; Forman and Alexander, 1998). The REZ is not linear, and depends on the species/community or natural component affected (viz., soil, streams) (Forman et al., 1997). The extent of the zone depends on road characteristics, landscape features such as availability of resources and type of ecosystem affected (Andrasi et al., 2021; Forman and Deblinger, 2000b; Shanley and Pyare, 2011; Torres et al., 2016).

For animals, the REZ is a culmination of species responses borne out of behavioural and ecological traits and consequent impacts on habitat use near roads as detailed in the preceding sections. Consequently, the extent of the REZ has been found to vary between animals, where relatively low traffic volumes can often create wider REZ for more sensitive

(Shanley and Pyare, 2011). This can lead to indirect habitat loss, reinforce the barrier effect for sensitive species, and also decrease the rate of crossing structures use by such species. Therefore, delineating REZ can help understand species responses to roads and consequently help mitigate adverse impacts beyond the physical road infrastructure.

Planning measures to mitigate impacts of roads on wild mammals

Recognition of the widespread impacts of roads on wildlife has necessitated infrastructure planners and conservation professionals to include mitigation measures such as crossing structures (underpasses and overpasses) (Mata et al., 2015; Mysłajek et al., 2020), automatic animal detection systems to alert drivers and alarm animals (Huijser, 2015), and wildlife fencing (Clevenger et al., 2001; Rytwinski et al., 2016; van der Ree et al., 2015) around the world. Such measures are increasingly being adopted in developing countries as well (Okita-Ouma et al., 2021; Poudel et al., 2020; Saxena and Habib, 2022).

Several factors are considered while deciding strategies to mitigate the impacts of roads on wildlife – impacts to be mitigated, the focal species or community for which the measure is targeted, the design, location and type of mitigation measure to be deployed, cost and long-term viability of the measures (Cain et al., 2003). Several researchers have formulated guiding principles for planning mitigation based on criteria such as habitat patch and corridor size, likelihood of animal collisions and crossings, optimal combinations of mitigation measures etc., (Ford et al., 2011; Forman, 2005; Jaarsma et al., 2006; Polak et al., 2014; Saxena et al., 2020; Spanowicz et al., 2020).

Pragmatic on-ground mitigation solutions, however, are based on a combination of ecological guiding principles, and spatially delineated priority habitats in a landscape, and priority segments in a road network. As a first step, the mitigation hierarchy requires identification of sites where no new road development should occur (Kiesecker et al., 2010; Phalan et al., 2018) based on some guiding principles (Forman, 2005). This is ideally followed by identification of areas where mitigation options would yield the most benefits for multi-species conservation (Polak et al., 2019).

Most often, placement of mitigation measures like crossing structures are decided based on information on roadkill hotspots (Fedorca et al., 2021; Gunson et al., 2011; Nelli et al., 2018; Shilling and Waetjen, 2015), movement and road crossing data from radio-collared animals (Zeller et al., 2020), and a combination of both collision and crossing data (Zeller et al., 2018). However not all road planners and conservation professionals have pre-construction data on animal movement and animal collision hotspots. In such cases, limited roadkill and animal movement and habitat use/suitability information is modelled and/or simulated on larger landscapes to delineate collision hotspots and crossing zones (Visintin et al., 2016; Wierzchowski et al., 2019).

1.1. Rationale for the study

With the construction and upgradation of about 2,00,000 km of roads planned under different government schemes till the year 2022 (Carter et al., 2020; “Ministry of Road Transport & Highways, Government of India”), India is also going through a phase of rapid road network expansion. Consequently, the impacts of roads on wildlife and natural areas are also expected to increase manifold. The study area i.e., the central Indian landscape (CIL), is considered to be the heart of India’s wildlife, and is also recognised to be one of the landscapes with the highest potential for long-term viable tiger conservation. It is home to 838 tigers (nearly 35% of Indian tiger population) distributed across 19 tiger reserves and other protected areas (Jhala et al., 2020). These tiger reserves are connected through a network of corridors that are tracts of forests in the midst of multiple land uses. The landscape is also witnessing accelerated levels of road development and expansion. In anticipation of increasing vehicular traffic, several 2-lane roads in India are rapidly being up-graded to 4 or more lanes.

Linear infrastructure, particularly roads, have been identified as one of the major causes of loss of connectivity for tigers and associated wildlife within this landscape (Habib et al., 2021; Thatte et al., 2020, 2018). Highly fragmented landscapes such as CIL are more prone to negative impacts of connectivity loss (Kuipers et al., 2021). Moreover genetic measures indicate adverse fragmentation-caused impacts on large-bodied (especially herbivores), terrestrial and arboreal forest dependent species living in highly fragmented regions (Lino et al., 2019).

Road up-gradation plans and consequent increase in vehicular traffic would endanger the functional integrity of these corridors. This will affect long term wildlife conservation in the landscape. Gathering baseline information on the impacts of roads on wildlife is thus the first step towards planning roads in tiger landscapes and, where unavoidable, mitigating these impacts to ensure long-term viable conservation in such landscapes. The study therefore aims to quantify the scale of road-related impacts on wildlife in this landscape in order to provide ecologically sound and viable solutions for mainstreaming biodiversity concerns in road development plans.

The need for combining wildlife science, landscape ecology principles and road planning approaches becomes real and instant for securing and enhancing connectivity between natural areas with an overarching goal of conserving biodiversity in landscapes fragmented by road development corridors. In a rapidly developing country like India, delay in ecologically-informed decision-making and implementation of mitigation measures will always have negative impacts on wildlife till permanent measures are in place. This delay may result in disconnected wildlife populations and loss of precious wildlife.

Information on the impacts of roads on wildlife is largely missing from developing countries (Barrientos et al., 2021), particularly the global tiger range. While predictions for the extent of wildlife habitats potentially affected by roads have been made for forests in the global tiger range (Carter et al., 2020), these are based mostly on studies from the global west. Considering differences in species ecology, road development and conservation imperatives between developed western countries and developing tropical nations, there is an urgent need to base mitigation strategies in these countries on site, species/community and landscape specific empirical studies.

However, road ecology in most of the developing world, especially south and south-east Asia, has not been keeping up with the rapid pace of infrastructure growth in these regions. Most road ecology studies have been carried out in the west, particularly high income countries (Barrientos et al., 2021). While exceptions do exist (Gubbi et al., 2012; Gubbi and Poornesha, 2015; Vidya and Thuppil, 2010), most research has focused on wildlife roadkill (Baskaran and Boominathan, 2010; Behera and Borah, 2010; Das et al., 2007; Pragatheesh and Rajvanshi, 2013; Selvan et al., 2012; Sur et al., 2022). With notable exceptions (Pragatheesh and Rajvanshi, 2013), most of the information generated on impacts of roads on wildlife has been a by-product of other monitoring and research activities. Moreover studies not primarily focused on assessing effect of road infrastructure on wildlife have identified road networks as landscape-scale impediments to animal movement often through genetic, GIS-based landscape assessments and combined approaches (Jayadevan et al., 2020; Joshi et al., 2013; Nayak et al., 2020; Thatte et al., 2020, 2018; Yumnam et al., 2014). Notably Habib et al. (2021) identified home range characteristics of wild carnivores in human-dominated landscapes with respect to the local road network.

For high investment and long-term infrastructure development plans, the decisions are taken at a strategic level. Thus large-scale and cumulative impacts of linear developments on landscapes and associated ecological processes necessitate the study of these impacts at the landscape level (Saxena et al., 2016). This type of study is more inclusive than a study at the ecosystem level (Mortberg et al., 2007), whereby suitable and accessible habitat can be planned in habitat networks consisting of core areas sufficient for species' persistence in the landscape, linked together through corridors that enable dispersal (Opdam et al., 2002). Consequently, the present study aims to fill these gaps by creating baseline information on species responses to and impacts of road. This would help design species and site-specific mitigation measures to alleviate road impacts. Further considering the rapid growth of the Indian road network and rampant road up-gradation plans, the study aims to delineate priority mitigation sites in the landscape based on species responses to roads. The resulting knowledge can help stakeholders involved in road planning to ensure biodiversity protection and social and economic well-being at the same time.

1.4. Study objectives

Despite being one of the leading causes of landscape fragmentation and animal mortality in India and CIL, field studies to assess the effect of roads have rarely been conducted in the region, with the exception of Pragatheesh and Rajvanshi (2013). In order to keep pace with the rapidly expanding road network and up-gradation plans in the landscape, assessment of species and community ecology, and their responses to roads would aide in better decision-making and mitigation planning in this vital tiger conservation landscape. Consequently, I framed the following objectives for my study:

A. *Determine the extent of the ecological impacts of existing road network on mammals in the Central Indian Tiger Landscape.*

Sub-objectives:

1. Identify the effect of roads and associated traffic on the behaviour, activity patterns and habitat use of selected mammalian species,
2. Identify the effect of roads and associated traffic on the species diversity and relative abundance of mammalian species.

B. *Predict road-related impacts on the integrity of the Central Indian Tiger Landscape*

Sub-objective:

1. Delineate species-specific road-effect zones under different road and traffic scenarios in the landscape

C. *Identify and prioritise crossing zones in different corridors for planning mitigation measures to improve permeability and integrity of the Central Indian Tiger Landscape.*

1.5. Organisation of thesis

The thesis has been organised into 7 chapters. Chapter 1 introduces the issue of road development in a bio-diversity rich developing country context, the impact of roads and road networks on mammals, and rationale and objectives of the present study. Chapter 2 introduces the study area, its importance in terms of tiger conservation, the road network in the landscape, division of study area into complexes for ease of analysis and reporting, and a brief description of these divisions and of the selected study species. The three study objectives – including the aims, methods, results and discussion, have been organised in the subsequent chapters (3 – 6). Chapter 3 deals with the relative abundance, activity and diversity of mammals near NH 44 (parts of Objective A1 and 2). Chapter 4 deals with the behaviour of chital near NH 44 (part of Objective A1). Chapter 5 deals with use of roadside habitat by ungulates in the central Indian landscape (Objective A1), and delineation of species-specific road effect zones (Objective B). Finally, Chapter 6 deals with the identification and prioritisation of crossing zones in corridors of central India (Objective C). The final chapter contains a synthesis, conclusions, and management implications of the study (Chapter 7).

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Chapter 2

Study area

2.1. The Central Indian Landscape

The central Indian tiger landscape (henceforth used interchangeably with 'Central Indian Landscape'), comprising of a network of protected areas, and 23 (of the 50) tiger reserves, is often called the heart of India's wildlife. The landscape, along with the Eastern Ghats, comprises the semi-arid zone of Rajasthan, and the central Indian plateau in the states of Maharashtra, Madhya Pradesh, Chhattisgarh, Jharkhand and Odisha (Fig. 2.1). The landscape also extends to the Eastern Ghats in Telangana, Andhra Pradesh and Odisha. The geography of the landscape is diverse, with the Aravalli hills, the oldest mountain ranges in India, to the north-west, the vast Chhota Nagpur plateau in the north-east, and the hills of the Eastern Ghats to the south-east in Odisha.

The landscape has characteristically high human population densities, mostly dependent on agricultural activities. The area is also known for its rich mineral deposits, and burgeoning cities like Nagpur, Chhindwara, Kota, and Chandrapur that are in proximity to some of the landscape's best forested tiger habitats. Lying geographically in the central part of India, multiple major transportation corridors i.e., roads and railway lines connecting different parts of the country pass through the landscape. Consequently, the forests in the landscape are facing tremendous pressures because of the rich mineral deposits, especially coal in the Chhota Nagpur plateau. Infrastructure development associated with mining, coupled with high human densities in the landscape and regional development aspirations have led to additional pressures of land-use conversion for agriculture, expansion of linear infrastructure including railway lines, roads, power transmission lines and irrigation canals. These activities have been associated with decrease in forest cover across the landscape, causing the landscape to become one of the most fragmented in the country.

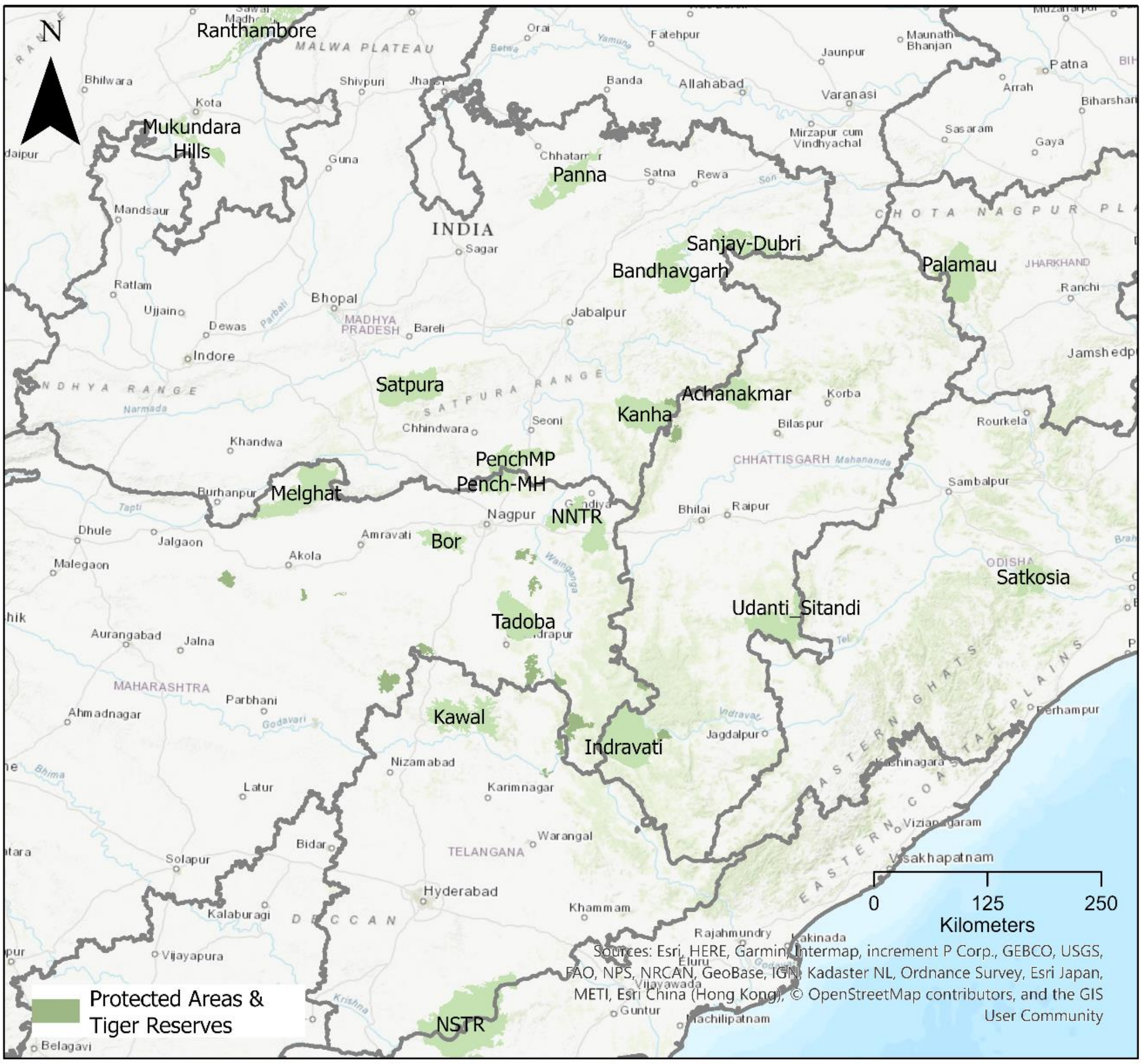

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Figure 2.1. The central Indian landscape spread across Madhya Pradesh, Telangana and Chhattisgarh states, and parts of Rajasthan, Jharkhand, Odisha and Maharashtra, with 35% of India’s estimated tiger population residing in the landscape’s tiger reserves, protected areas and intervening forests.

2.2. Flora and fauna

The landscape is a mix of semi-arid and peninsular forests, with diverse habitats. The major forest types in the landscape include tropical moist and dry deciduous forests, and tropical thorn forests. The moist peninsular forests that are restricted to areas with high soil moisture and rainfall in Madhya Pradesh and Chhattisgarh are dominated by *Syzygium cumini*, *Dendrocalamus strictus, Shorea robusta, Bauhinia* spp.*, Albizia chinensis, Emblica officianalis, Terminalia* spp.*, Adina cordifolia, Mitragyna parviflora, Lagerstroemia* spp.*, Anogeissus latifolia* and *Gmelina arborea*. *Dendrocalamus* breaks are common in parts of Madhya Pradesh and Maharashtra. Vegetation in the dry deciduous forests include *Tectona grandis, Anogeissus latifolia, Terminalia* spp.*, Diospyros tomentosa, Hardwickia binata, Dalbergia latifolia, Cassia fistula, Butea monosperma, Bridelia retusa, Aegle marmelos* and *Helicteres isora*.

The landscape is home to five canid species (golden jackal *Canis aureus*, wolf *Canis lupus pallipes*, fox *Vulpes bengalensis*, desert fox *Vulpes vulpes,* and the Asiatic wild dog *Cuon alpinus),* eight felid species (leopard *Panthera pardus*, tiger *Panthera tigris*, jungle cat *Felis chaus*, desert cat *Felis sylvestris*, caracal *Caracal caracal*, rusty spotted cat *Prionailurus rubiginosus*, leopard cat *Prionailurus bengalensis*, and fishing cat *Prionailurus viverrinus*), six bovid species (blackbuck *Antilope cervicapra*, gaur *Bos gaurus*, nilgai *Boselaphus tragocamelus*, wild buffalo *Bubalus arnee,* chinkara *Gazella benetti,* and chowsingha *Tetracerus quadricornis*), along with several other ungulate species (chital *Axis axis*, hard ground barasingha *Rucervus duvacelli branderi*, sambar *Rusa unicolor*, barking deer *Muntiacus vaginalis*, mouse deer *Moschiola indica*, wild pig *Sus scrofa* and Asiatic elephant *Elephas maximus*).

2.3. Tiger Conservation in the Central Indian Landscape

Central India is one of the strongholds of tiger conservation in India holding 1033 (885-1193) estimated tiger individuals, comprising about 35% of India’s estimated tiger population (Jhala et al., 2020). Tiger occupancy in the landscape has seen an increase of about 40% during the past 12 years, with simultaneously decreasing patch extinction (Jhala et al., 2020). This can be attributed to the increase in protection status accorded to several forest patches designated as protected areas over the years. More recently, corridor management and regulation of activities therein is increasingly being practised. Despite fragmentation of forested habitats and high human densities, tigers of Central India have been found to be the most genetically diverse (Kolipakam et al., 2019).

However, long-term survival of the central Indian tiger population is only possible if these protected areas and tiger reserves are connected with functional corridors which can aid in the movement of tigers, their co-predators and prey. Currently not a single tiger population in the landscape is viable in the long run by itself. Therefore, immigration and emigration of tigers within the landscape is a prerequisite for long term tiger conservation. This movement between habitat patches in the landscape is highly dependent on the suitability of corridors – patches of forests that connect prime/core tiger habitats to each other. These corridors act as connecting links between the habitats.

2.4. Study landscape within Central India

I conducted my study in a smaller and relatively more connected subset of the landscape (Fig. 2.2), which includes the Achanakmar, Kanha, Navegaon-Nagzira, Pench (Maharashtra and Madhya Pradesh), Satpura, Melghat, Bor, Tadoba-Andhari, Kawal and Indravati tiger reserves, nearby wildlife sanctuaries and intervening forests that form connecting links or corridors between these tiger populations.

The tiger reserves within the selected study area are home to 392 tigers (Jhala et al., 2020). Tiger occupancy in the landscape has also been detected in the non-protected forests of the Satpura-Melghat corridor, Kanha-Pench corridor, Chandrapur and Gadchiroli districts of Maharashtra, and Pranhita Wildlife Sanctuary. Tiger presence was found to have increased substantially in the forests and corridors that are in the proximity of protected areas and tiger reserves including Kanha, Pench, Saptura, Melghat, Navegaon Nagzira, Bor and Tadoba, including the Balaghat, Yawal, Chandrapur, Brahmapuri, Umred Karhandla, Central Chanda, Nagpur and Gondia forest divisions (Jhala et al., 2020). Overall, an increase in tiger occupancy over the past decades has been observed in areas that were characterised by low densities of roads and human settlements (Jhala et al., 2020).

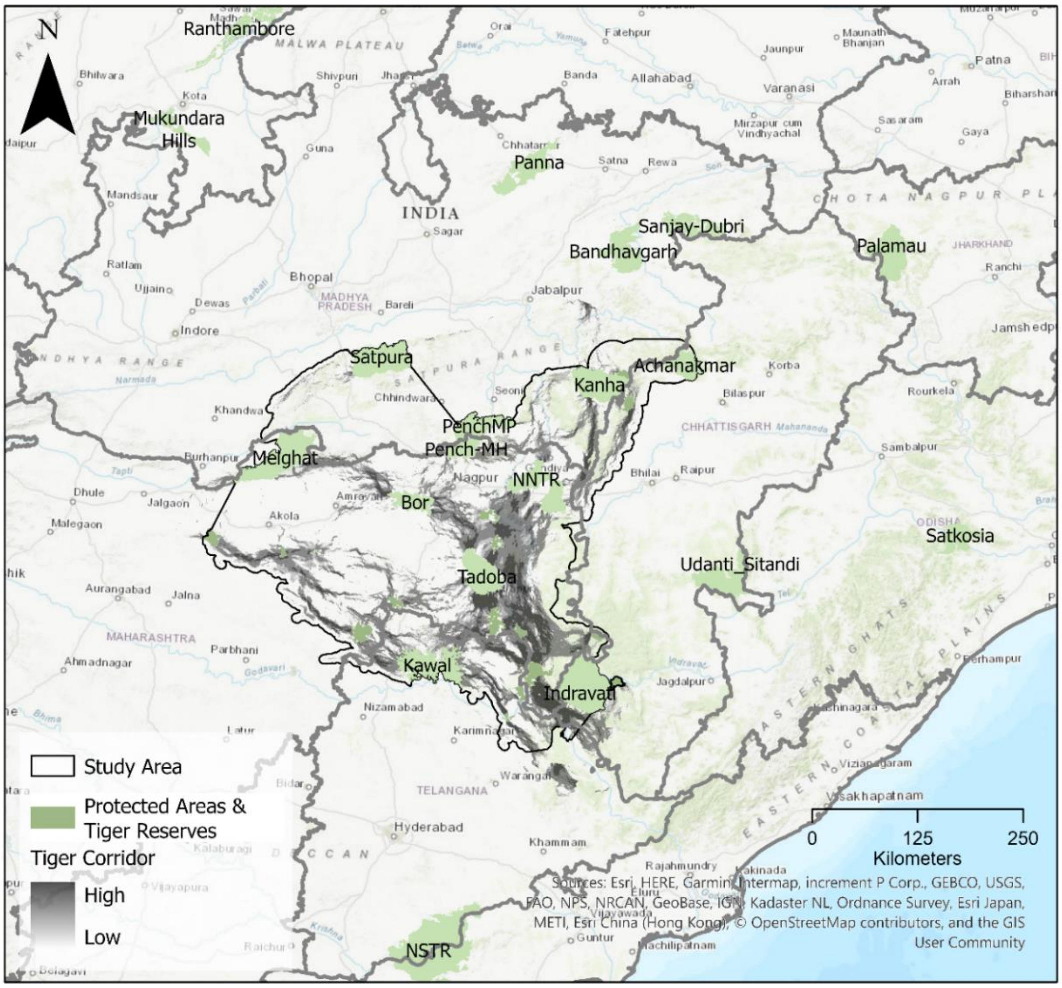

Figure 2.2. The study area within the central Indian landscape comprising 11 tiger reserves, nearby wildlife sanctuaries and intervening forests and corridors (Habib et al., 2021b).

For ease of analysis and reporting, I further divided the study area into complexes of adjacent and connected tiger reserves, protected areas and intervening forests. These complexes have been collectively referred to as ‘corridors’ hereon. For example, the Kanha-Achanakmar corridor refers to the PAs (Kanha, Achanakmar, Bhoramdeo, Phen) and the intervening forests acting as corridors (Habib et al., 2021b). Given below is a brief description of the six divisions of the study area.

a. Kanha-Achananakmar corridor

The Kanha-Achanakmar corridor consists of Kanha and Achanakmar TRs, Phen WLS and Bhoramdeo NP (Fig. 2.3). Along with the Pench Tiger Reserves (Madhya Pradesh and Maharashtra), the Kanha-Achanakmar complex together form the largest contiguous tiger population in the country holding 308 (252-370) tigers, with Kanha being an important tiger source (Jhala et al., 2020). However, the conservation status of Achanakmar continues to decline. The corridor sustains the Achanakmar tiger population from the Kanha source population. The corridor is potentially endangered by the National Highway 12A that cuts through the core zone of Kanha and Phen.

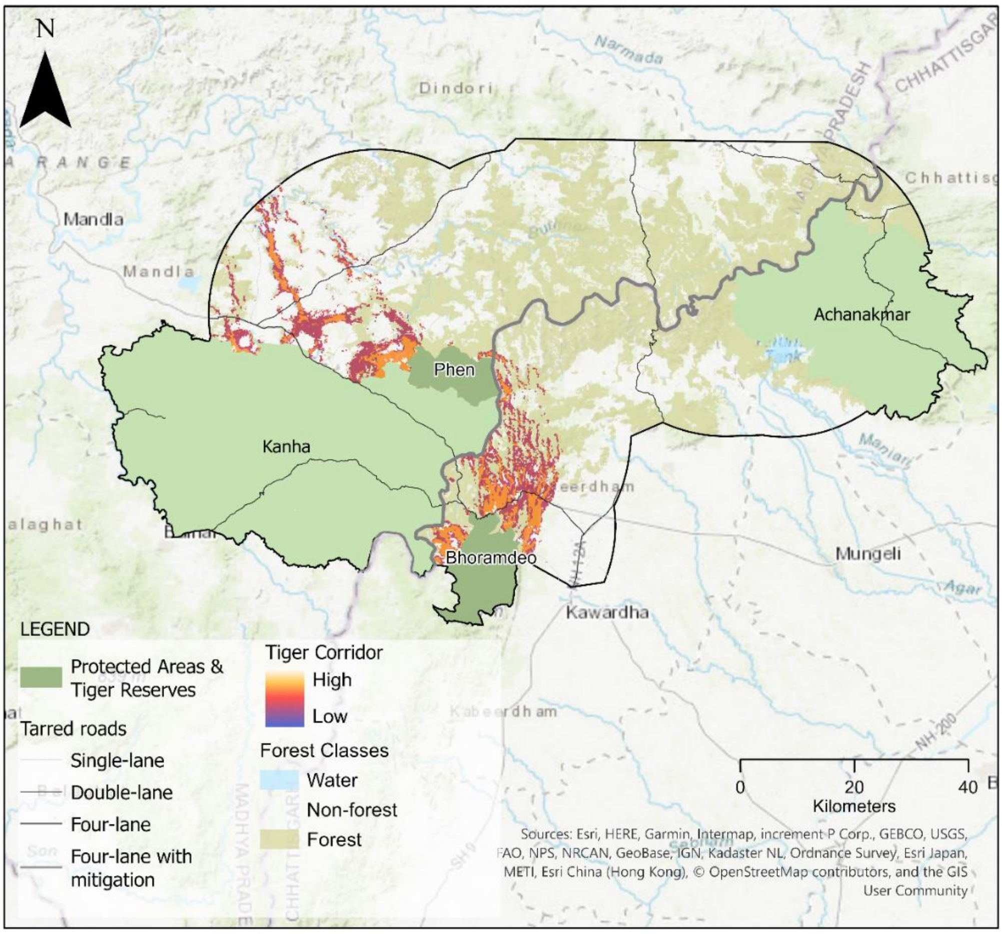

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Figure 2.3. The Kanha-Achanakmar corridor complex comprises of the Kanha and Achanakmar tiger reserves, Phen and Bhoramdeo wildlife sanctuaries, and intervening forests.

b. Pench-Kanha-NNTR corridor

The Pench-Kanha-NNTR corridor is comprised of the Pench, Kanha and Navegaon-Nagzira tiger reserves and intervening forests (Fig. 2.4). One of the most vital corridors in the landscape, the Kanha-Pench corridor connects two vital tiger source populations of Central India – Kanha and Pench TRs – with each other. There is evidence of regular use of this corridor by tigers (Yumnam et al., 2014), with the considerable tiger populations in the intervening Seoni and Balaghat territorial divisions. The corridor is adequately forested, with large parts under the Forest Development Corporation of Madhya Pradesh state. The expansion of the National Highway 7 (now 44) and the broad-gauge conversion of the Gondia-Mandla railway line have the potential to impede the connectivity of this corridor. However, inclusion of wildlife crossing structures during the expansion of National Highway 44, and the subsequent use of the structures by wildlife (Saxena and Habib, 2022) have set a precedent in road construction through sensitive habitats in the country. Further Kanha tiger population is connected to the southern tiger sink populations in NNTR and further south in Indravati through the forests in Chhattisgarh and eastern Madhya Pradesh. The National Highway 6 cuts through this corridor at two spots, once through the forests connecting northern and southern parts of NNTR, and then in Chhattisgarh. However, the on-going construction of wildlife passages on the former stretch of NH 6 is expected to mitigate the impacts of the highway within NNTR and the corridor.

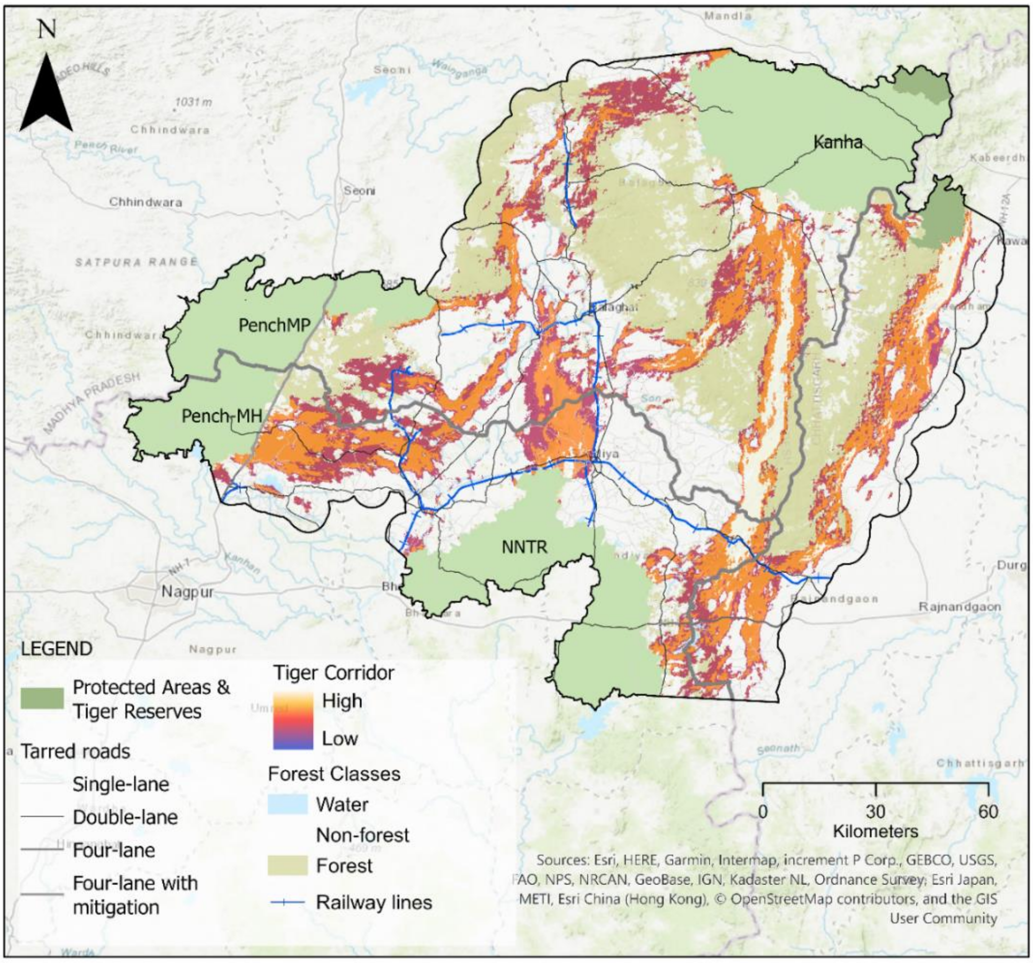

Figure 2.4. The Pench-Kanha-NNTR corridor complex comprises of the Pench (Madhya Pradesh and Maharashtra), Kanha and Navegaon-Nagzira tiger reserves and intervening forests.

c. Pench-Satpura-Melghat-Bor corridor

The Pench-Saptura-Melghat-Bor corridor comprises of the Pench (Madhya Pradesh and Maharashtra), Satpura, Melghat and Bor tiger reserves and intervening forests (Fig. 2.5), with Pench being the major tiger source. Both Satpura and Melghat are recognised to have high potential to sustain more tigers and have shown recoveries through incentivised village relocations. Pench and Saptura are connected through a matrix of patchy forests, agricultural lands, human settlements and mines, and have been found to be functionally connected (Yumnam et al., 2014). Satpura and Melghat are connected through habitat linkages.

Melghat and Pench are also connected via Bor. National and state highways, and railway lines are potential barriers to movement in this corridor.

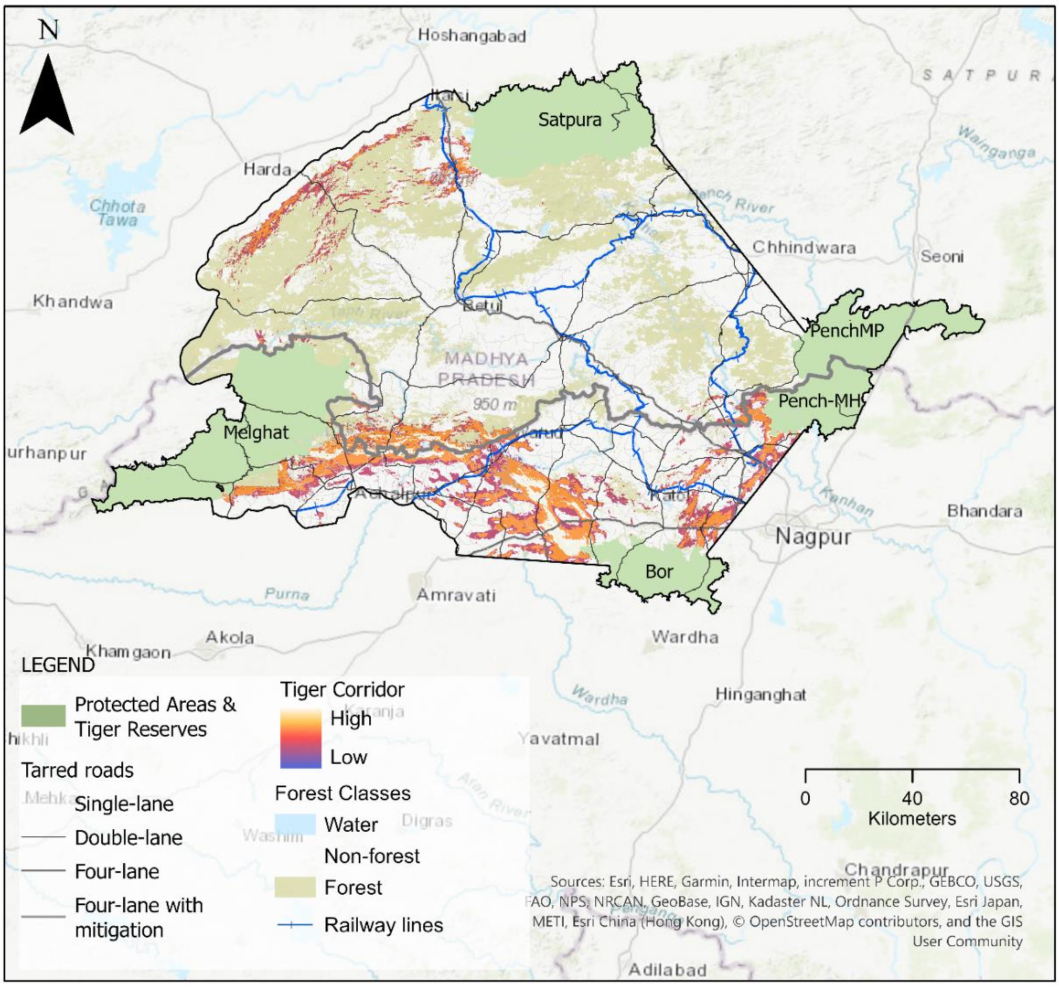

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Figure 2.5. The Pench-Satpura-Melghat-Bor corridor complex comprises of the Pench (Maharashtra and Madhya Pradesh), Satpura, Melghat and Bor tiger reserves and intervening forests.

d. NNTR-Bor-TATR corridor

The NNTR-Bor-TATR corridor connects the tiger populations of Bor, Navegaon-Nagzira and Tadoba Andhari TRs, and tigers residing in the Umred Karhandla and Ghodazari WLS, and the Brahmapuri, Central Chanda, Chandrapur and Pandharkawda forest divisions (Fig. 2.6). The area is characterised by high tiger densities that often cause conflict with humans.

There is regular movement of tigers between these habitats (Habib et al., 2021b), though this connectivity is endangered by multiple national and state highways, and railway lines.

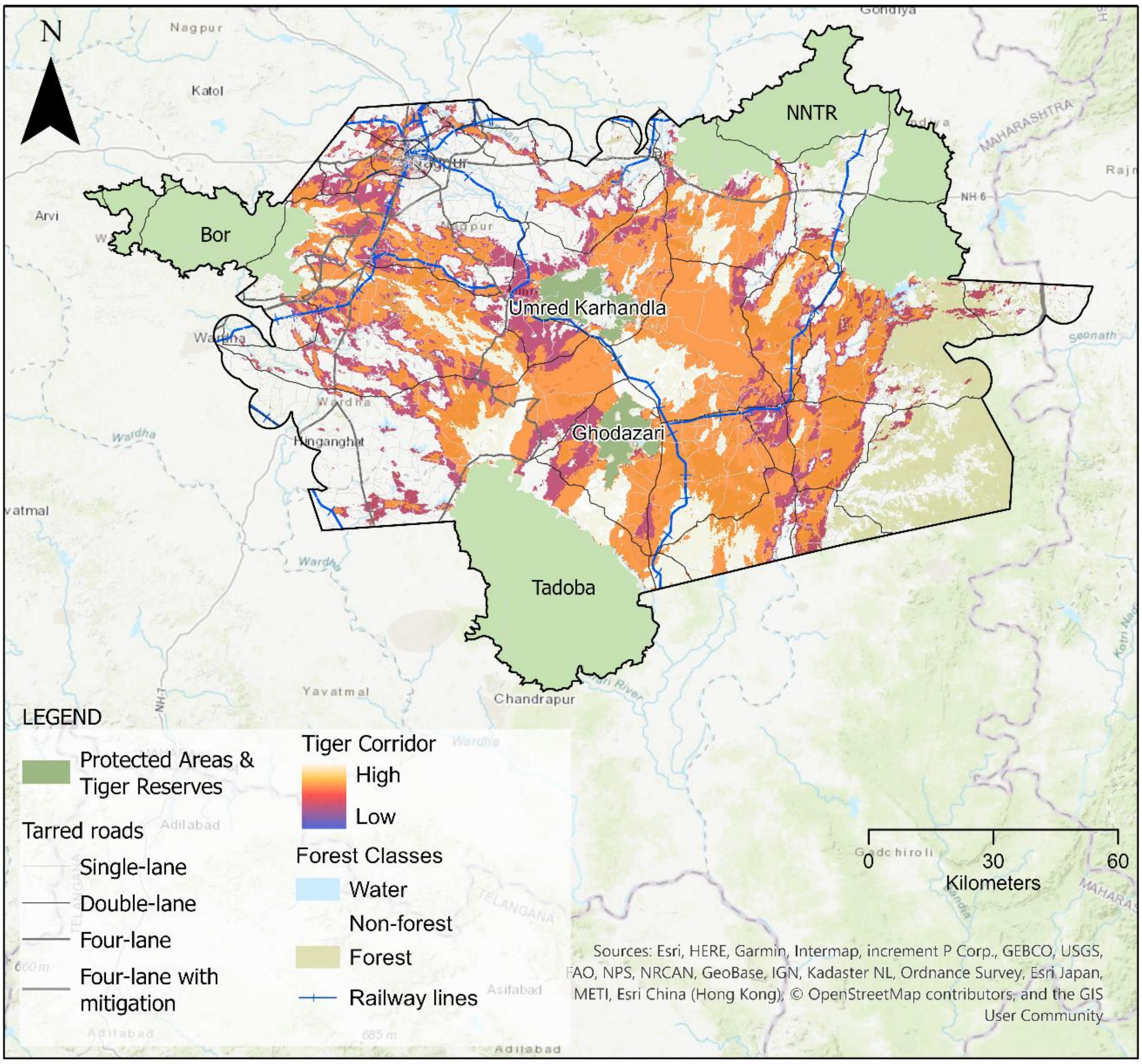

Figure 2.6. The NNTR-Bor-TATR corridor complex comprises of the Navegaon-Nagzira, Tadoba and Bor tiger reserves, Umred Karhandla and Ghodazari wildlife sanctuaries, and intervening forests.

e. TATR-Indravati corridor

The TATR-Indravati corridor connects the tiger populations in Tadoba Andhari, Kawal and Indravati TRs, and is interspersed with PAs like Kanhargaon, Chaprala, Bhamragarh, Pranhita WLS (Fig. 2.7). Though the forests south of Chaprala are dense, wildlife occupancy in the forests is low owing to extremism. Kanhargaon has been recently declared as a wildlife sanctuary, and acts as an important stepping stone habitat for tigers dispersing from Tadoba through the Central Chanda forest division.

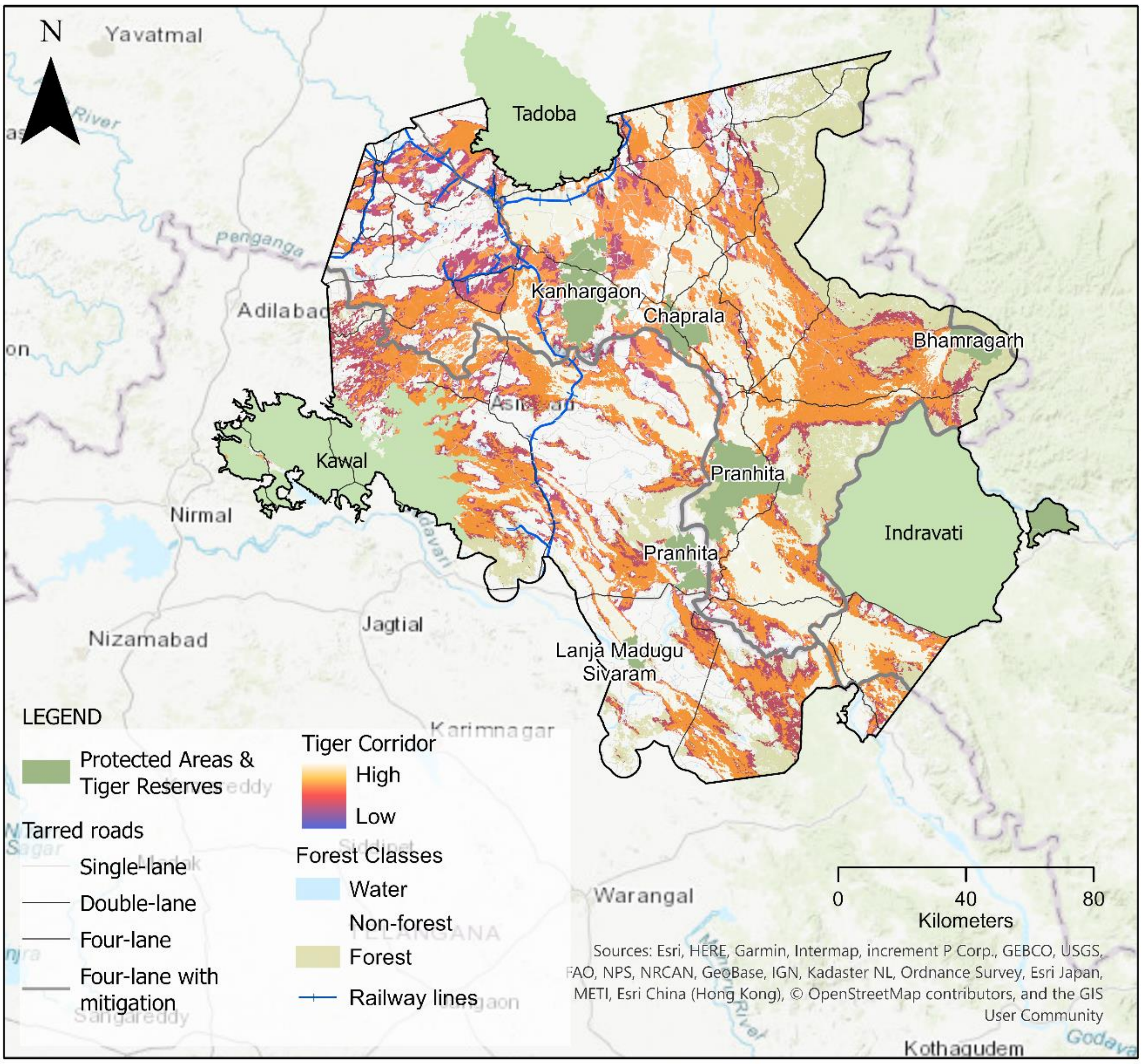

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Figure 2.7. The TATR-Indravati corridor complex comprises of the Tadoba Andhari, Kawal and Indravati tiger reserves, Kanhargaon, Chaprala, Pranhita and Lanja Madugu Sivaram wildlife sanctuaries, and intervening forests.

f. Kawal-Tipeshwar-Dhyanganga corridor

The Kawal-Tipeshwar-Dhyanganga corridor comprises of the Kawal tiger reserve, and the Painganga, Tipeshwar, Karanjasohol, Katepurna and Dhyanganga WLS (Fig. 2.8). The egion is connected via weak corridor links between Kawal TR, and up to the Dhyanganga WLS through the Tipeshwar WLS Tipeshwar is home to resident tigers. Recently one of the longest recorded tiger dispersals of a male tiger was documented through radio-telemetry from Tippeshwar to Dhyanganga (Hussain et al., 2022), that highlighted the functional connectivity of this corridor, and the role of fragmented but refuge islands for dispersing individuals.

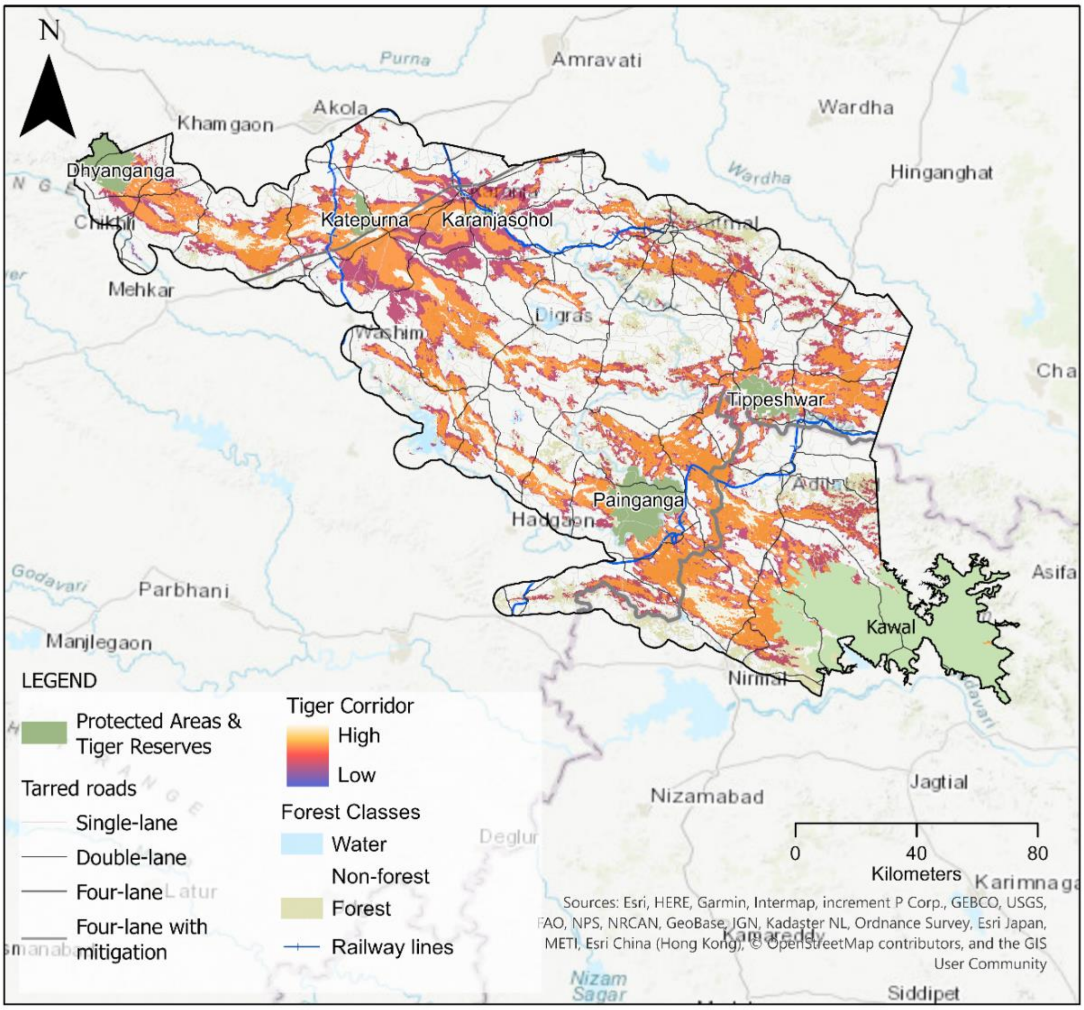

Figure 2.8. The Kawal-Tipeshwar-Dhyanganga corridor complex comprises of the Kawal tiger reserve, Painganga, Tipeshwar, Karanjasohol, Katepurna and Dhyanganga wildlife sanctuaries, and intervening forests.

2.5. Road network in the landscape

The central Indian landscape has one of the densest road networks in the country (Fig. 2.9), especially in the state of Maharashtra. The highest proportion of roads in the landscape comprises of tertiary roads, that are small, village level roads. Primary and trunk highways make up the least proportion of roads in the landscape, though the high traffic volumes on these highways can potentially cause high animal mortalities and create barriers to animal movement. Major national highways and expressways connecting different parts of the country like the North-South and East-West transportation corridors, and the recently completed Nagpur-Mumbai expressway intersect animal habitats and movement corridors.

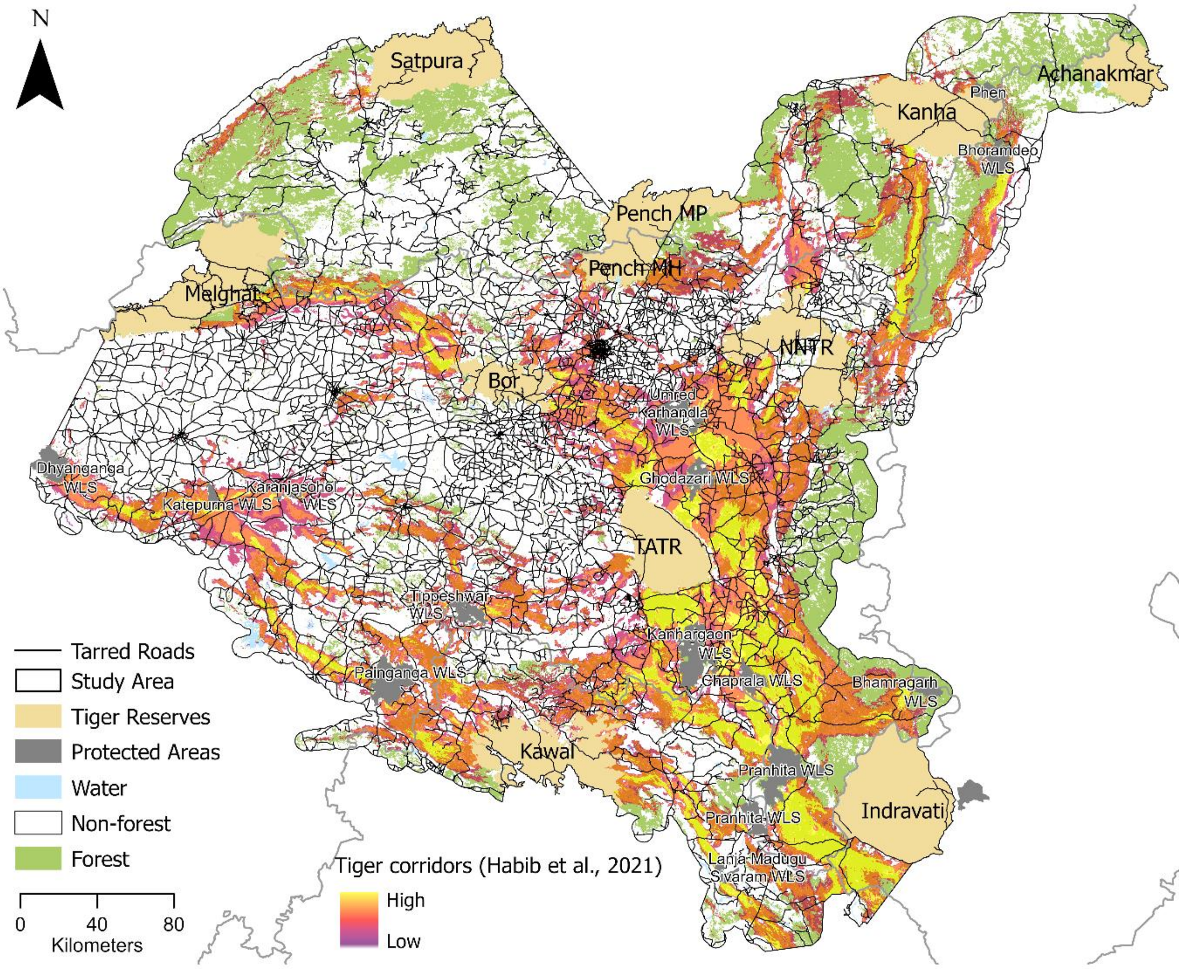

Figure 2.9. The road network in the selected study area comprises of a dense network of different road types intersecting tiger habitats and corridors.

High road densities exist near major cities such as Nagpur, Amravati and Chandrapur, while roads are sparsely distributed near Kanha, Achanakmar and south-eastern parts of the landscape near Indravati (Fig. 2.10).

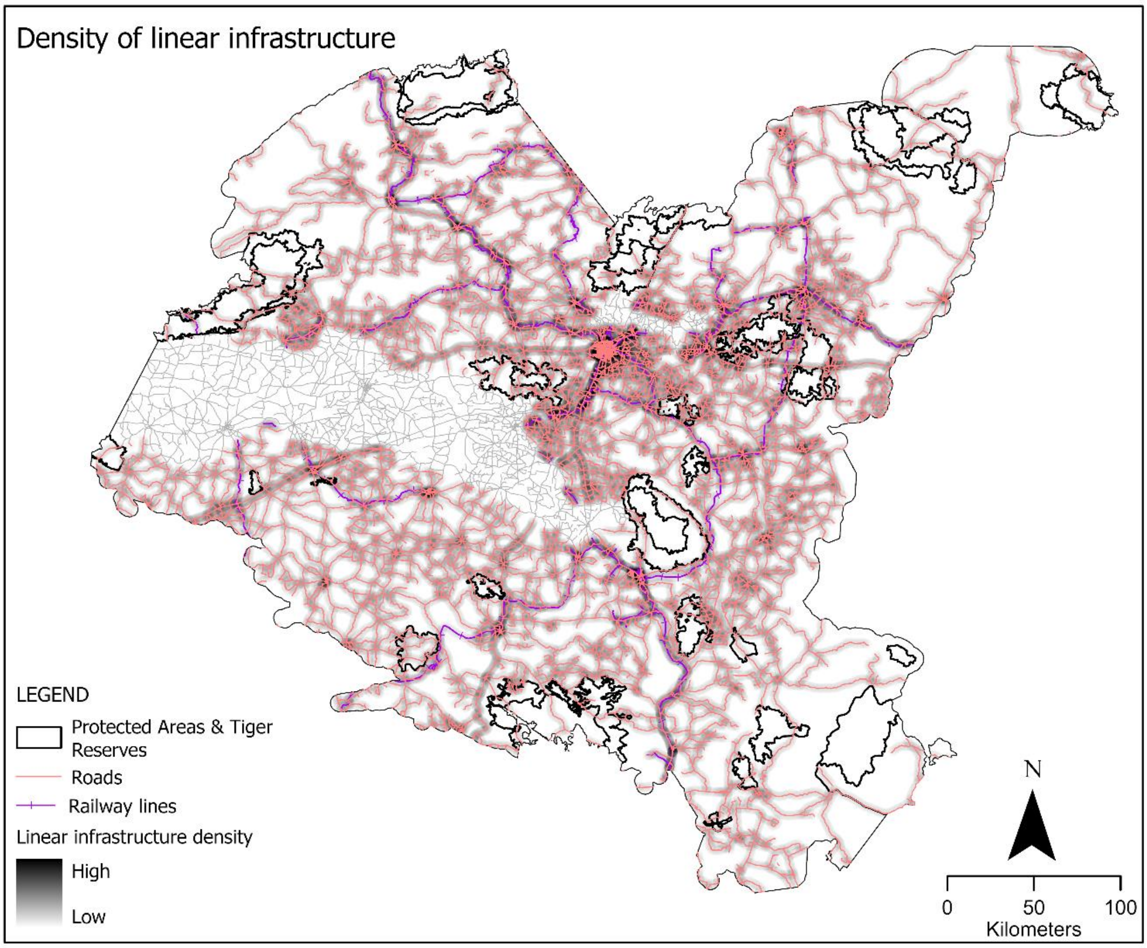

Figure 2.10. Linear infrastructure (roads and railway lines) density in the selected study area in central India.

2.6. Intensive study site

National Highway 44 passing through Pench Tiger Reserves, Madhya Pradesh and Maharashtra

The Pench landscape, consisting of Pench Tiger Reserves (PTR) and surrounding forests in Madhya Pradesh and Maharashtra states, harbours an important tiger source population in the central Indian tiger landscape (Fig. 2.11). Both tiger reserves are contiguous, but administratively separated by the state boundary. On the eastern side, PTR MP is connected with Kanha Tiger Reserve through the Pench-Kanha corridor, while PTR MH is connected to the Navegaon-Nagzira-Tadoba-Indravati Tiger Reserve populations. The Pench landscape is part of the Deccan peninsular central highlands biogeographic province

(Rodgers and Panwar, 1988). With a combined area of 1631.63 km^2, both tiger reserves are named after the river Pench that flows through the reserves. Major forest types in the landscape are southern Indian tropical moist deciduous, southern dry mixed deciduous and southern tropical dry deciduous forests, dominated by teak (*Tectona grandis*) and other associates. The tiger densities in the two reserves are similar (Pench MP: 5.5 ± 0.85/100 km^2; Pench MH: 4.78 ± 0.7/100 km^2) (Habib et al., 2022; Jhala et al., 2020). The major co-predators of the tiger found in the area are leopard, wild dog, and sloth bear. Major prey species of tigers and co-predators include gaur, sambar, chital, wild pig, barking deer, and four-horned antelope. The landscape is also home to grey wolf, striped hyena (*Hyena hyena*), and the golden jackal (Habib et al., 2022).

The National Highway 44 (previously known as NH 7, hereafter NH 44) is a vital highway that is part of the north-south transportation corridor connecting multiple economic and urban centres along the northern and southern limits of India. A 60 km stretch of the highway passes through PTR, surrounding forests and two vital tiger dispersal corridors. As part of the National Highways Development Plan, the former 2-lane highway was proposed for up-gradation to 4-lane configuration. Considering the importance of the PTR as a tiger source for the landscape, and to mitigate the impacts of the highway on wildlife within PTR, wildlife crossing structures (CS) or animal underpasses were proposed along the entire stretch of the highway passing through forests in both states (Fig. 2.11). The traffic volume on the highway during the study period was 5425±553 vehicles per day.

The Maharashtra section of the highway was under construction during the initial phase of the study (beginning 2017), and up-gradation of the highway and construction of CS in this segment was completed by end of the year 2018. In the Maharashtra section of the highway, the mitigation measures consist of 9 CS measuring 50 – 750 m in width, and 5 m in height (Habib et al., 2015). The Madhya Pradesh section of the highway remained a 2-lane road until the year 2019, and up-gradation to 4-lane with CS was recently completed. The highway passing through the forest areas does not have wildlife fencing, except for guide walls on either side of the CS measuring 50-250 m in length.

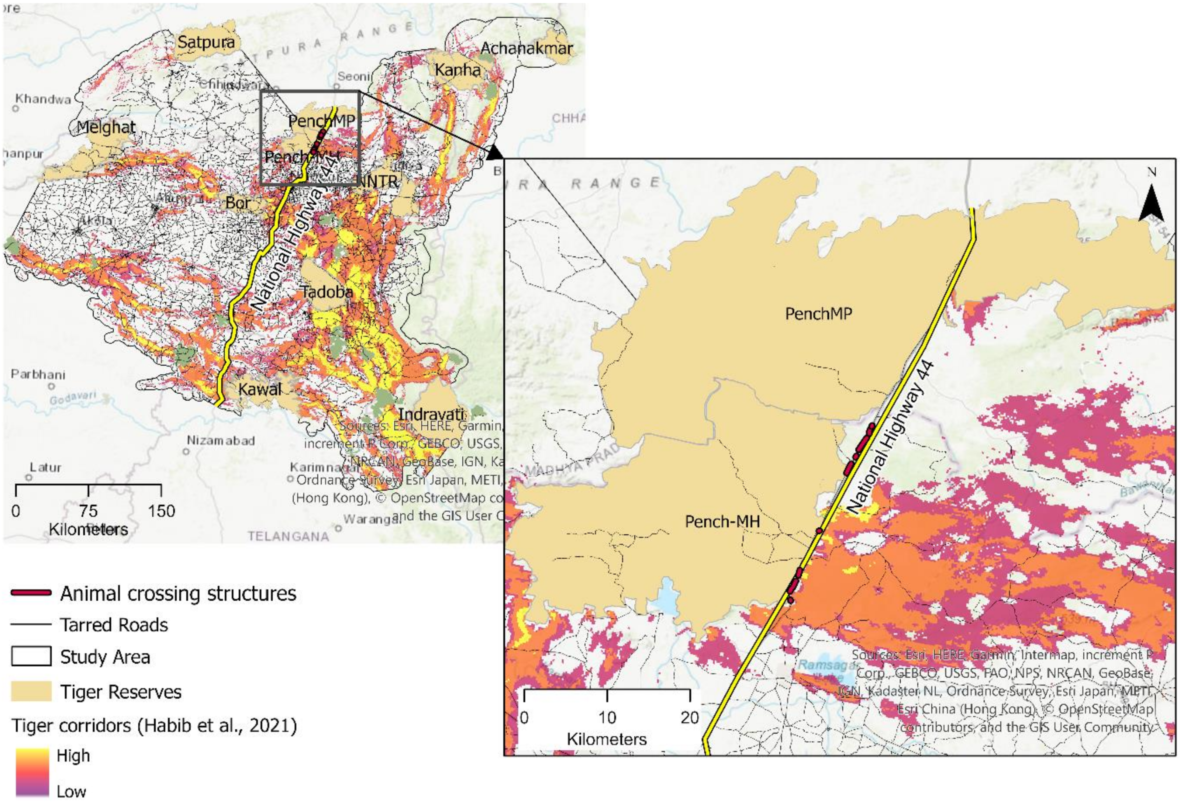

Figure 2.11. The National Highway 44, a vital north-south highway, passes through the forests and corridors in the study area in central India [Left]. It passes through the eastern edge of the Pench Tiger Reserve, Maharashtra, and intersects the forest ranges of Pench Tiger Reserve, Madhya Pradesh. In the Maharashtra section of the highway, 9 animal crossing structures have been constructed.

2.7. Study species

For the study, I selected the tiger, which is the umbrella species for conservation in this landscape, its major co-predators i.e., leopard and wild dog, and the five most commonly occurring prey species i.e., chital, gaur, nilgai, sambar and wild pig. Given below is a brief description of the eight mammals selected for the study. Descriptions have been restricted to animal characteristics that may have a bearing on the animals' responses to and impacts because of roads and fragmentation.

a. *Tiger*

Scientific Name: *Panthera tigris*

Conservation status: Schedule I (Wildlife (Protection) Act, 1972

Endangered (IUCN Red List)

Figure 2.12. A tiger using one of the 9 wildlife crossing structures on National Highway 44 passing through the Pench Tiger Reserve, Maharashtra.

The tiger is one of the world's most charismatic large carnivores and acts as an umbrella species for the conservation of forested habitats it inhabits. In India, it is accorded the highest level of protection. In central India, tigers inhabit forests inside protected areas, but are increasingly found to occupy forests and matrices composed of forests, agricultural fields, power plants, and scrub forests. Nonetheless, road networks have been identified as one of the most imminent threats to long-term tiger conservation.

Tigers are wide-ranging and territorial. This, combined with large tiger home ranges especially outside protected areas (Habib et al., 2021a), increases the chances of tigers encountering roads and other linear infrastructure. Roads have also been found to reduce survival, tenure longevity and cub survival of tigers, and also significantly decrease kill consumption (Kerley et al., 2002). Spatio-temporal habitat use patterns by tigers are also affected by presence of human disturbance, and tigers have been found to temporally avoid humans (Yang et al., 2019). In India, tigers were found to avoid crossing roads during the day when the traffic is at its highest (Hussain et al., 2022). Higher movement rates outside protected areas and in the vicinity of human infrastructure (Habib et al., 2021a) directly translates to high energetic costs to dispersing individuals. While the solitary behaviour of tigers can reduce the probability of collision with vehicles at low-medium traffic volumes (Saxena et al., 2020), wide roads with high traffic volumes and dense road networks would increase roadkill probability and the barrier effect for tigers.

b. Leopard

Scientific name: *Panthera pardus*

Conservation status: Schedule I (Wildlife (Protection) Act, 1972)
Vulnerable (IUCN Red List)

The leopard is one of the most widespread carnivores in India and in the Central Indian landscape given its generalist and highly adaptive behaviour. Leopards were found to occupy all PAs and major forest tracts within corridors in the landscape, with highest leopard occupancy in Madhya Pradesh followed by Odisha and Maharashtra (Jhala et al., 2020).

Figure 2.13. A leopard using one of the 9 wildlife crossing structures on the National Highway 44 passing through the Pench Tiger Reserve, Maharashtra.

Leopards are adept at surviving in human-dominated landscapes through their behavioural plasticity. This includes altering activity patterns to avoid interacting with humans (Ngoprasert et al., 2007). Leopards have one of the lowest collision probabilities given their solitary nature, fast movement and body size (Saxena et al., 2020). However, leopard mortality caused by road and railway traffic is regularly reported in the landscape. Like tigers, leopards are also highly vulnerable to genetic fragmentation caused by anthropogenic infrastructure (Thatte et al., 2020).

c. Asiatic wild dog or dhole

Scientific name: *Cuon alpinus*

Conservation status: Schedule I (Wildlife (Protection) Act, 1972)
Endangered (IUCN Red List)

Figure 2.14. A pack of Asiatic wild dogs using one of the 9 wildlife crossing structures on National Highway 44 passing through Pench Tiger Reserve, Maharashtra.

The Asiatic wild dog or dhole is a social canid found in the forests of south and south-east Asia. The dhole is monophyletic i.e., it is the only species of its genus *Cuon*. Dholes are primarily found in forests occupied by tigers within central India (Jhala et al., 2020), where one of the largest numbers of dholes is thought to exist in the country (Johnsingh and Acharya, 2013). Genetic studies have revealed up to 85% declines in major dhole sub-populations, with protected areas being highly important in maintaining the last remaining genetically differentiated dhole populations (Modi et al., 2021).

Dholes are known to occur exclusively in forests and thick scrub jungles, with home ranges relatively smaller than other carnivores in the guild (Habib et al., 2021a). Moreover, compared to other predators in the landscape, dholes have relatively smaller dispersal distances and require relatively more intact corridor patches to disperse (Modi et al., 2022). Consequently, the greatest threat to dholes from roads would be within and near protected areas.

In landscapes near protected areas, dholes have been found to avoid areas used intensively by tigers and human disturbance, and prefer areas used by their principal prey (Ghaskadbi et al., 2023). Apart from this, little research has been done to document responses of dholes to human disturbance, particularly roads.

d. Chital or spotted deer

Scientific name: *Axis axis*

Conservation status: Schedule II (Wildlife (Protection) Act, 1972)
Least Concern (IUCN Red List)

Figure 2.15. Chital or spotted deer using one of the 9 wildlife crossing structures on National Highway 44 passing through Pench Tiger Reserve, Maharashtra.

Chital is a common cervid native to most parts of the Indian subcontinent and Sri Lanka, and is a habitat generalist, inhabiting grasslands interspersed with forests, in addition to thriving in forest edges (Dinerstein, 1980). Chital herd sizes vary greatly with habitat structure and time of the day (Shankar Raman, 1997). In the central Indian landscape, chital distribution is contiguous with tiger occupancy, and is among the primary prey species of tiger *Panthera tigris* and other co-predators in the landscape (Ghaskadbi et al., 2022;

Majumder et al., 2013). It is found in both within and outside PAs, being one of the most widely distributed wild ungulates in the landscape (Jhala et al., 2020).

Chital are known to approach human habitations and raid agricultural fields. Use of forest habitat by chital near the National Highway 44 was also found to be among the highest compared to other large mammals in the study area, with no significant temporal avoidance of roadside habitat (Saxena and Habib, 2022). However Gubbi et al. (2012) found significantly less use of habitat by chital near roads with traffic > 40 vehicles/hour. Chital have relatively high roadkill probabilities owing to their large body and group sizes. Additionally, use of roadside habitat by chital, often coinciding with high traffic hours, also makes the species more vulnerable to roadkill as compared to other guild members (Saxena et al., 2020). Few studies have addressed the responses and impacts of anthropogenic disturbance on chital.

e. Gaur

Scientific name: *Bos gaurus*

Conservation status: Schedule I (Wildlife (Protection) Act, 1972)
Vulnerable (IUCN Red List)

Gaur is the largest wild bovid distributed across forests in India and parts of south-east Asia. In India, the central Indian landscape is a stronghold of gaur population (Ashokkumar et al., 2011). In Central India, gaur distribution is primarily restricted to PAs, where they primarily prefer undisturbed rugged forested areas. Gaur avoid disturbed areas, and are mostly diurnal in undisturbed areas (Ashokkumar et al., 2011). Gaur populations are mostly threatened because of habitat fragmentation.

Figure 2.16. A gaur using one of the 9 wildlife crossing structures on National Highway 44 passing through the Pench Tiger Reserve, Maharashtra.

While the large body size of gaur and slow speed makes gaur vulnerable to roadkill, low overlap with traffic owing to avoidance of roadside habitat makes it unlikely that gaur would encounter traffic during peak traffic hours (Saxena et al., 2020). In Malaysia, intermediate levels of disturbance were found to be beneficial, while intense infrastructure development led to fragmentation of gaur populations (Conry, 1989). Apart from this, research on the responses of gaur to anthropogenic disturbance is lacking.

f. *Nilgai*

Scientific name: *Boselaphus tragocamelus*

Conservation status: Schedule II (Wildlife (Protection) Act, 1972)

Least Concern (IUCN Red List)

Figure 2.17. A nilgai or bluebull using one of the 9 wildlife crossing structures on National Highway 44 passing through the Pench Tiger Reserve, Maharashtra.

Nilgai or bluebulls are group-living large antelopes distributed majorly across India, Nepal and Pakistan. Nilgai avoid dense forests, and are found in agro-pastoral patches, forested areas and scrubland-grassland mosaic habitats in the central Indian landscape (Jhala et al., 2020). Nilgai are said to be tolerant of human footprint, and are often involved in incidents of crop raiding. However rapid land use conversion and ability of nilgai to use habitats near human settlements has led to incidents of conflict with humans, predation by feral dogs and road-related mortality (Bajwa and Chauhan, 2019).

g. Sambar

Scientific name:	*Rusa unicolor*
Conservation status:	Schedule I (Wildlife (Protection) Act, 1972)
	Vulnerable (IUCN Red List)

The sambar is the largest Indian deer, distributed across the Indian subcontinent and southeast Asia. In Central India, sambar is mostly confined to PAs, and relatively large and intact forested patches near PAs and intervening corridors. Sambar prefers forested hillsides, preferably near cultivation, and are mainly nocturnal. Sambar avoid areas with human presence (Griffiths and van Schaik, 1993), and can be used as indicators of disturbance by their absence (Cheyne et al., 2016).

Figure 2.18. A herd of sambar using one of the 9 wildlife crossing structures on National Highway 44 passing through the Pench Tiger Reserve, Maharashtra.

Because of their nocturnal habit, sambar activity does not overlap with peak traffic activity periods, although it has the least collision probability given its small average group size (Saxena et al., 2020). Nonetheless, avoidance of disturbed habitats by sambar can intensify the barrier effect and lead to population fragmentation.

h. *Wild pig*

Scientific name: *Sus scrofa*

Conservation status: Schedule II (Wildlife (Protection) Act, 1972)
Least Concern (IUCN Red List)

Figure 2.19. A sounder of wild pigs using one of the 9 wildlife crossing structures on National Highway 44 passing through the Pench Tiger Reserve, Maharashtra.

The wild pig or wild boar is the most widely distributed wild ungulate worldwide. In India and in the study landscape as well, wild pig is the most widely distributed wild ungulate. Wild pigs inhabit a range of habitats, ranging from forests, grasslands and scrublands. They are also known to be highly adaptable to thrive in human-dominated areas (Stillfried et al., 2017), and may also increase daytime activity, given persecution by humans is absent (Johann et al., 2020).

Wild pig is omnivorous, feeding on crops, roots, tubers, insects, snakes and carrion. Crop depradation by wild pigs often leads to conflict with humans in agricultural areas near forests. The attraction of wild pigs to roadside habitat for feeding and scavenging, activity overlap with peak traffic hours (Saxena et al., 2020), and tolerance of human footprint is possibly the reason why wild pigs are observed to be among the most frequently encountered roadkilled ungulates in the landscape. Additionally, the large group sizes (Saxena et al., 2020), and high abundance (Torres et al., 2023) makes them more vulnerable to collision with vehicles

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Chapter 3

Relative abundance, activity and diversity of mammals near National Highway 44, Pench Tiger Reserves, Madhya Pradesh and Maharashtra

3.1. Introduction

Roads impact wildlife in direct and indirect ways including wildlife-vehicle collisions, habitat loss, degradation and fragmentation, and by creating barriers to movement (van der Ree et al., 2015, 2011). The presence of anthropogenic infrastructure such as roads near wildlife habitats also elicit avoidance of adjacent habitat by wildlife (Gaynor et al., 2018; Griffiths and van Schaik, 1993; Meisingset et al., 2013) because of disturbance from road and traffic emissions (D'Amico et al., 2015; Leblond et al., 2013). Wildlife are known to alter their temporal activity patterns to avoid overlaps with human activity (Gaynor et al., 2018). Patterns of avoidance at different scales can be a function of disturbance intensity (Gubbi et al., 2012; Leblond et al., 2013; Mccown et al., 2009), road type (Burson et al., 2000); (Mulero-Pázmány et al., 2016), and other road-related factors (D'Amico et al., 2015). Avoidance of roads can alter resource accessibility for wildlife, and increase the barrier effect (Prokopenko et al., 2017). While seemingly non-lethal, avoidance of anthropogenic infrastructure like roads by wildlife (Baigas et al., 2017) may decrease the habitat available to wildlife (D'Amico et al., 2015; Madadi et al., 2017; Mattson et al., 1987), alter interspecific interactions like predator-prey dynamics (Kerley et al., 2002; Kuijper et al., 2016), and create physical (Alexander et al., 2005; Wadey et al., 2018) and genetic barriers for wildlife populations (Riley et al., 2006).

However, species responses to road-related disturbance have been found to vary, mainly as a function of behavioural traits and differential levels of threat perception from humans (Jacobson et al., 2016; Rytwinski and Fahrig, 2013). While habituation to 'predictable' human behaviour has been observed among carnivores (Wheat and Wilmers, 2016), roadside habitat may be attractive for foraging by some ungulates (Marino et al., 2012; Meisingset et al., 2013; Munro et al., 2012; Shannon et al., 2014a, 2014b), possibly because of the absence of top predators (Shannon et al., 2014b). The cost of foraging by ungulates near moderately disturbed sites may be less than that in the absence of human disturbance, leading to higher than expected use of these areas (Laurian et al., 2012; Shannon et al., 2014b). Conversely, ungulates may trade-off foraging opportunities against keeping away from roads by avoiding peak traffic hours (Eldegard et al., 2012). While habituation to human presence may make carnivores more vulnerable to mortality (Wheat and Wilmers, 2016), enhanced activity of herbivores in the absence of top predators may lead to trophic alterations (Kuijper et al., 2016; Shannon et al., 2014b), and increased vulnerability to roadkill (Mayer et al., 2021).

Varying tolerance to road-related disturbance (Fahrig and Rytwinski, 2009a) among members of an animal community can also reduce species richness near roads as compared with undisturbed habitats (Berthinussen and Altringham, 2012), with some mammal species completely avoiding roadside habitat. This reduction in diversity can occur through habitat degradation because of noise and light emissions from traffic (Berthinussen and Altringham, 2012), and activities associated with roads (Vanthomme et al., 2013).

Avoidance of roadside habitat could accentuate the barrier effect for some species by creating isolated populations with restricted movement between habitat patches (Forman and Alexander, 1998). This would further reduce the probability of habitat recolonisation, use of wildlife crossing structures by such species, and increase the barrier effect further by road widening or increase in traffic (Forman and Alexander, 1998; Saxena and Habib, 2022).

With rapidly increasing road networks and the need to mitigate effects of roads and traffic, information on modifications in animal space use patterns and species richness are required to design effective and innovative mitigation strategies. Identifying species most affected by indirect habitat loss near roads because of traffic emissions (noise, disturbance) can help direct mitigation measures towards alleviating these effects. Moreover, while roadkill remains the most investigated impact of roads on wildlife, it is equally important to complement our understanding of wildlife roadkill with species space use patterns in adjacent habitats (Ascensão et al., 2019). Further, since high animal activity in the vicinity of roads increases species roadkill probability (Kušta et al., 2017; Saxena et al., 2020), alterations in activity near roadsides provide critical information for mitigating roadkill, and barrier effects for animal movement, and in managing other long-term indirect effects viz., trophic cascades (Mata et al., 2017).

In a forested habitat near a high-traffic highway in Central India, I quantified large mammal species richness and functional diversity under different road treatments (different road types and control), and the factors influencing the same. I also assessed the influence of environmental and road-related factors on eight select large mammals in the roadside habitat. Finally, I quantified large mammal temporal activity overlaps and similarities between (a) species' activity near roadside and control habitat, (b) species and traffic activity patterns, and (c) predator-prey activity overlap patterns. I also used differences in hourly activities between different roadside habitats and natural activities (control) as a metric to assess degree of avoidance of roadside habitat by wildlife.

Within the mammal community in the study site, I expected (a) low species richness and functional diversity near roads as compared with control, and variation in species diversity between the different road sites, (b) variation in spatial and temporal responses to different road types as a function of species' tolerance to anthropogenic disturbance, (c) reduced predator-prey temporal overlaps near roadside sites as compared with control habitat. The study adds to the understanding of mammal responses to anthropogenic presence and infrastructure, and can potentially help inform management strategies for mitigating impacts of roads on wildlife.

3.2. Methodology

3.2.1. Field methods

I carried out camera trapping on 5 km contiguous habitat patches along National Highway 44 in the Maharashtra (4-lane) and Madhya Pradesh (2-lane) sections passing through the Pench Tiger Reserves in the two states (Fig. 3.1). In 2017, camera trapping was carried out once each near the 2-lane and 4-lane segments of the highway (site referred to as '2-lane' and '4-lane' respectively hereafter). In 2019, the survey was repeated in the 4-lane segment after construction of nine CS (site referred to as '4-lane_mitigated' hereafter).

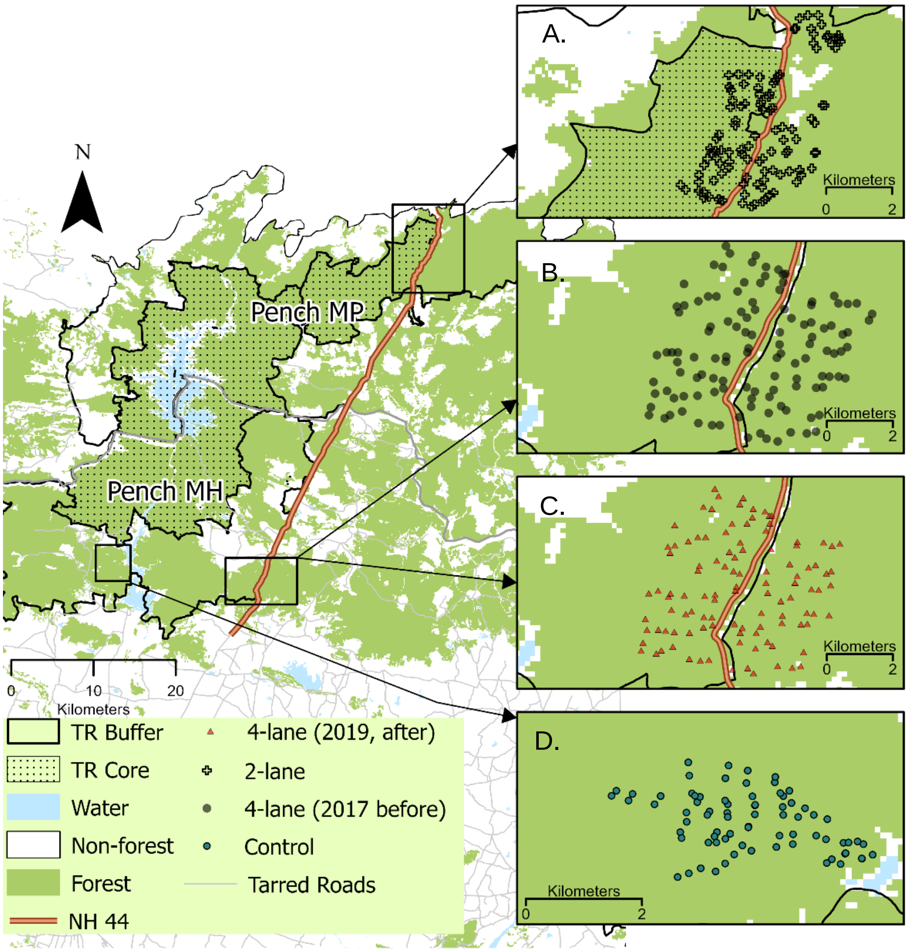


Figure 3.1. Location of Pench Tiger Reserves (PTR), Maharashtra (MH) and Madhya Pradesh (MP) and the National Highway 44 passing through PTR. [right from top]

Camera trapping locations near A. 2-lane, B. 4-lane, C. 4-lane (after construction of crossing structures), and D. control habitat inside PTR.

I deployed single-sided Cuddeback (“Cuddeback, Green Bay, Wisconsin”) C1 camera traps at increasing distances (0 – 2000 m) from the highway in the forest habitat adjacent to the highway at intersections of multiple forest trails, stream beds and dirt roads for 15-20 days at each site. An effort was made to deploy camera traps such that captures of ungulates, carnivores and small mammals was maximised. Camera traps were tied to trees near the selected sites at a height of approximately 1 m allowing us to capture species ranging from small to large mammals, without the use of any baits. The general habitat and vegetation structure near all sites was assumed to be similar, since all sites were part of the tiger reserve. I also deployed camera traps within the tiger reserve in Maharashtra at a distance of 6 km from the highway as the control setting (road-related disturbance absent; site referred to as ‘control’ hereafter). To avoid spatial autocorrelation, I avoided deploying consecutive camera traps on the same forest trails.

3.2.2. Analytical methods

I sorted photo-captures of all wild mammals photographed during the exercise at the species level. I considered photos of a species taken 30 minutes apart to be independent events (O’Brien et al., 2003) to account for spatial autocorrelation. Date, time of capture and other information of independent captures was extracted using the function recordtable in the package camtrapR (Courtiol et al., 2017) in R (RStudio Team, 2020).

3.2.2.1. Species relative abundances between road and control sites

I used the Relative Abundance Index (RAI) calculated as capture rates of species x trapping effort and scaled up to 100 camera days, to compare relative abundances between roadside sites and control site of select species. I then estimated the significance of difference among relative species abundances at the four sites using pairwise Wilcoxon tests at 95% significance level.

3.2.2.2. Impact of roads on species richness and functional diversity

Traditional species richness indices like total count of species (richness), Shannon entropy and Simpson diversity are not sensitive to relative abundances of rare species (Roswell et al., 2021), as these indices treat species as equally distinct from each other. Moreover, to assess the impact of human disturbance on community composition, it is important to measure the sensitivity of community diversity to loss of rare and less abundant species. Functional diversity indices quantify the range and relative abundance of particular functional traits within a community (Kirkpatrick et al., 2018), and help in assessing ‘environmental filtering’ i.e. the process of abiotic factors limiting the establishment or persistence of species with a particular functional trait.

I assessed mammalian species richness and functional diversity across the three road sites and control site using Hill’s diversity indices (Hill, 1973) – naïve species diversity i.e., richness (q=0), Hill-Shannon diversity (q=1), and Hill-Simpson diversity (q=2). For calculation of richness and diversity, I only used data from camera traps that were functional for 14 days. I used species traits in diversity calculations to quantify the effective number of equally abundant and functionally equally distinct species following Kirkpatrick et al. (2018). Functional diversity (q=1 and q=2) was calculated using species traits that have been previously identified as predictors of mammal species’ vulnerability to road-related effects (Rytwinski and Fahrig, 2012), viz., reproductive rate (calculated as the mean litter size multiplied by the number of litters per year), mobility (defined as the mean home range) and body mass (Table 3.1). Species-specific values for these traits were derived from Menon (2014), Johnsingh and Manjrekar (2013), Minhas et al. (2013), Anand et al. (2021) (rhesus macaque), Sankar et al. (2013) (gaur), Moczygemba et al. (2012) (nilgai), Chatterjee et al.

(2014) (sambar), Katna et al. (2022) (jungle cat), and Gupta et al. (2012) (ratel). The home ranges of four-horned antelope and Indian pangolin were estimated using equation in Swihart et al. (1988).

Table 3.1. Species functional traits identified as predictors of mammal species' vulnerability to road-related effects by Rytwinski and Fahrig (2012) used for calculation of Hill's functional diversity indices.

	Body mass (g)	**Reproductive rate (mean litter size x number of litters per year)**	**Mobility (mean home range in m^2)**
Gray langur *Semnopithecus entellus*	12679.29	0.714	305
Rhesus macaque *Macaca mullata*	6614	1	534.5
Four-horned antelope *Tetracerus quadricornis*	19000	1.8644	443.0463
Chital or spotted deer *Axis axis*	45500	1.03323	364.77
Gaur *Bos gaurus*	809000	1.053	19400
Nilgai *Boselaphus tragocamelus*	180000	1.575	8855.5
Sambar *Rusa unicolor*	177522.9	1	2042.5
Wild pig *Sus scrofa*	135000	8.35125	792.7
Jungle cat *Felis chaus*	10000	6	590
Leopard *Panthera pardus*	53075	2.14	50494
Mongoose *Herpestes edwardsii*	1008	8.58	309.99
Ratel or honey-badger *Mellivora capensis*	10000	4.66	625
Sloth bear *Melursus ursinus*	77500	0.9702	1000
Small Indian civet *Viverricula indica*	3000	0	65

Tiger *Panthera tigris*	128800	1.028	5358.3
Asiatic wild dog *Cuon alpinus*	15750	4.515	6875
Black-naped hare *Lepus nigricollis*	2196.875	11.3685	1.389
Common palm civet *Paradoxurus hermaphroditus*	17325	4.06	531.85
Indian pangolin *Manis crassicaudata*	11963.78	1	638.5653
Porcupine *Hystrix indica*	17325	4.06	141.198

For these traits, I constructed taxonomic and functional distance matrices (for each functional trait), where distance values ranged from 0 (total similarity) to 1 (total dissimilarity). Distance matrices with species traits and capture rates were then used to calculate Hill's diversity indices ($q = 1$ and 2) for all sites. I further assessed the significance of difference between calculated Hill's diversity indices at all sites with control using non-parametric paired Wilcoxon rank sum tests at $p=0.05$ significance level.

I tested for the impact of road type and road characteristics on naïve species richness using generalised linear models (GLM), and on normalised Hill's diversity indices using generalised linear mixed models using package glmmTMB (Magnusson et al., 2020). I used poisson distribution for naïve species richness and Gaussian distribution for Hill's diversity indices. I used site (2-lane, 4-lane and 4-lane_mitigated), functional constraint applied (species traits), protection level (core, buffer and others), and distance to road (in meters) as independent variables, and camera ID as random variable. I also included interaction between road type, protection, site and distance to road as independent variables. Model evaluation was done manually using AIC values. I also constructed rank abundance curves for the four sites using function rankabunplot in package 'vegan' (Oksansen et al., 2022) in R.

3.2.2.3. Impact of road on species roadside habitat use

I tested the effect of road-related and environmental variables on the capture rates of three large carnivores (tiger, leopard, wild dog), and five major prey species (chital, gaur, nilgai, sambar and wild pig). I did not measure the functional relationship of relative species capture rates with animal densities, and species capture rates were interpreted as a measure of habitat use (Ngoprasert et al., 2007). I defined the response variable as species capture rates i.e., the number of captures of species (scaled) on camera trapping sites (Gaussian error distribution) offset by the number of camera trap days at each trapping site to account for differential camera days at each site.

I ran separate models for each species using generalised linear mixed effects models (GLMM) in R package glmmTMB (Magnusson et al., 2020) using multiple environmental, anthropogenic and road-related variables of interest (Table 3.2). I used environmental variables (distance to human settlement (m), distance to tiger reserve (m), distance to water body (m), terrain roughness, protection status, anthropogenic disturbance), road-related variables (distance to road and road type) and interaction terms (protection status x distance to road, and road type x distance to road) as fixed variables, and camera trapping site ID as a random variable to account for inter-site variations. I calculated anthropogenic disturbance as the capture rates of human, livestock and free-ranging dogs at each camera trapping site. I checked for correlation between continuous explanatory variables using package PerformanceAnalytics (Peterson and Carl, 2020), and found that none of the variables had correlation coefficients greater that |0.7|. I carried out manual model selection, by step-wise removal of non-significant explanatory variables and variables that led to non-convergence of models from a global model containing all individual explanatory variables and interaction terms. For each species, I evaluated model performance using Akaike

Information Criterion (AICc) values and AIC weights (wAICc), and averaged models with ΔAICc < 2 using package MuMIn (Barton, 2020).

Table 3.2. Details of environmental and road-related variables used to assess use of roadside habitat by wild mammals near National Highway 44 passing through Pench Tiger Reserves, Madhya Pradesh and Maharashtra.

	Variable	***Source/Description***	***Range/Levels***
Environmental	Distance to human settlement (m)	Calculated using 'near' tool in ArcGIS Pro	1088.98 – 10780.56
	Distance to tiger reserve (m)		0 – 1674.89
	Distance to water body (m)		82.83 – 4219.61
	Terrain roughness	Calculated from digital elevation model (DEM)	0.44 – 0.64
	Protection status		Core Buffer Other
	Anthropogenic disturbance	Calculated as capture rate of humans, free-ranging dogs and livestock at each camera trap	0 – 23.02
Road-related	Distance to road (m)	Calculated using 'near' tool in ArcGIS Pro	23.70 – 1748.53
	Road type	Classified on the basis of number of lanes and presence of mitigation measures	2-lane 4-lane 4-lane_mitigated

3.2.2.4. Impact of roads on animal activity

I calculated activity overlaps between species activity at different road sites with corresponding species' control activity and traffic using package overlap (Meredith and Ridout, 2017) in R. Traffic data for the years 2017 and 2019 was obtained from the National

Highways Authority of India's toll check-post at NH 44. I used overlap coefficient Dhat1 when, in a pair of temporal data series, the smaller sample size was less than 50, and Dhat4 when the smaller sample size was more than 50 observations. Robust bootstrap confidence intervals were also estimated using the 'bootest' function of package overlap (Meredith and Ridout, 2017). I assessed significance of similarity or difference between activity patterns of a species at different sites using non-parametric Watson-Wheeler tests of circular homogeneity (Batschelet, 1981) at $p=0.05$ significance level using package circular (Agostinelli and Lund, 2022) in R. I plotted hourly capture densities at different sites using density plot in package ggplot2 (Wickham, 2016) for visualising more than two activity patterns and their overlaps. I also calculated hourly differences between species activities at road sites and control sites – negative values denoted lesser and positive values denoted higher roadside species activity compared to control site. All confidence intervals were calculated at 95% significance.

3.3. Results

The sampling effort across all four sites equalled 5773.4 camera days (n=385 camera sites). I obtained 6360 independent captures including those of 20 mammal species and anthropogenic activities (humans, livestock and free-ranging dogs) from the camera trapping exercise (Table 3.3). The highest number of unique species were captured near the 4-lane roadside (before mitigation) (n=20), followed by 4-lane road after mitigation (n=19) and the least near the 2-lane road (n=17) and control site (n=17).

Table 3.3. Site-specific camera trapping details at control (within Pench Tiger Reserve, Maharashtra) and roadside habitat along National Highway 44, Pench Tiger Reserves, Madhya Pradesh and Maharashtra.

Details	*Control*	*2-lane*	*4-lane (before mitigation)*	*4-lane_mitigated (after mitigation)*
Number of camera locations	66	108	106	105
Mean camera days	15	14.9	13.7	16.4
Total camera days	990	1609.2	1452.2	1722
Total wildlife captures	890	1960	1297	1385
Number of wild species detected	17	17	20	19

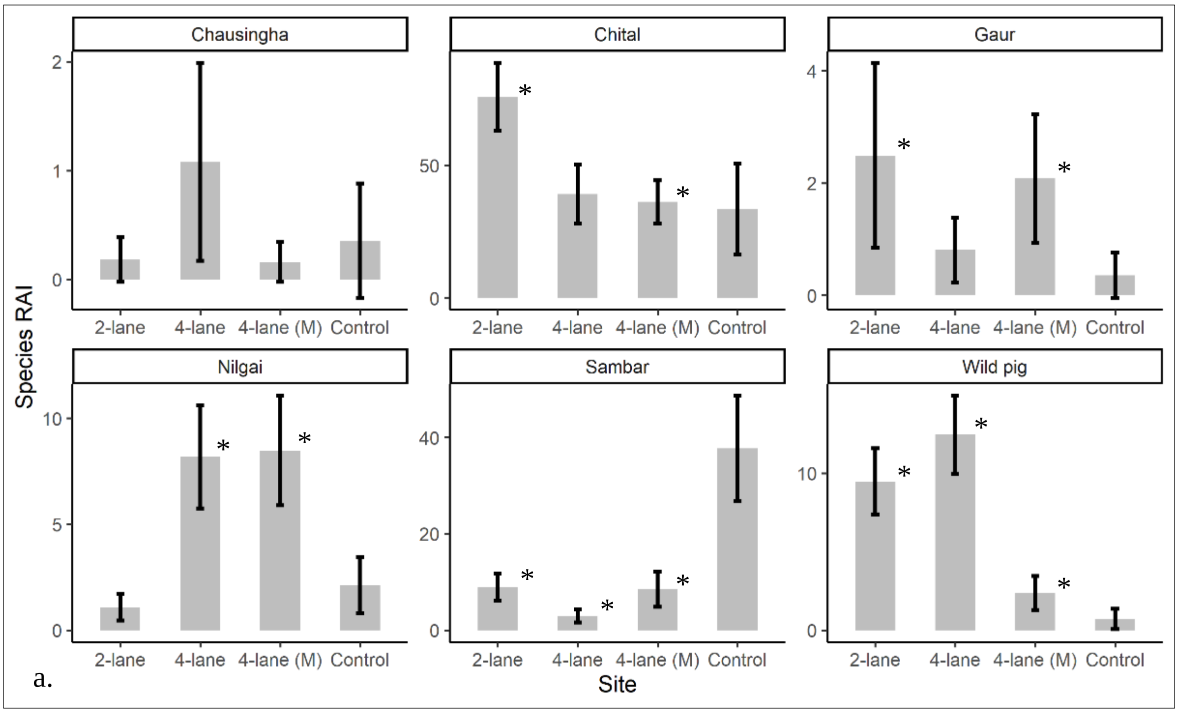
3.3.1. Species relative abundances between road and control sites

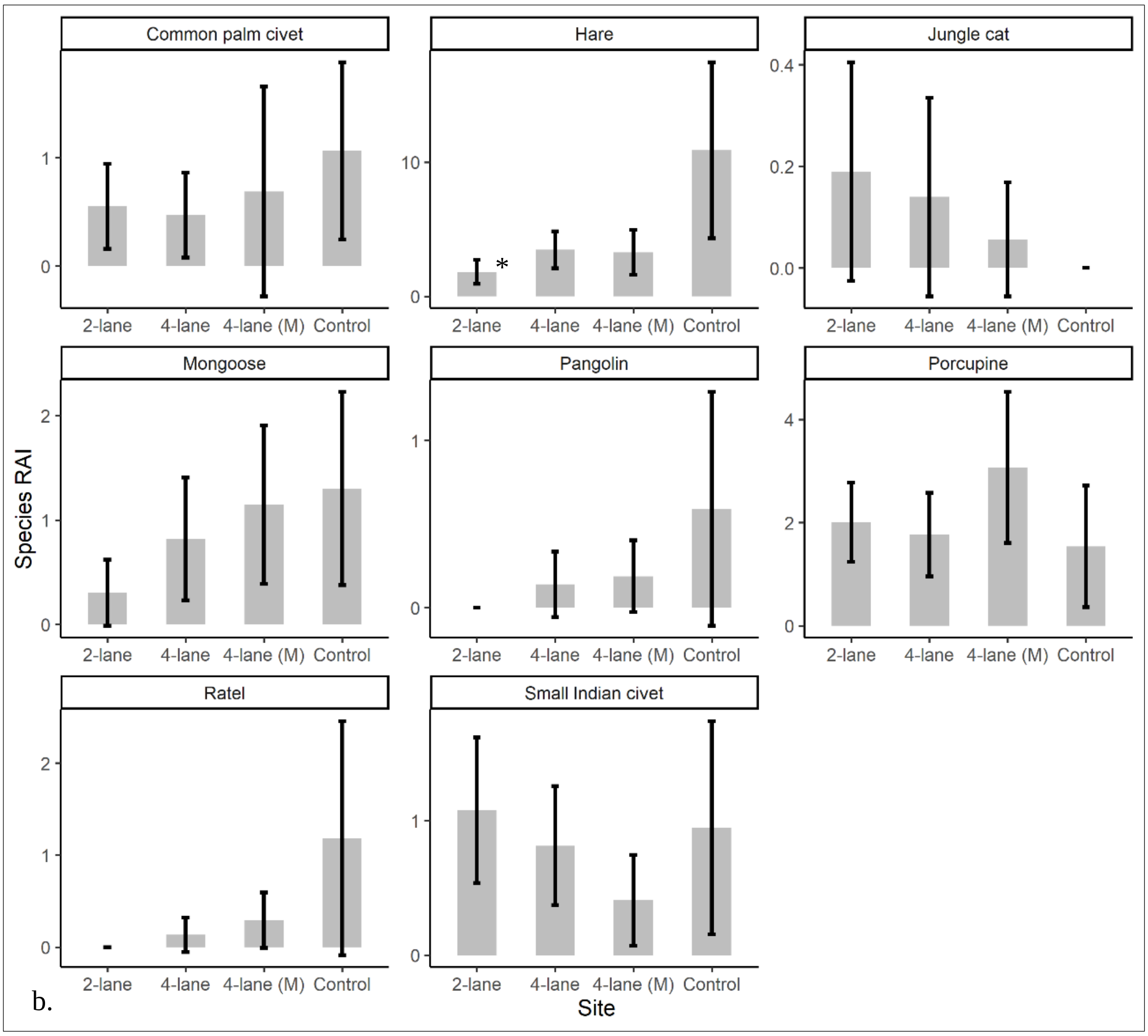
I found varying species abundances in the roadside forests as compared to the control site (Fig. 3.2 (a-d)). Among ungulates, sambar relative abundance was significantly lower than that in control ($p < 0.05$). Chital and gaur relative abundances were signficantly higher at roadside sites near 2-lane and 4-lane (mitigated) roads as compared with control ($p < 0.05$), while wild pig was significantly more abundant near all roadside sites ($p< 0.05$). Nilgai was singificantly more abundant at 4-lane roadside habitat as compared with control ($p < 0.05$), both before and after construction of mitigation measures. Chausingha captures at all sites were low.

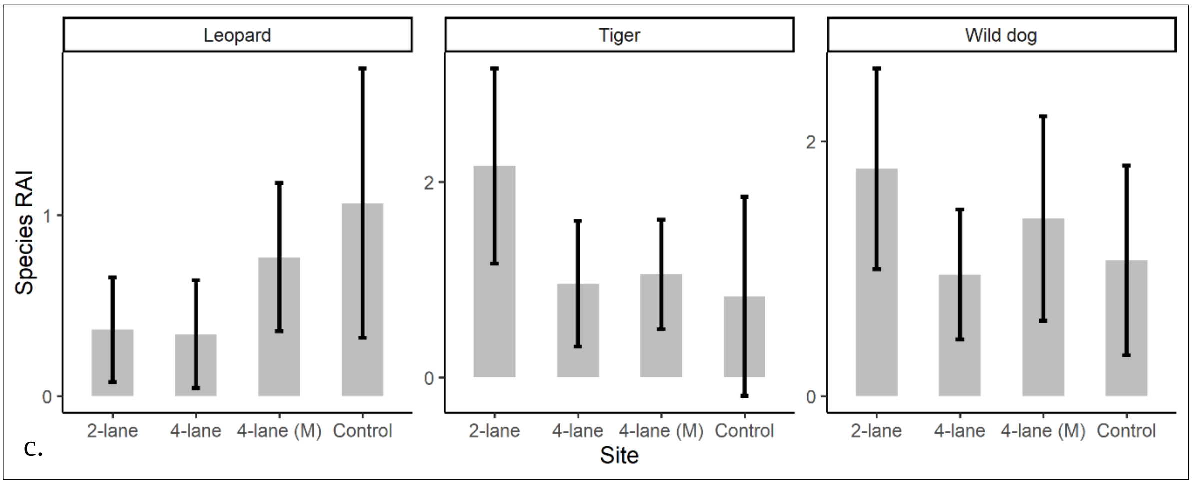
Among small mammals, no significant differences in relative species abundances were observed between the four sites for common palm civet, mongoose sp., porcupine and small Indian civet ($p > 0.05$). Hare relative abundance was significantly less near 2-lane roads as compared with control. No captures of jungle cat were obtained at control site, and no captures of pangolin and ratel were obtained near 2-lane road.

Among large carnivores, no significant differences in relative species abundances were observed between the four sites.

Among the two primate species, I found no significant difference in langur abundance between the four sites ($p>0.05$), while rhesus macaque relative abudance was significantly higher near 2-lane roads as compared with control ($p < 0.05$).




Common palm civet
Hare
Jungle cat
Mongoose
Pangolin
Porcupine
Ratel
Small Indian civet
Species RAI
Site
2-lane
4-lane
4-lane (M)
Control
*
b.


Leopard
Tiger
Wild dog
Species RAI
Site
2-lane
4-lane
4-lane (M)
Control
c.

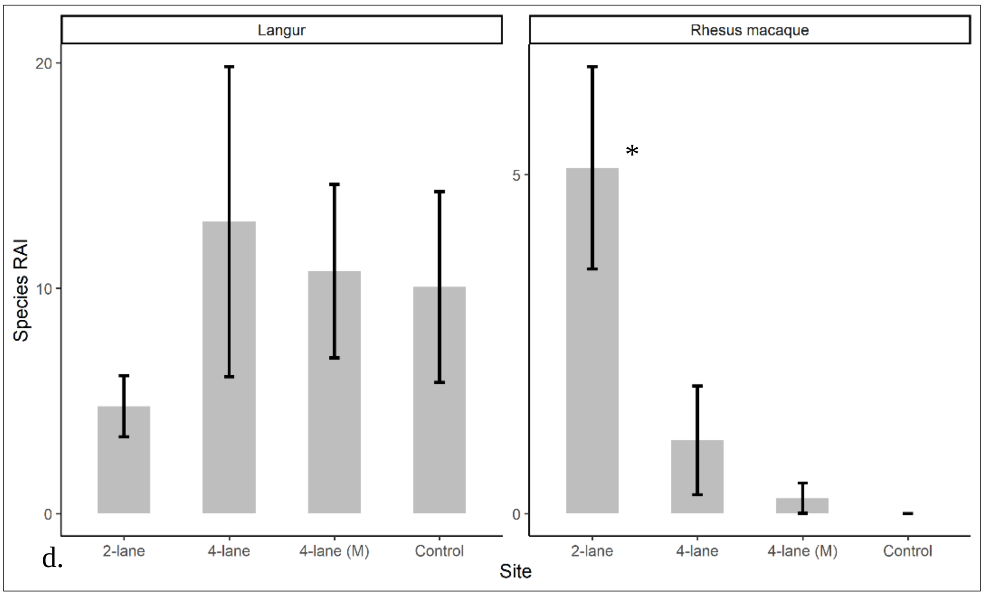


Figure 3.2. Relative Abundance Indices (RAI) for (a) six ungulate, (b) eight small mammal, (c) three large carnivore, and (d) two primate species in habitat near different road types (2-lane road, and 4-lane road before and after mitigation) and control site (Pench Tiger Reserve, Maharashtra). Relative abundance values that are signficantly different from control values are indicated by an asterisk.

3.3.2. Impact of roads on species richness and functional diversity

A total of 20 mammal species were photocaptured between the four sites, with the highest species richness being in the forest habitat near the 4-lane road. The four sites had 15 common mammal species. Honey badger and Indian pangolin were not captured near the 2-lane road in PTR Madhya Pradesh, while sloth bear was only captured near the 4-lane road before construction of mitigation measures (Fig. 3.3).

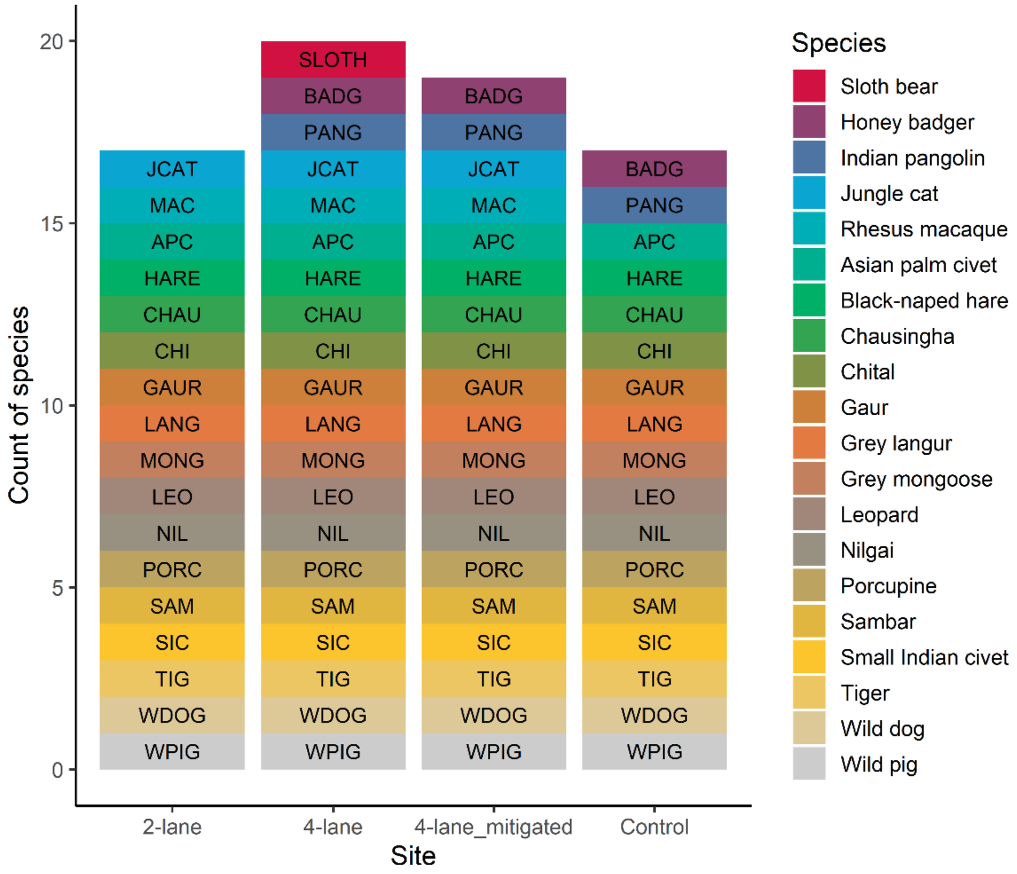


Figure 3.3. Species richness in roadside sites (2-lane, 4-lane and 4-lane mitigated) and control site (Pench Tiger Reserve, Maharashtra). Colour bar represents rarity of captures with grey being most captured while red represents rarely captured species.

The rank abundance curves for the three road sites (2-lane, 4-lane and 4-lane mitigated) and control site show that the control site and habitat near 2-lane road has strong dominance by species such as chital and sambar. The longest tail of rare species is observed near 4-lane roads (Fig. 3.4). Relative abundance of chital and other common species is highest in the control site and habitat near 2-lane road and declines with width of road (habitat near 4-lane road). The 4-lane roads (before and after construction of mitigation measures) have the lowest proportion of species with intermediate rarity, while forest near the 2-lane road has the lowest species richness.

The mammal community within the control habitat is dominated by ungulates (chital, sambar, and wild pig), followed by rhesus macaque and gray langur. The most dominant carnivores are tiger and wild dog. Jungle cat, chausingha and mongoose were rarely captured here.

In forest near 2-lane road, chital and sambar are the dominant ungulates, followed by gray langur and hare. In the forests near the 4-lane road, chital, gray langur, wild pig and nilgai are the most dominant mammals. Chital, gray langur, nilgai and sambar were among the dominant mammals near 4-lane roads after construction of mitigation measures. Rarely photocaptured species near roadside sites (2-lane, 4-lane and 4-lane after mitigation) included Indian pangolin, ratel and chausingha.

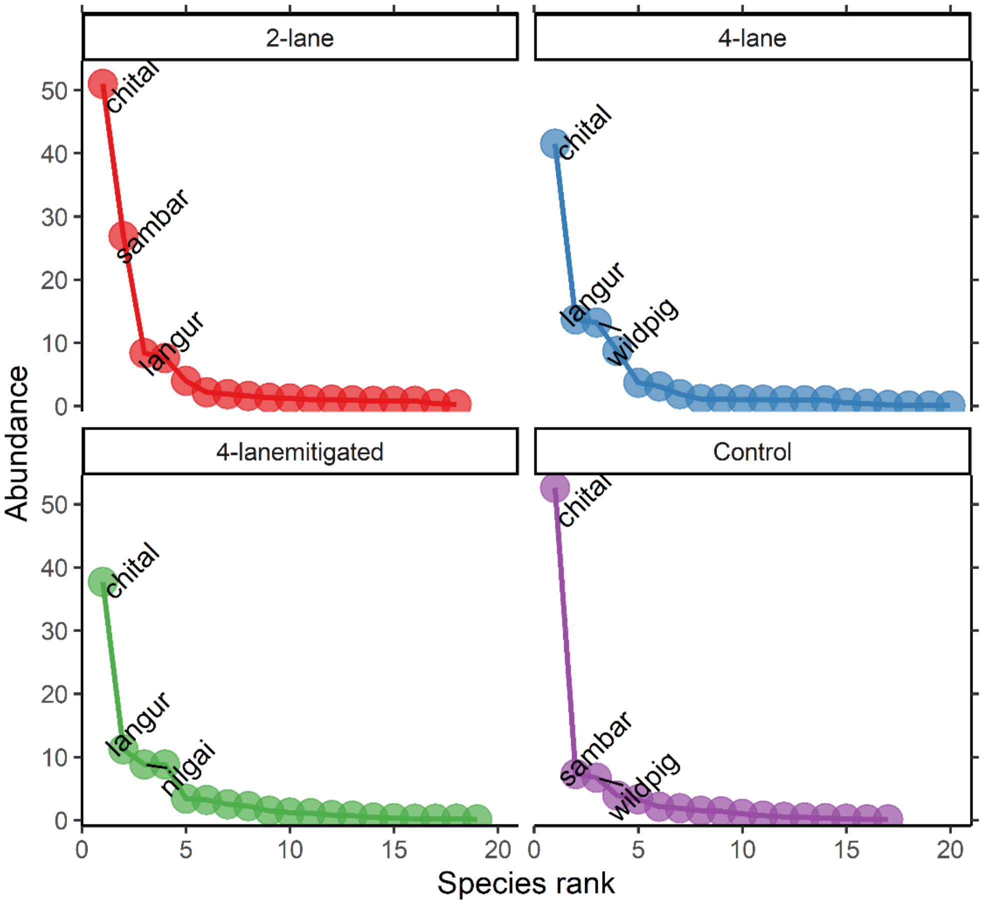
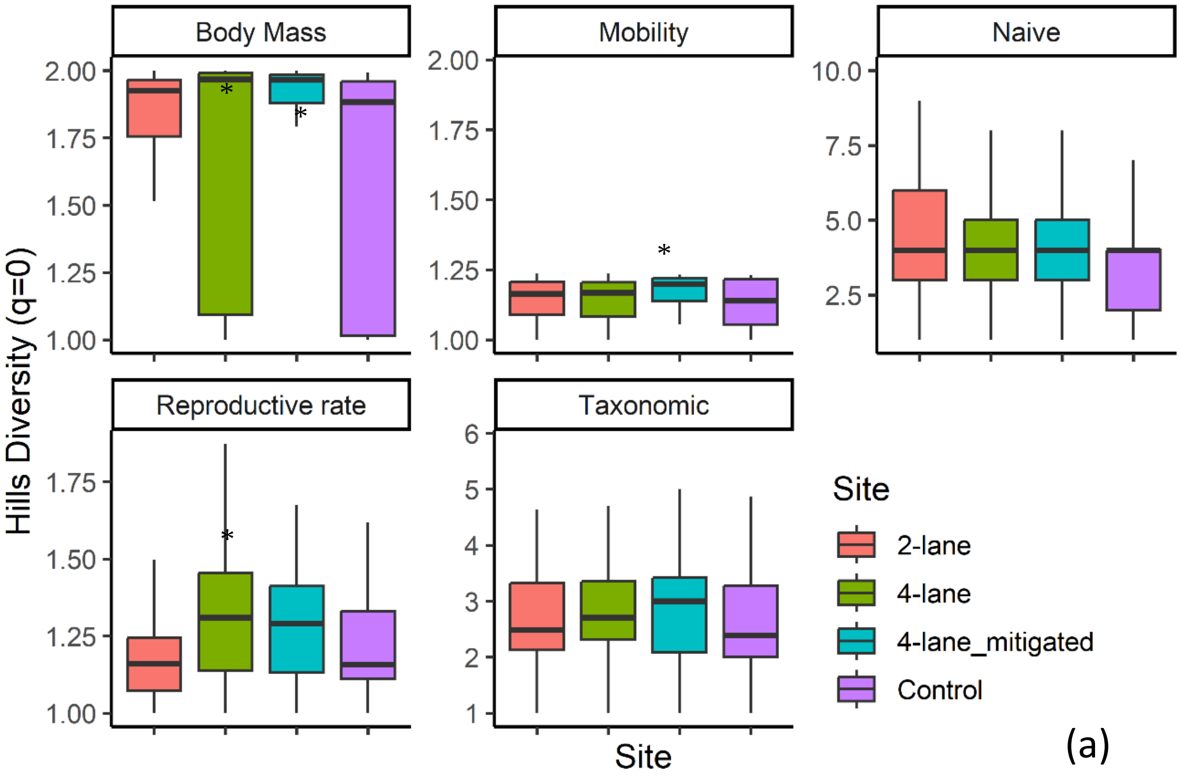


Figure 3.4. Rank abundance plot showing the number of unique species across the four sites ranked according to the abundance of each species, with labels of three most abundant species in each site. A long tail indicates higher species richness, while fewer species with high abundance indicate dominance of few species in the community.

Among the calculated diversity indices, diversity of trait body mass near 2-lane roads (q=0) was significantly different from that in control, while the trait diversity near 4-lane mitigated road (q=0, 1 and 2) was significantly different from control (paired Wilcoxon rank sum test $p < 0.05$). Diversity of trait mobility near 4-lane (mitigated) road (q=0 and 1) was significantly greater than that in control, while diversity of trait reproductive rate significantly higher near 2-lane road (q=0) as compared to control. I found no significant difference in trait diversity (q=0, 1 and 2) among other traits (naïve and taxonomic) and sites (Fig. 3.5).



(a)

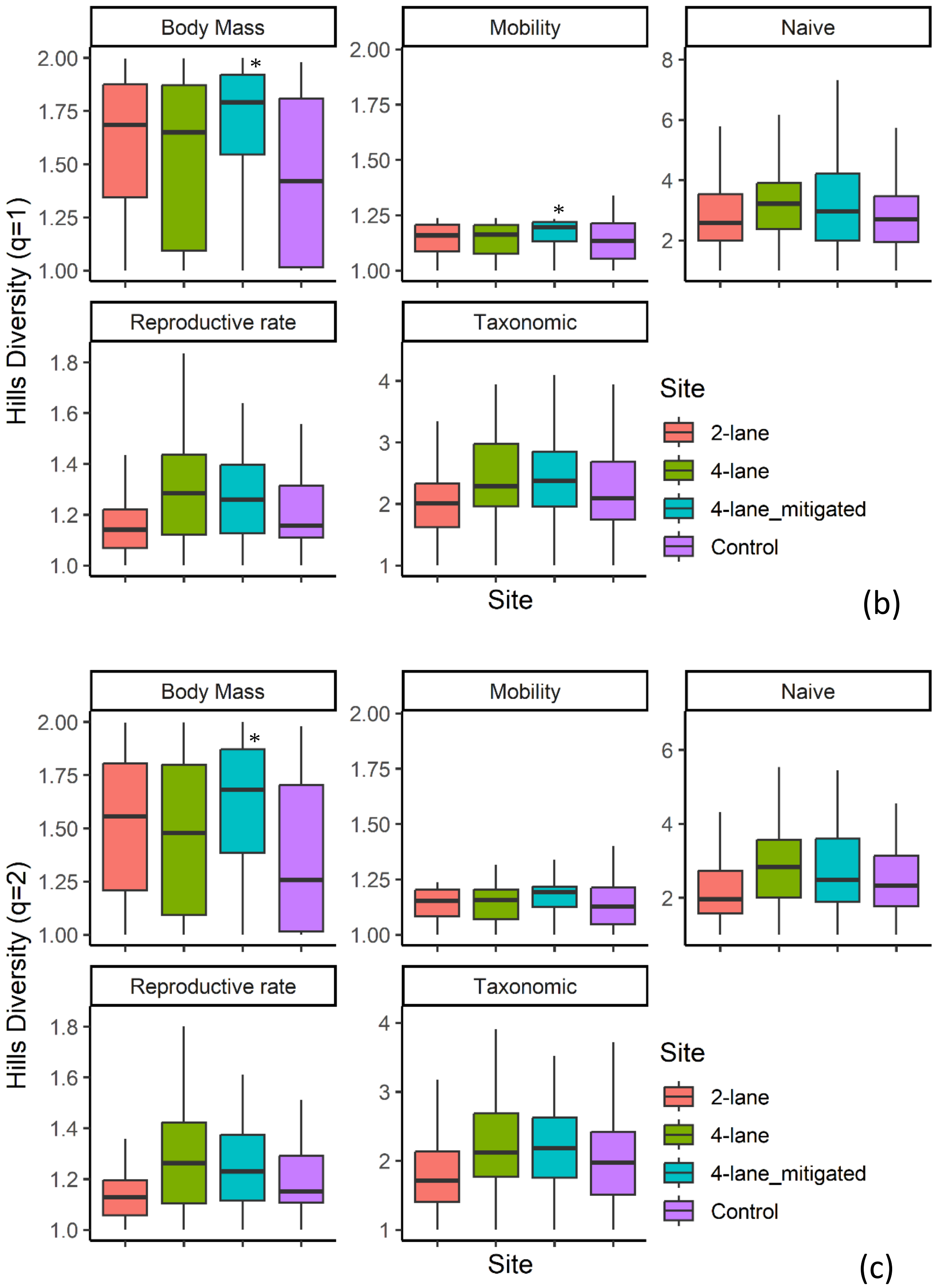


Figure 3.5. Calculated (a) naïve (q=0), (b) Shannon (q=1), and (c) Simpson's (q=2) diversity metrices for different road sites (colours) and across different species functional

traits (facets). Asterisks indicate signficant difference from control species diversity indices.

Only naïve and taxonomic diversities (q = 0, 1 and 2) were significantly influenced by protection, site and distance to road (Table 3.4). I found that naïve and taxonomic diversities significantly varied between sites- both increased with increasing distance to the road, were the lowest in forests with the least protection, and were higher in forests near 4-lane and 4-lane (mitigated) roads as compared with forests near 2-lane road (Fig. 3.6).

Table 3.4. Best approximating GLMMs assessing the difference between different road sites and factors affecting naïve and functional species diversity indices.

Predictors	**q=0**		**q=1**		**q=2**	
	Estimates	*SE*	*Estimates*	*SE*	*Estimates*	*SE*
(Intercept)	1.7958 ***	0.1491	1.6477 ***	0.1117	1.5718 ***	0.1002
Body Mass	*Reference*		*Reference*		*Reference*	
Mobility	-0.6637 ***	0.1842	-0.5088 ***	0.1357	-0.4316 ***	0.1215
ConstraintMobility:Dist_road	0.0002	0.0001	0.0002	0.0001	0.0001	0.0001
ConstraintMobility:ProtectionCore	-0.1716	0.2024	-0.1409	0.1491	-0.1237	0.1335
ConstraintMobility:ProtectionOther	-0.1946	0.1489	-0.0897	0.1097	-0.0568	0.0982
ConstraintMobility:Site4-lane	0.0331	0.1880	0.0139	0.1385	0.0078	0.1240
ConstraintMobility:Site4-lane(mitigated)	-0.0459	0.1868	-0.0936	0.1376	-0.1002	0.1232
Naive	1.7141 ***	0.1842	0.7230 ***	0.1357	0.3846 **	0.1215
ConstraintNaive:Dist_road	**0.0005 *****	**0.0001**	**0.0007 *****	**0.0001**	**0.0007 *****	**0.0001**
ConstraintNaive:ProtectionCore	**0.8201 *****	**0.2024**	-0.1302	0.1491	**-0.3854 ****	**0.1335**
ConstraintNaive:ProtectionOther	**-1.5384 *****	**0.1489**	**-1.3489 *****	**0.1097**	**-1.1597 *****	**0.0982**
ConstraintNaive:Site4-lane	**0.8777 *****	**0.1880**	**1.0527 *****	**0.1385**	**1.0186 *****	**0.1240**
ConstraintNaive:Site4-lane(mitigated)	**0.7018 *****	**0.1868**	**0.8149 *****	**0.1376**	**0.7140 *****	**0.1232**

Reproductive rate	**-0.6174** ***	**0.1842**	**-0.4921** ***	**0.1357**	**-0.4309** ***	**0.1215**
ConstraintReproductive rate:Dist_road	0.0002	0.0001	**0.0002** *	**0.0001**	**0.0002** *	**0.0001**
ConstraintReproductive rate:ProtectionCore	-0.2433	0.2024	-0.2070	0.1491	-0.1869	0.1335
ConstraintReproductive rate:ProtectionOther	-0.2171	0.1489	-0.1348	0.1097	-0.1098	0.0982
ConstraintReproductive rate:Site4-lane	0.1261	0.1880	0.1214	0.1385	0.1186	0.1240
ConstraintReproductive rate:Site4-lane(mitigated)	-0.0183	0.1868	-0.0426	0.1376	-0.0428	0.1232
Taxonomic	**0.7328** ***	**0.1842**	**0.3196** *	**0.1357**	0.1849	0.1215
ConstraintTaxonomic:Dist_road	0.0002	0.0001	**0.0003** **	**0.0001**	**0.0003** ***	**0.0001**
ConstraintTaxonomic:ProtectionCore	-0.0222	0.2024	-0.2003	0.1491	-0.2462	0.1335
ConstraintTaxonomic:ProtectionOther	**-0.4245** **	**0.1489**	**-0.4202** ***	**0.1097**	**-0.3997** ***	**0.0982**
ConstraintTaxonomic:Site4-lane	**0.4171** *	**0.1880**	**0.4822** ***	**0.1385**	**0.4751** ***	**0.1240**
ConstraintTaxonomic:Site4-lane(mitigated)	0.3459	0.1868	**0.3671** **	**0.1376**	**0.3366** **	**0.1232**
Dist_road	-0.0002	0.0001	**-0.0002** *	**0.0001**	**-0.0002** *	**0.0001**
ProtectionCore	0.2095	0.1639	0.1766	0.1227	0.1580	0.1101
ProtectionOther	0.1673	0.1205	0.0792	0.0903	0.0517	0.0810
2-lane	*Reference*		*Reference*		*Reference*	
4-lane	0.0054	0.1522	0.0096	0.1140	0.0100	0.1022
4-lane(mitigated)	0.1211	0.1512	0.1480	0.1132	0.1476	0.1016
Random Effects						
σ^2	0.55		0.30		0.24	
τ_{00}	0.17 $_{\text{SiteID}}$		0.11 $_{\text{SiteID}}$		0.09 $_{\text{SiteID}}$	
ICC	0.24		0.26		0.27	
N	317 $_{\text{SiteID}}$		317 $_{\text{SiteID}}$		317 $_{\text{SiteID}}$	
Observations	1585		1585		1585	
Marginal R^2 / Conditional R^2	0.651 / 0.734		0.604 / 0.708		0.553 / 0.672	

* $p<0.05$ ** $p<0.01$ *** $p<0.001$

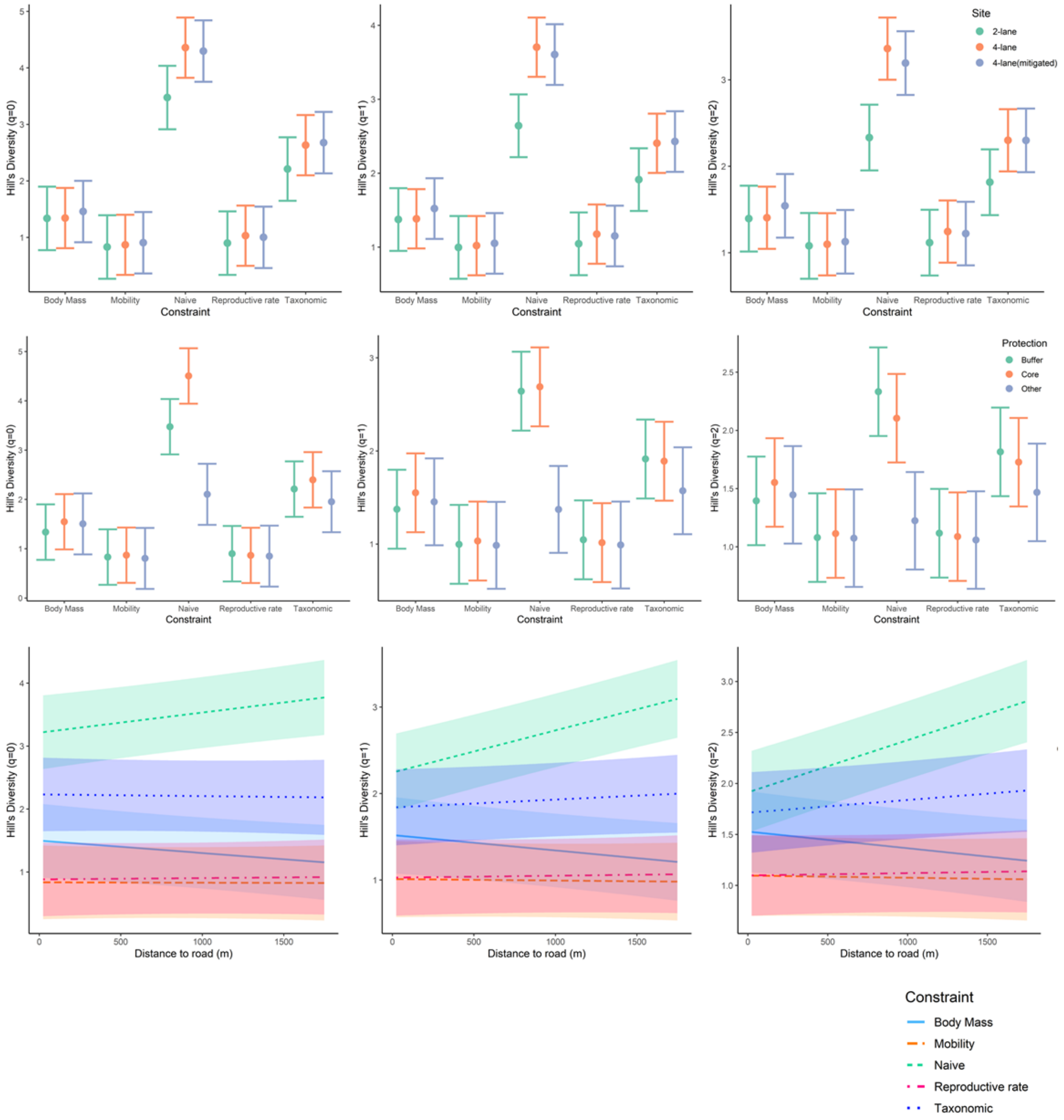


Figure 3.6. Model predictions of naïve and functionally constrained measures of species richness (q=0), Shannon (q=1) and Simpson's (q=2) diversity indices at different road sites, protection levels and distance from road.

3.3.3. *Impact of road on species roadside habitat use*

Among GLMM candidate models, I found that the interactive effect of road type and distance to road explained habitat use by chital, gaur, nilgai and wild dog, while interaction between protection status and distance to road explained habitat use by nilgai. Distance to road, rather than interactive effects, best explained roadside habitat use by sambar, while road type explained roadside habitat use by sambar, wild pig, leopard and tiger (Table 3.5).

Table 3.5. Species-wise best generalised linear mixed models with road-related factors best explaining use of roadside habitat of eight mammals near the National Highway 44, Pench Tiger Reserves, Madhya Pradesh and Maharashtra, with model AICc, difference in AICc from best model (ΔAICc), and Akaike weight.

Species	***Best Performing Models***	***AICc****	***ΔAIC***	***Weight***
Chital	~ Distance to settlement + Protection + Road type x Distance to road	844.69	0	0.7
Gaur	~ Distance to settlement + Protection + Road type x Distance to road	892.13	0	0.42
	~ Distance to settlement + Distance to PA + Protection + Road type x Distance to road	892.35	0.22	0.38
Nilgai	~ Distance to settlement + Distance to water + Distance to PA + Protection x Distance to road + Road type x Distance to road	856.02	0	0.85
Sambar	~ Distance to settlement + Distance to water + Distance to road + Road type + Protection	865.44	0	0.46
	~ Distance to settlement + Distance to water + Distance to PA + Distance to road + Road type + Protection	866.25	0.81	0.31
Wild pig	~ Road type	885.98	0	0.38
	~ Road type + Protection	886.96	0.98	0.24
	~ Distance to PA + Road type + Protection	887.08	1.1	0.22
Leopard	~ Distance to settlement + Distance to water + Road type + Protection	911.54	0	0.46
	~ Distance to settlement + Distance to water + Distance to road + Road type + Protection	912.49	0.95	0.28
	~ Distance to settlement + Distance to water + Human + Distance to road + Road type + Protection	913.52	1.98	0.17
Tiger	~ Roughness + Distance to settlement + Distance to water + Distance to PA + Human + Road type + Protection	910.92	0	0.65
Wild dog	~ Distance to water + Human + Protection + Road type x Distance to road	915.94	0	0.35

	~ Roughness + Distance to water + Human + Protection + Road type x Distance to road	915.96	0.02	0.34
	~ Roughness + Distance to water + Human + Road type x Distance to road + Protection x Distance to road	916.93	0.99	0.21

[Models with ΔAICc < 2 were averaged.]
*Akaike's Information Criteria for small sample sizes

Use of roadside habitat by sambar increased with increasing distance to all road types (β=0.22, CI 0.06). Protection status (core or buffer zone) of roadside habitat positively influenced use of roadside habitats by tiger and chital (higher use of roadside core zone (β=0.65, CI 0.2 and β=0.75, CI 0.17 respectively)), while sambar and gaur used both core and buffer zones near roads more than unprotected forest near roads (β= -0.47, CI 0.21 and β=-0.24, CI 0.25 respectively) (Tables 3.5 and 3.6). Habitat use by nilgai was significantly high near road in unprotected forest (β=3.37, CI 1.67), and decreased with increasing distance to road.

While habitat use by sambar was least near 4-lane road before mitigation (β=-1.24, CI 0.42), leopard showed higher use of habitat near 4-lane road after mitigation (β=0.89, CI 0.44). Conversely, wild pig use of roadside habitat near 4-lane road after mitigation was the least (β= -0.76, CI 0.16).

I found differential wildlife responses to distances to different road types. Use of roadside habitat by gaur decreased with increasing distance to 2-lane road, and increased with increasing distance to 4-lane road (both before β=0.38, CI 0.14, and after mitigation β=0.52, CI 0.14). Conversely, while chital use of roadside habitat increased significantly closer to 4-lane roads before mitigation (β= -0.51, CI 0.12), there was no significant pattern after mitigation (Fig. 3.7 (a-m)).

Table 3.6. Model-averaged fixed effects estimates and standard errors for best supported models (ΔAICc <2) for carnivores- leopard, tiger and wild dog, explaining roadside habitat use near National Highway 44.

	Leopard		**Tiger**		**Wild Dog**	
Predictors	*Estimates*	*SE*	*Estimates*	*SE*	*Estimates*	*SE*
Intercept	-3.12 ***	0.30	-2.32 ***	0.34	-2.50 ***	0.14
Terrain roughness			0.10	0.08	-0.09	0.06
Distance to human settlement	0.32	0.21	-0.48	0.26		
Distance to protected area			-0.07	0.10		
Distance to road	0.063	0.05			0.09	0.12
Distance to water body	-0.17	0.10	0.22	0.12	-0.11	0.06
Anthropogenic capture rate	0.06	0.06	0.14 *	0.06	0.14 *	0.06
Road type: 4-lane	0.73	0.44	-0.83	0.51	-0.23	0.18
Road type: 4-lane (mitigated)	0.89 *	0.44	-0.81	0.50	-0.13	0.18
Protection: Core	-0.06	0.19	0.65 **	0.20	-0.03	0.19
Protection: Other	-0.33 *	0.14	0.16	0.19	-0.26	0.14
Distance to road x Road type: 4-lane					-0.24	0.17
Distance to road x Road type: 4-lane (mitigated)					0.23	0.17
Distance to road x Protection: Core					0.19	0.20
Distance to road x Protection: Other					-0.22	0.14
Observations	320		320		320	

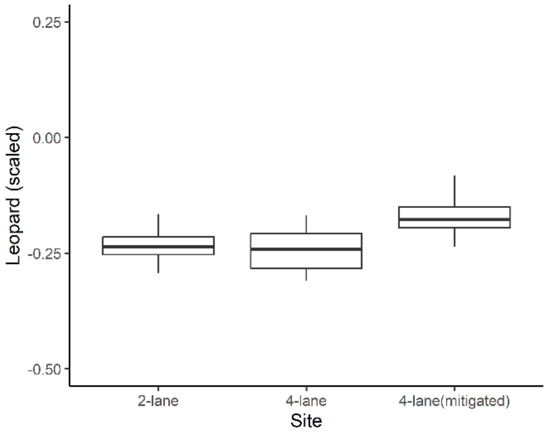
*p<0.05 **p<0.01 ***p<0.001

Table 3.7. Model-averaged fixed effects estimates and standard errors for best supported models (ΔAICc <2) for herbivores- chital, gaur, nilgai, sambar and wild pig, explaining roadside habitat use near National Highway 44.

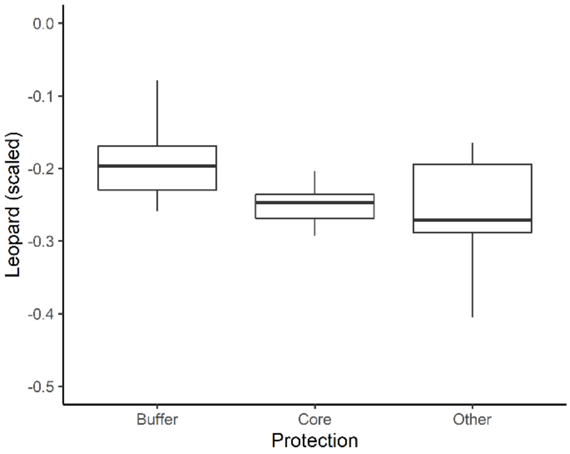
	Chital		**Gaur**		**Nilgai**		**Sambar**		**Wild Pig**	
Predictors	*Estimates*	*SE*	*Estimates*	*SE*	*Estimates*	*SE*	*Estimates*	*SE*	*Estimates*	*SE*
Intercept	-2.33 ***	0.19	-3.54 ***	0.22	-5.47 ***	0.81	-1.94 ***	0.29	-2.46 ***	0.14
Distance to human settlement	-0.32 **	0.11	0.50 ***	0.12	0.74 ***	0.20	-0.80 ***	0.20		
Distance to protected area			-0.16	0.12	-2.78	1.45	-0.12	0.11	0.14	0.10
Distance to road	0.10	0.09	-0.28 **	0.09	0.12	0.13	0.22 ***	0.06		
Distance to water body					-0.33 ***	0.09	0.31 ***	0.09		
Road type: 4-lane	-0.92 ***	0.27	1.21 ***	0.29	1.79 ***	0.41	-1.24 **	0.42	0.24	0.16
Road type: 4-lane (mitigated)	-1.00 ***	0.27	1.26 ***	0.29	1.85 ***	0.40	-1.00 *	0.41	-0.76 ***	0.16
Protection: Core	0.75 ***	0.17	0.53 **	0.19	0.17	0.17	0.61 ***	0.18	-0.24	0.18
Protection: Other	0.47 ***	0.12	-0.24	0.25	5.18 *	2.41	-0.47 *	0.21	-0.30	0.23
Distance to road x Road type: 4-lane	-0.51 ***	0.12	0.38 **	0.14	-0.08	0.16				
Distance to road x Road type: 4-lane (mitigated)	-0.08	0.12	0.52 ***	0.14	-0.40 *	0.16				
Distance to road x Protection: Core					-0.13	0.18				
Distance to road x Protection: Other					3.37 *	1.67				

Observations	320	320	320	320	320

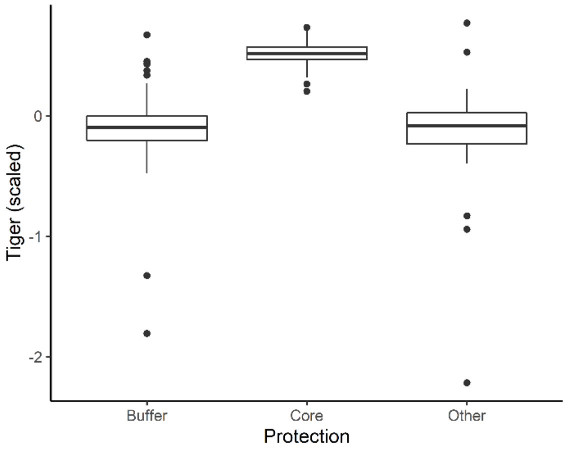
*p<0.05 **p<0.01 ***p<0.001



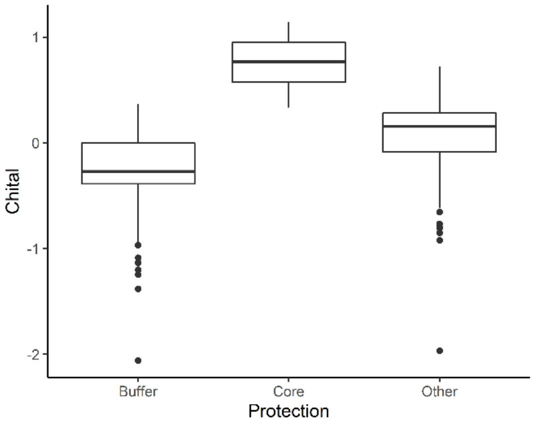
(a)



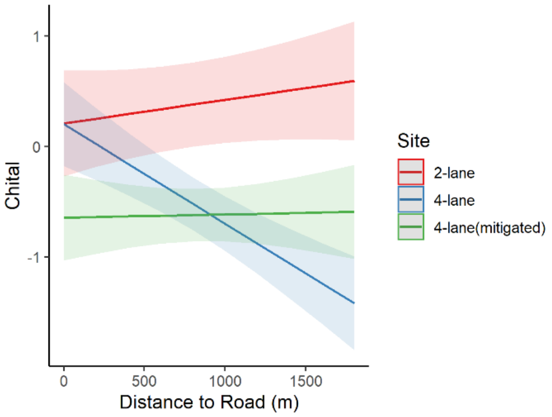
(b)



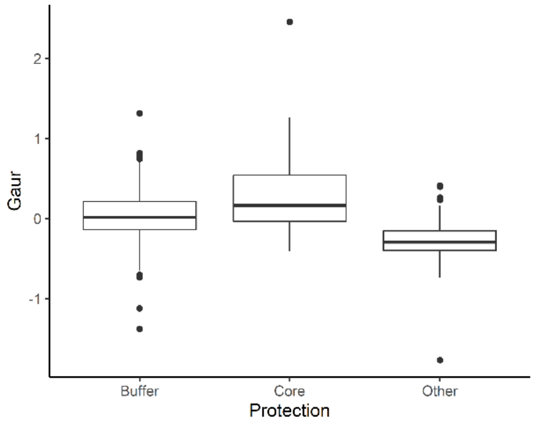
(c)

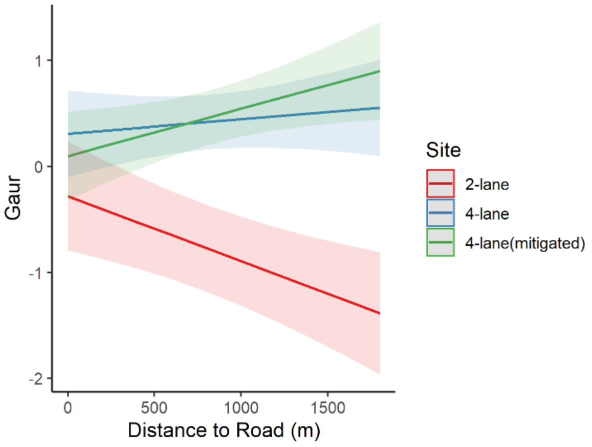


(d)



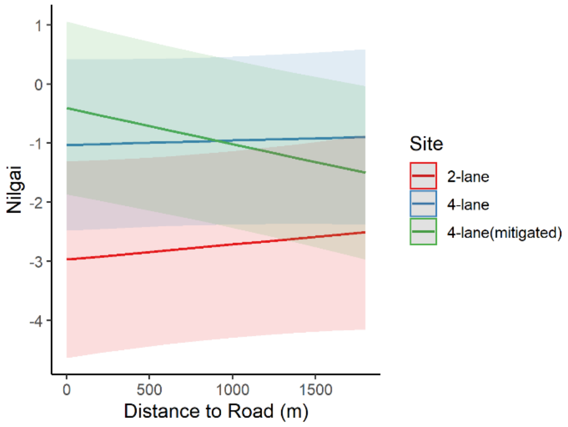
(e)

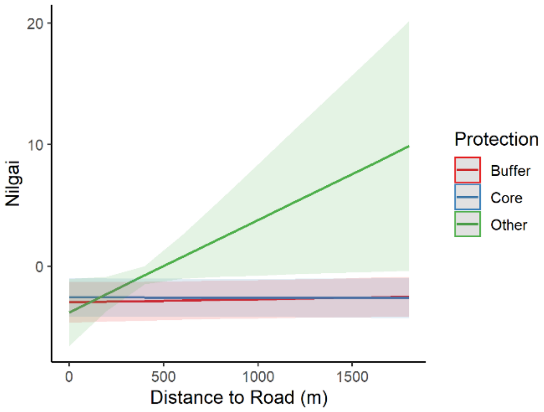

Gaur
2
1
0
-1
Buffer
Core
Other
Protection


Gaur
1
0
-1
-2
0
500
1000
1500
Distance to Road (m)
Site
2-lane
4-lane
4-lane(mitigated)

(f)

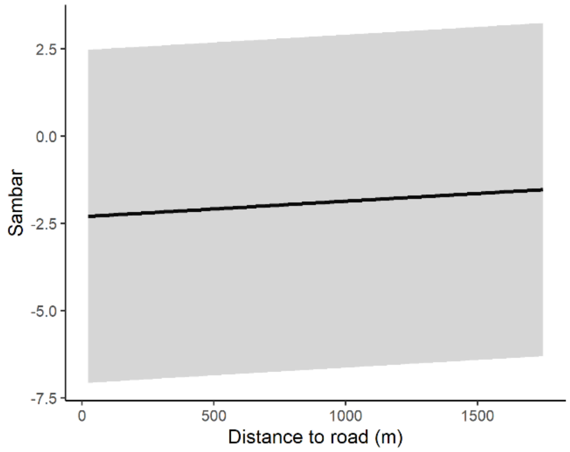
(g)

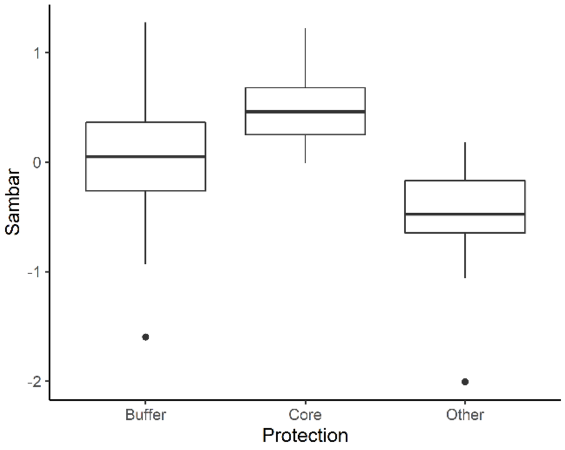

Nilgai
1
0
-1
-2
-3
-4
0
500
1000
1500
Distance to Road (m)
Site
2-lane
4-lane
4-lane(mitigated)


Nilgai
20
10
0
0
500
1000
1500
Distance to Road (m)
Protection
Buffer
Core
Other

(h)

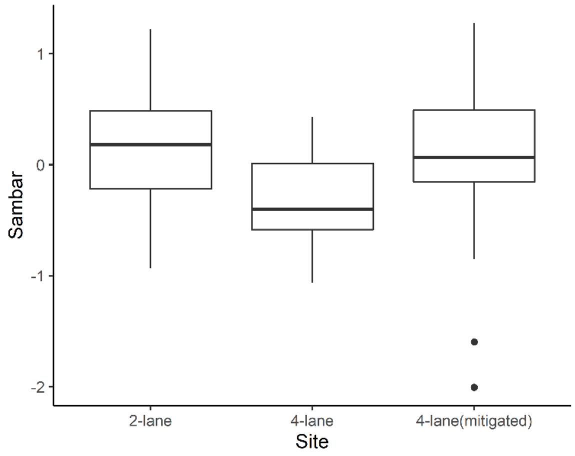
(i)


Sambar
2.5
0.0
-2.5
-5.0
-7.5
0
500
1000
1500
Distance to road (m)

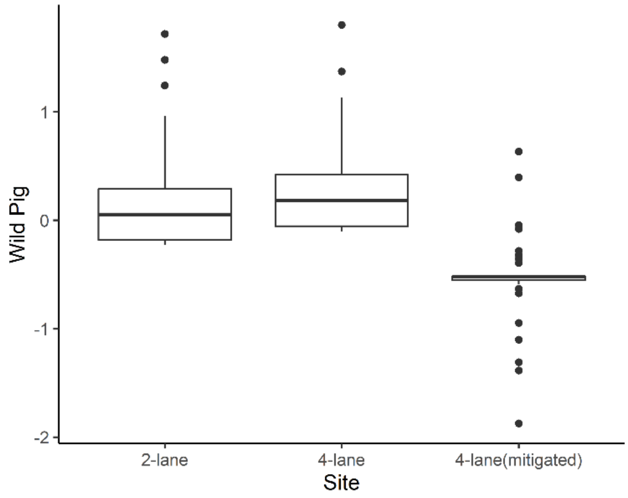

Sambar
1
0
-1
-2
Buffer
Core
Other
Protection

(j)

(k)



(l)



(m)

Figure 3.7. (a – m). Effect plots showing model predictions for road-related factors significantly affecting roadside habitat use by 8 mammal species near National Highway 44, Pench Tiger Reserves, Madhya Pradesh and Maharashtra.

3.3.4. Impact of roads on animal activity

All three predators showed similar activity patterns near roadsides and in control habitat (Fig. 3.8), though the hourly activities near all road types were significantly reduced as compared with activity in control site (Fig. 3.9). Tiger activity near 4-lane road before mitigation was significantly different from its natural activity pattern (Watson Wheeler test, W=7.4, p=0.02), and peaked during late night hours.

Chital activity near all road types was significantly different from control activity (Watson-Wheeler test W = 53.89, 34.28, 15.69, $p<0.05$). This activity overlapped the least with control activity near 2-lane road (0.67 CI 0.63-0.71), where chital activity outside of natural peak activity hours (early morning and late evening hours) was observed. After mitigation, chital activity near 4-lane road showed higher hourly activity, although within its peak natural activity hours. Wild pig activity near all road types did not differ significantly from its control activity (Watson Wheeler test $p > 0.05$). However I observed lesser overlaps with control activity near 2-lane and 4-lane roads, while after mitigation, there was an increase in diurnal hourly activity, with the least overlap with control among all roadside activities.

Among ungulates, hourly activities of gaur, nilgai and sambar near roadside habitat were generally reduced across all road types, with the exception of slightly increased diurnal nilgai activity near 4-lane road after mitigation (Appendix 3 Fig. A3.1 (c)). Sambar showed generally lesser hourly activities near all road types that were not significantly different from control activity (Watson Wheeler test W=3.34, 3.58, $p>0.05$), with the exception of activity near 4-lane road (Watson Wheeler test W=6.4, $p=0.04$). Gaur activity near all roadsides was not significantly different from control (Watson Wheeler test W=3.28, 0.77, 2.5, $p>0.05$), but with low overlaps with control activity (Dhat = 0.57 0.27-0.86 (2-lane), 0.47 0.18-0.76 (4-lane) and 0.47 0.18-0.76 (4-lane mitigated)). Nilgai activity near 4-lane road before mitigation was significantly different from control activity (Watson Wheeler test W=9.03, $p=0.01$). Nilgai activity overlap with control activity was highest near 4-lane road after mitigation (0.85 0.74-0.95).

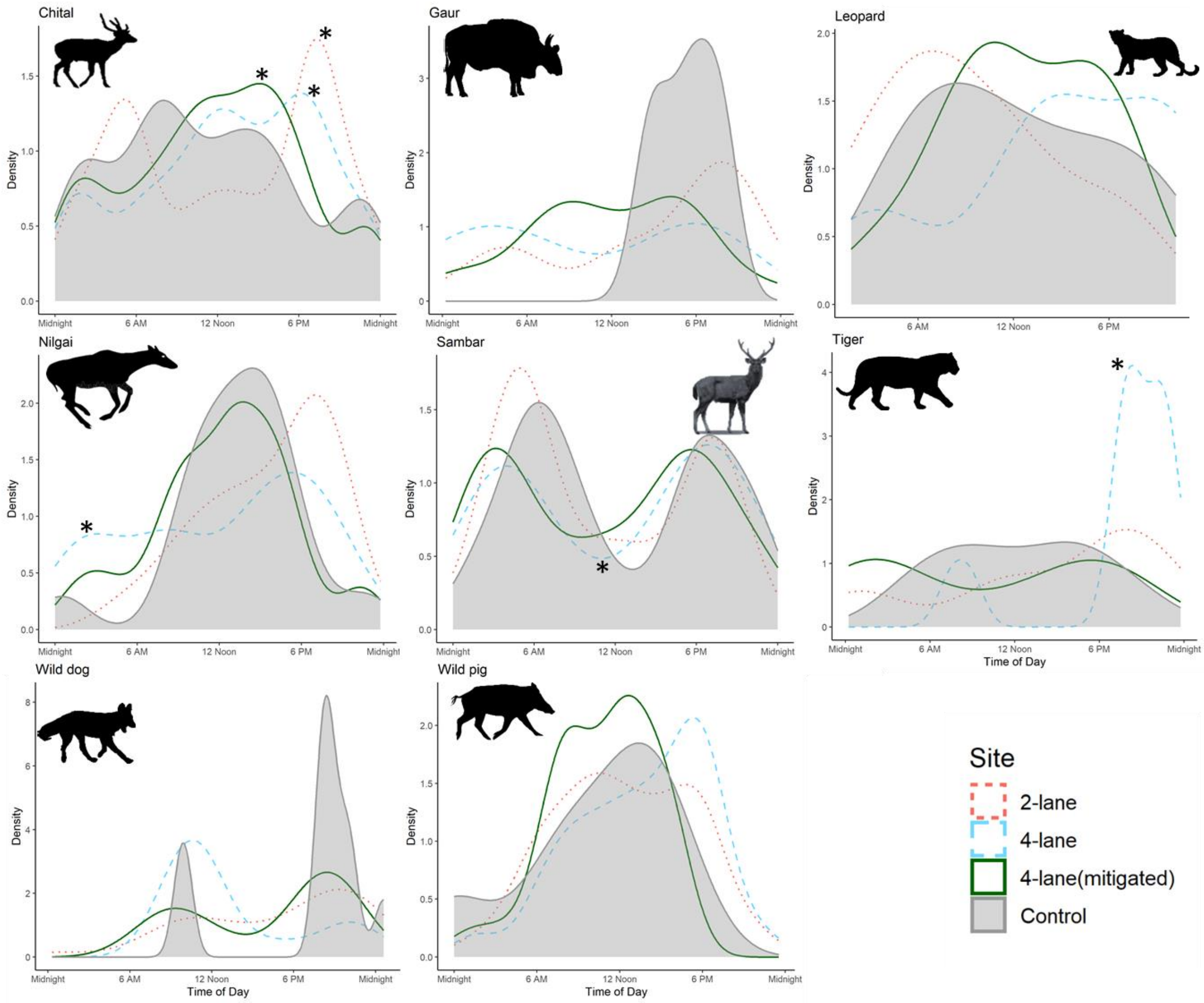


Figure 3.8. Temporal activity patterns of eight large mammals near National Highway 44 passing through Pench Tiger Reserve, Maharashtra and Madhya Pradesh, in control habitat (solid filled grey curves), near 2-lane road in Madhya Pradesh section (dotted red curves), near 4-lane road before (dashed blue curves) and after (solid green curves) construction of mitigation measures (crossing structures). Curves marked with * (asterisk) were significantly different from species' control/natural activity.

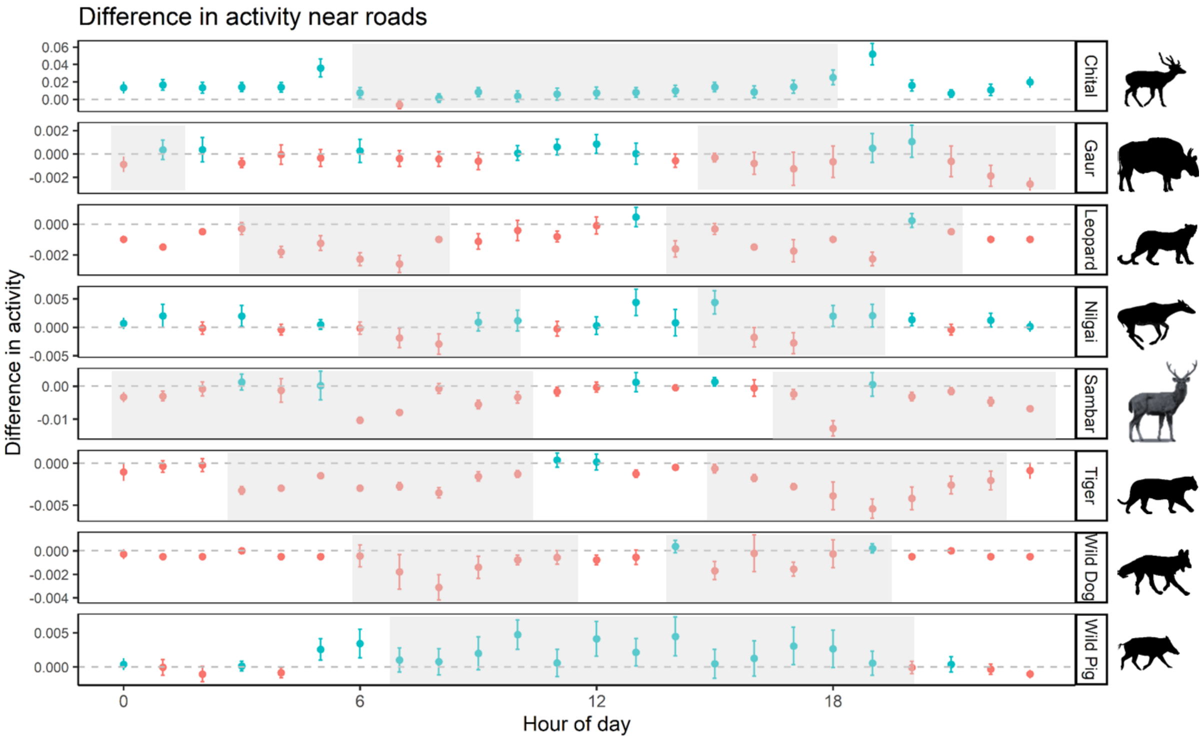


Figure 3.9. Difference in hourly activity patterns of eight large mammals near National Highway 44 (all road types). Solid dots represent mean difference in activity and bars represent upper and lower limits of confidence intervals. Grey shaded areas represent peak activity hours in control habitat. Horizontal dashed grey line represents zero.

Predator-prey overlaps between road sites

Near-natural leopard-prey overlaps near 2-lane road were observed. I found near-natural prey-leopard activity overlaps near 4-lane road after mitigation with all prey species, particularly with chital and wild pig (Fig. 3.10). I found relatively less activity overlap between tiger and prey near 4-lane road, as compared with that near 2-lane road. After mitigation, near-natural prey-tiger activity overlaps were observed particularly with chital and wild pig. Conversely we found no significant change in wild dog-prey overlap near any of the 3 road sites. Near-natural activity overlap of wild dog after mitigation was observed with gaur, which is not a principal prey of wild dog.

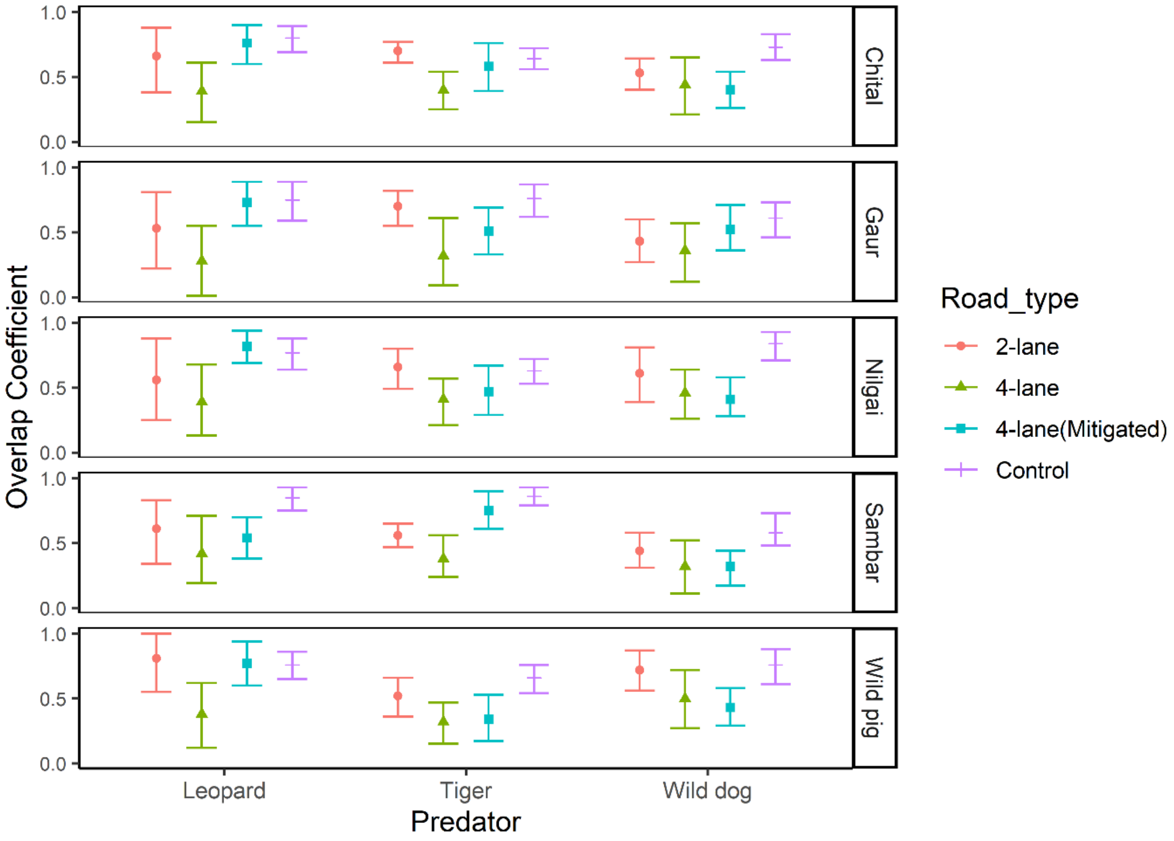


Figure 3.10. Coefficient of activity overlap between predators (x-axis) and prey species (panels) in different roadside habitats (red dot – 2-lane, green triangle – 4-lane (before mitigation), blue square (4-lane (after mitigation)) and violet bar (control). Bars represent bootstrapped confidence intervals.

Species-traffic activity overlap

The average daily traffic volume on NH 44 in 2015 (before construction of mitigation measures was 5833±693.06 vehicles, while it was 5425±553 after construction of mitigation measures (2019). Traffic activity on the 4-lane road before (2015) and after construction of mitigation measures (2019) showed a similar pattern (Fig. 3.11).

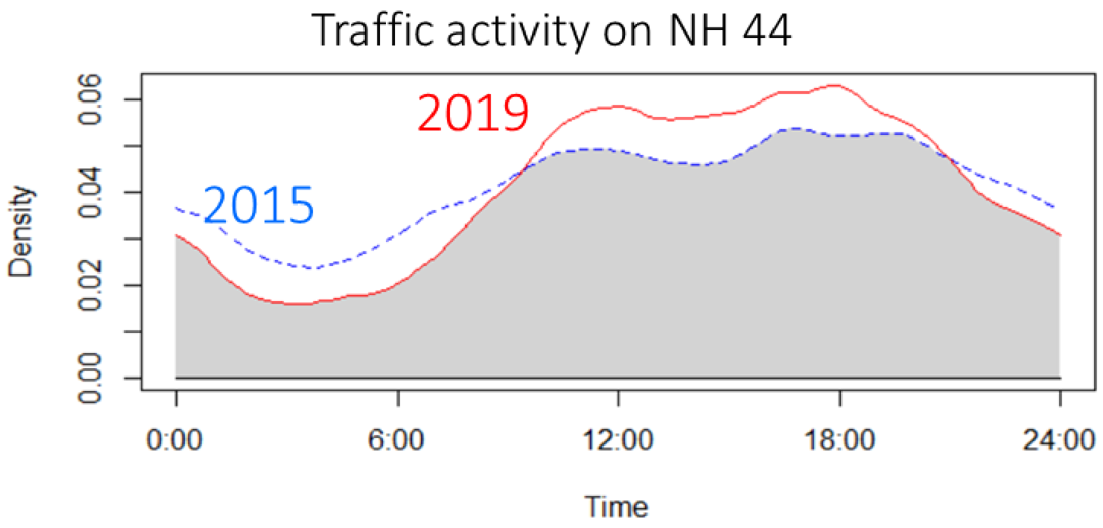
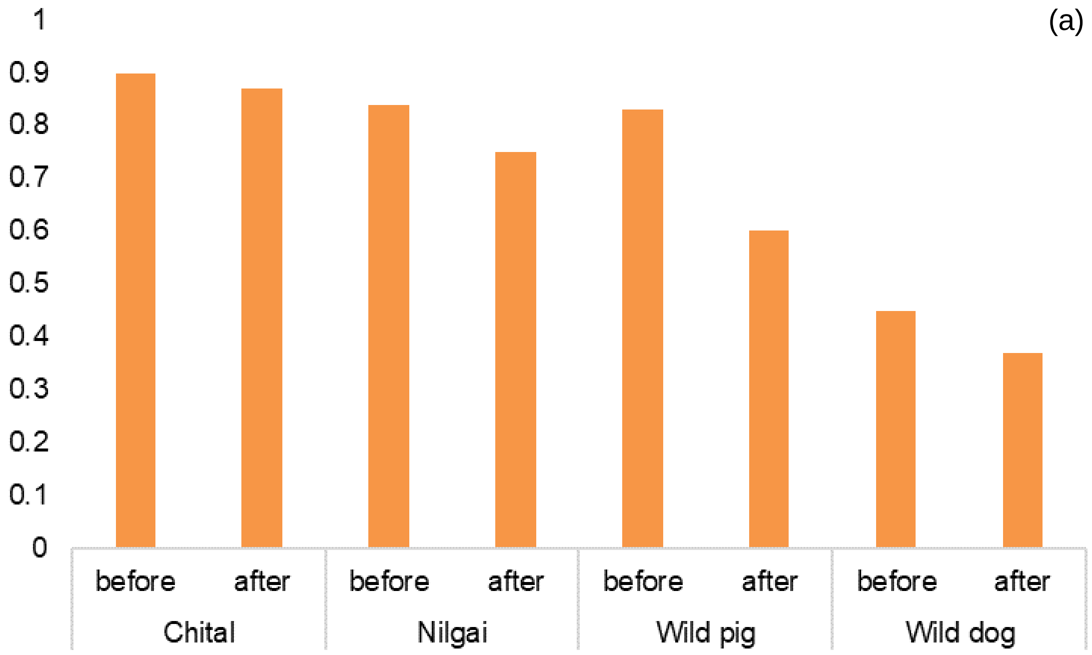


Figure 3.11. Daily activity pattern of vehicular traffic on National Highway 44 passing through Pench Tiger Reserve, Maharashtra before (2015) and after construction of mitigation measures (2019).

Chital and nilgai showed similar activity overlaps with traffic on 4-lane road and after construction of mitigation, while wild pig and wild dog activity overlaps with traffic decreased after contruction of mitigation measures (Fig. 3.12(a)). Conversely for primarily nocturnal/crepuscular species like gaur, sambar, leopard and tiger, activity overlap with traffic increased after construction of mitigation measures (Fig. 3.12(b)).



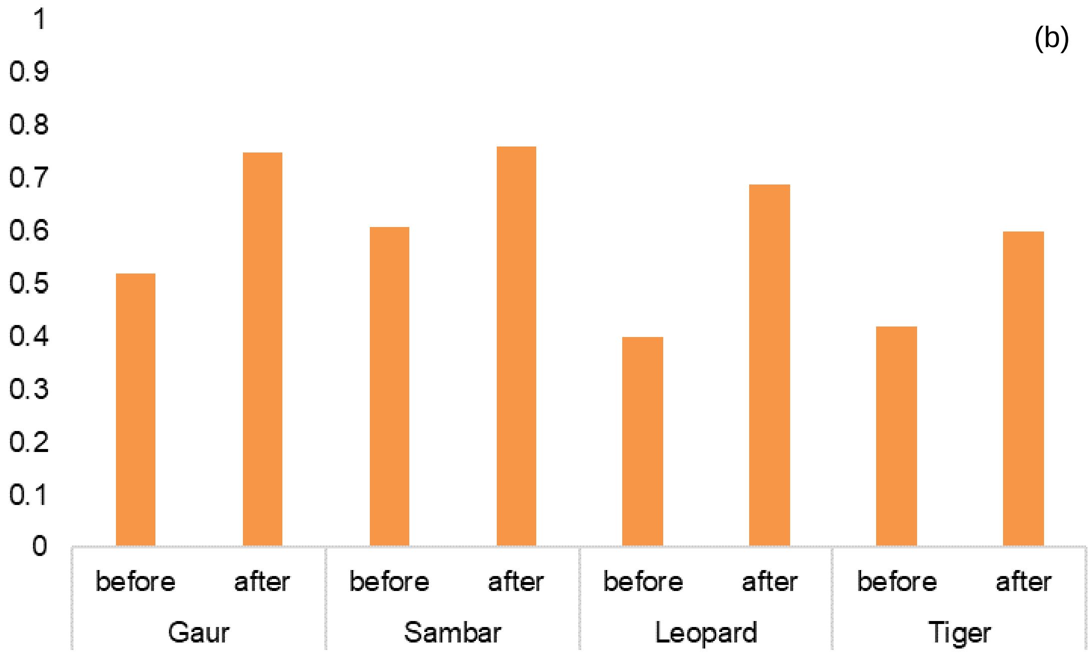


Figure 3.12. Activity overlaps with traffic on National Highway 44 passing through Pench Tiger Reserve, Maharashtra with (a) chital, nilgai, wild dog and wild pig, and (b) gaur, sambar, leopard and tiger.

3.4. Discussion

The study provides evidence that roads impact species differently (Rytwinski and Fahrig, 2013, 2012). Roadsides and control habitat harboured similar species richness. The functional species diversity across sites were also not significantly different, with the exception diversity indices (q= 1 and 2) measured in terms of body mass near 4-lane roads that were significantly less than that in control habitat. Species diversity could further decrease near roadside forests that are away from protected areas, since availability of favourable and protected habitat in the vicinity of roads may lead to less significant effects of roads on species diversity and richness (Sangiwa et al., 2019).

Among the mammals studied, broadly I found three types of spatio-temporal responses to roads and mitigation measures: (a) reduced use before, and increased/near-natural use after construction of mitigation measures, (b) reduced use irrespective of road type and mitigation measures, and (c) high habitat use before construction of mitigation measures through increased activity, and reduction in activity after mitigation. In terms of altered activity patterns of the study species near roads, I observed shifts towards both nocturnal as well as diurnal activity patterns, and reduced as well as significantly high hourly activities compared to natural activity during peak as well as non-peak activity hours. The study duration and siting allowed me to first compare effect of road type (2-lane and 4-lane) with the same traffic volume between both road types, and subsequently the effect of CS construction in the roadside habitat along the same segment.

Large carnivores are most vulnerable to road related effects (Grilo et al., 2015) owing to their large area requirements, low reproductive rates, high mobility and large body sizes (Rytwinski and Fahrig, 2012). In accordance with predictions, carnivores showed significantly less use of roadside habitats as compared with use in undisturbed habitat (control). This could be a result of carnivores actively choosing home ranges away from roads in response to the risks associated with roads (Basille et al., 2013). While low activity near roads may reduce probability of roadkill (Murray and St. Clair, 2015), such avoidance may also lead to social and genetic isolation among carnivores (Riley et al., 2006). Further nocturnal activity of tiger and leopard near unmitigated roads may indicate attempts to cross roads at low traffic hours (Baigas et al., 2017; Kautz et al., 2021; Meisingset et al., 2013). Using stripe patterns of individual tigers, I identified two individuals along the habitat near 4-lane highway before construction of the CS, only one of which was captured on both sides. After construction of the CS, I photo-captured 6 individuals (including the two individuals photo-captured before construction of CS), two of which were found using habitat on both sides of the highway. Interestingly, all individuals were found to be using the CS regularly (Saxena and Habib, 2022).

Responses of the predators to construction of mitigation measures also varied – while leopard showed an increase in use of roadside habitat with an increase in daytime activity, construction of mitigation structures helped recover natural tiger activity patterns. Moreover, tiger and wild dog activity overlaps with traffic near 4-lane road were low both before and after mitigation, while leopard overlap with traffic increased, largely owing to diurnal shift in leopard activity post-mitigation. I observed low overlaps of wild dog activity with traffic both before and after construction of mitigation measures. Among carnivores, wild dogs were found to use the CS most frequently (Saxena and Habib, 2022).

In the context of ungulates' responses to road-related disturbance, I observed variation in response to different road types (Cappa et al., 2019; Polfus et al., 2011) and alterations in activity patterns (de Oliveira, 2018; Eldegard et al., 2012) at different sites, either within or outside of natural peak activity hours. Use of habitat near unmitigated roads by sambar and gaur was lower than or similar to their natural relative abundances respectively. Both ungulates are forest-dwelling and disturbance-averse species that are rarely encountered as roadkill in the study area, possibly because of high degree of avoidance of roadside habitat. Activity patterns of both species near roads also indicates a similar possibility. However, while no significant alterations or shift from natural sambar activity near roads was observed, gaur activity post-mitigation showed a diurnal shift. This could be attributed to perceived reduction in disturbance after mitigation structures were constructed, and consequent shift to diurnal activity by gaur (Ashokkumar et al., 2011).

Prey species have also been found to increase use of moderately disturbed habitat that are mostly avoided by predators (Muhly et al., 2011; Rogala et al., 2011), also perceived by prey as 'predation *refugia'*. Chital and wild pig showed significantly high activity near unmitigated roads (2-lane and 4-lane roads respectively). Higher-than-natural chital and wild pig activities were observed near 2-lane and 4-lane roads (with significantly higher chital activity during hours outside of natural activity peaks). This indicates greater exploitation of roadside habitat during low traffic hours. Owing to factors such as their attraction to roads for forage, ability to avoid vehicular traffic, tolerance to traffic disturbance and negative responses of their primary predators (Fahrig and Rytwinski, 2009b), the two species are possibly positively affected by roads. However, after construction of mitigation measures, a significant decline in peak hour activity and relative abundance of wild pig, and a decline in non-peak hour temporal activity of chital was also observed. This could be because of increased probability of encountering predators near roadsides after mitigation (as evidenced by increase in predator-prey overlap), and increase in intraguild competition for forage near roadside habitat. Both chital and wild pig were the most frequently encountered large mammal roadkill on the highway, possibly because of their increased activities near roadsides (Kušta et al., 2017; Saxena et al., 2020). A decline in activity-driven vulnerability to roadkill for both species could be expected post construction of CS (since the highway remains unfenced), and this would require further assessment.

Overall, leopard, sambar and gaur showed avoidance of vicinity of 4-lane road without mitigation since no photocaptures of these species were obtained near 500 m from the road. These species can be said to have adverse vulnerability to road-related effects, possibly exhibiting high noise and road surface avoidance (Jaeger et al., 2005).

Protected areas can buffer the effect of anthropogenic footprint as compared to unprotected areas (Burson et al., 2000), particularly for carnivores (Habib et al., 2021). Similarly herbivores are expected to exploit high quality foraging sites in the vicinity of roads (Eldegard et al., 2012), since such habitat is actively managed and protected. Relatively high abudances of chital, gaur, tiger and wild dog were observed near 2-lane roads compared to that near other road types, possibly because of the presence of core and buffer zones of tiger reserve on both sides of the road. Therefore it is most vital to implement mitigation measures on roads passing through protected areas, as wildlife mortality is also expected to be high in such areas because of high local abundances (Grilo et al., 2011).

NH 44 (previously NH 7) is one of the oldest highways of India. Thus, the response of wildlife to this highway has probably evolved over decades. Protection against human disturbance associated with roads (Laurance et al., 2009) along PTR has probably been possible because of the protected status of the forest. Initial results of CS monitoring have revealed that species behaviour in terms of response to traffic and clearing of forest influences differential use of CS by wildlife (Saxena and Habib, 2022). However, the effect of increased traffic load and expansion the highway, albeit with large mitigation measures, and the consequent effect on CS use, would require long-term synchronous studies at different time periods. Further investigation into predator-prey dynamics would also require studying predation patterns near roadsides. Even though I attempted to account for seasonal variation by conducting the study during the same season, the data was collected over a short study period. An interesting result of the study was the increase in diurnal activities of nocturnal species like leopard and gaur after mitigation measures were constructed. A more detailed assessment of carnivore activity patterns near mitigation measures and implications for interspecific interactions is required to assess such changes in activity.

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Chapter 4

Chital behaviour near National Highway 44, Pench Tiger Reserves, Madhya Pradesh and Maharashtra

4.1. Introduction

Human infrastructure such as roads passing through natural areas bring wildlife in close contact with humans and vehicles. While certain human-wildlife interactions in such interfaces are fatal to wild animals (for example, roadkill), human footprint and associated disturbance also have non-lethal effects that cause decreased use or avoidance of such habitats by wildlife (D'Amico et al., 2015; de Oliveira, 2018; Dyer et al., 2002; Wattles et al., 2018). High degrees of spatio-temporal avoidance of human contact and infrastructure is usually exhibited by wildlife species that are sensitised to perceived anthropogenic threats, with or without previous experience of negative interactions with humans (Ciuti et al., 2012a; Donadio and Buskirk, 2006; Paton et al., 2017; Stankowich, 2008, Bonnot et al., 2013). While this avoidance leads to indirect loss of habitat, such mechanisms help animals avoid potentially risky or costly situations (Blumstein, 2016).

However, human presence and footprint have also been found to elicit varied responses among wildlife that use these areas, particularly prey species. According to the risk disturbance hypothesis, wildlife perceive humans as predators, and consequently respond to human-caused disturbance the same way they would respond to their natural predators (Frid and Dill, 2002). High vigilance has been observed among many ungulates near disturbed areas (Loehr et al., 2005; Tsunoda, 2021), such as habitats in the vicinity of roads (Gavin and Komers, 2006; Lian et al., 2011; St. Clair and Forrest, 2009). Moreover, in highly disturbed areas, ungulates tend to be in smaller groups as compared with habitats with low human disturbance (Manor and Saltz, 2003), in accordance with the 'group size effect' or the 'dilution hypothesis' (Creel et al., 2014).

Conversely, the role of humans as super predators also extends to their effect on carnivores by reducing their use of disturbed areas (Kuijper et al., 2016). This results in a ‘predator release’ situation wherein prey exploit moderately disturbed sites in the absence of their natural predators (Berger, 2007; Laurian et al., 2015), often exhibiting behaviours that indicate reduced predatory threat from natural predators, that is, associating human presence as predator shields (Shannon et al., 2014). Multiple studies have demonstrated the use of disturbed habitat by wildlife without any evidence of increased threat perception in some species (Brown et al., 2012; Cappa et al., 2017; Schuttler et al., 2016).

However, exploiting disturbed areas is not without its costs. Cues of human presence have been found to decrease foraging opportunities in certain prey species, sometimes in optimal habitats (Ciuti et al., 2012b; Crawford et al., 2022; Dwinnell et al., 2019), leading animals to trade-off foraging opportunities against staying away from disturbed but resource-rich areas (Benhaiem et al., 2008). Additionally, increased vigilance can also involve trade-offs with and disruptions in natural social interactions, that can be adverse for social group living species living in disturbed areas (St. Clair and Forrest, 2009).

In Pench Tiger Reserves (PTR), Madhya Pradesh and Maharashtra, chital (*Axis axis*) are the most widely distributed and abundant wild ungulates (Habib et al., 2020; Jhala et al., 2020), and are among the primary prey species of tiger and other co-predators in the landscape (Ghaskadbi et al., 2022; Majumder et al., 2013). Similarly use of habitat near the National Highway 44 (NH 44) by chital is also among the highest compared to other large mammals in the study area, with significantly different activity patterns as compared to forest interiors (Chapter 3). Use of roadside habitat by chital, often coinciding with high traffic hours, also makes the species more vulnerable to roadkill as compared to other guild members (Saxena et al., 2020). Consequently, understanding behavioural mechanisms which enable chital to use areas with road-related disturbance, and at the same time make them vulnerable to impacts of linear infrastructure can lend clues to mitigate such impacts (St. Clair et al., 2019). In addition to these factors, chital were more visible and abundant during daytime near the highway, as compared to other ungulates, making them suitable for such a study.

In the present study, I assessed whether road-related disturbance had an effect on the behaviour of chital by comparing the same with chital behaviour inside PTR, with special focus on the vigilance behaviour. I also examined whether this vigilance had costs in terms of other individual and group/social behavioural activities. Specifically, I asked whether:

a. Chital group size varied between different gradients of road-related disturbance (assuming increasing distance to road as a proxy of decreasing levels of road-related disturbance),
b. Chital behaviour near roadsides differed with that inside PTR i.e., in the absence of road-related disturbance, and
c. Chital feeding and vigilance behaviours near roadsides and inside PTR varied.

I hypothesised that given the differential perceived threat from predators inside PTR, and the threat from vehicles and humans near roadsides, vigilance behaviour by chital would vary between the two sites. I expected smaller chital group sizes, increased levels of vigilance, and consequently less time spent on feeding by chital in roadside habitat. I also expected lesser proportional time allocated to non-vigilance behaviours by chital at roadsides considering the high fitness costs of being non-vigilant near humans.

4.2. Methodology

4.2.1. Field methods

4.2.1.1. Chital group size

Chital herds along the NH 44 passing through PTR, Madhya Pradesh (2-lane) and Maharashtra (4-lane), and within both tiger reserves (TR) were observed during January-December 2017 and 2019, and their group sizes and compositions were noted (Fig. 4.1).

Distance from the highway for chital herds observed near the highway was estimated using a rangefinder, while the distance from highway for herds observed within the TRs was estimated using the near tool in ArcGIS Pro (ESRI Inc., 2021).

4.2.1.2. Chital behaviour

I drove along NH 44 to record the behaviour of chital herds near the highway (Fig. 4.1) using a digital camera ("DSC-H400 Specifications | Sony IN") during April – December 2019 between 6:00 – 9:30 AM and 3:30 – 7:00 PM. Video recording of chital herds near the highway was done such that herds or individuals were not aware of the presence of our stopped vehicle (Fig. 4.1 (inset)). Similarly, behaviour of chital herds within PTR was also recorded. The recording was continued till such time that the herds had moved away from visibility or till darkness. I also noted down the group size, age-sex composition, and distance from highway (using a rangefinder), GPS location on the highway, and road type (2-lane or 4-lane). I also categorised the vegetation density as 'low' (grassy patch open without tree cover), 'medium' (moderately dense with 90% visible individuals), and 'dense' (dense tree and understory foliage).

I categorised chital herds observed <150 m away from the highway (all observations made from the highway) as 'roadside' and further as those near 2-lane and 4-lane segment of the highway, while all other herds within PTR were classified as 'control'. Group density is a determinant of proactive anti-predator strategy among ungulates (Iranzo et al., 2018); however I could not estimate group density as the group formation kept changing near the highway. I classified male chital individuals as AM (adult males) when they had fully formed antlers that were at or above the shoulder level while feeding, and sub-adult males (with antlers smaller than that of adult males) and spikes (males with unbranched antler points) as SAM (sub-adult males). Because chital observations made near the highway were often in moderate-dense vegetation and on slopes, it was difficult to tell apart female age-sex categories. Therefore, female adult and sub-adult chital were categorised as AF (adult females), while fawns and juveniles (smaller than adult females) were classified as 'juvenile'.

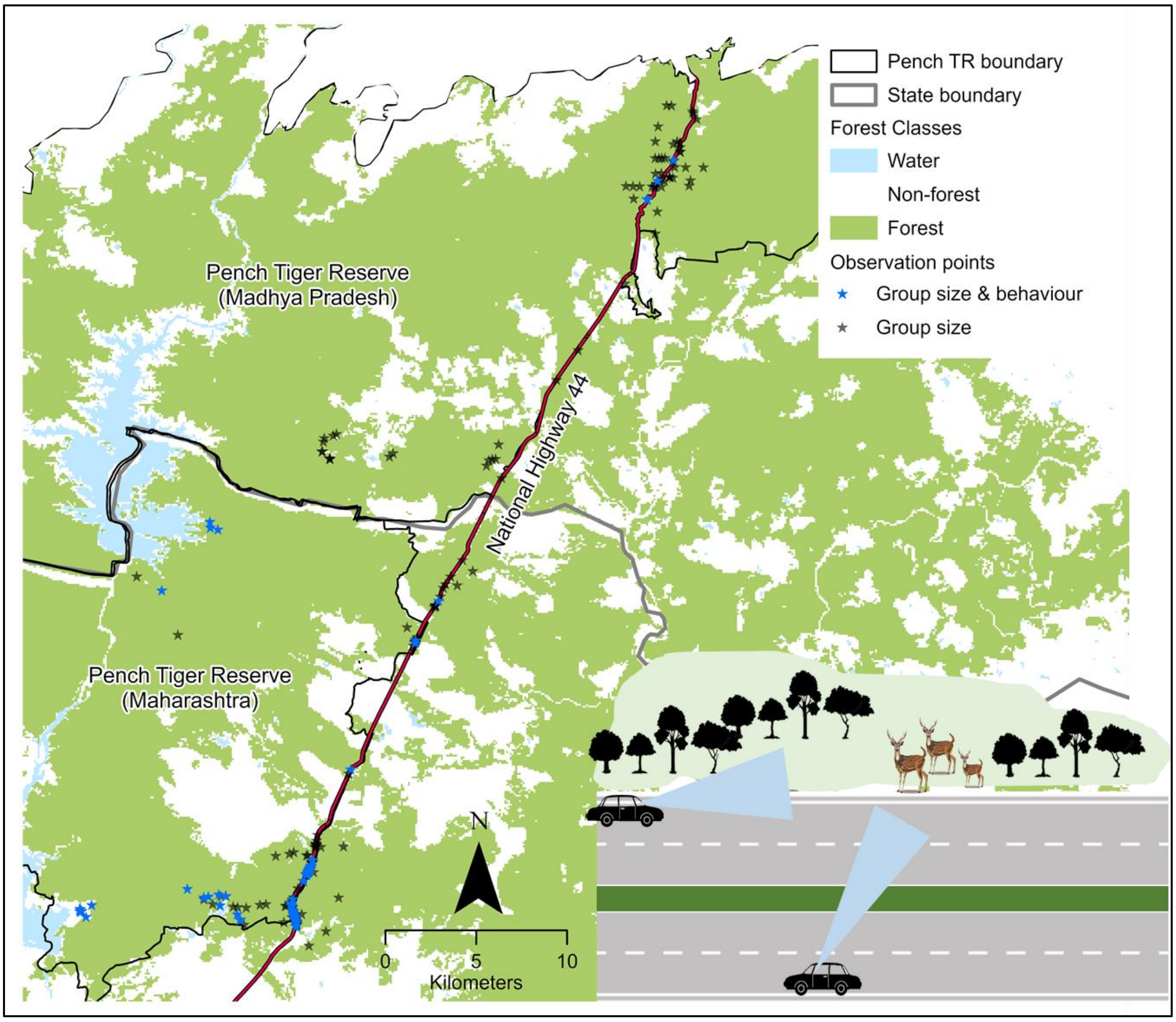

Figure 4.1. The National Highway 44 passes along the eastern boundary of the Pench Tiger Reserve, Maharashtra, and through the northern ranges of the Pench Tiger Reserve, Madhya Pradesh. Black stars indicate locations where only group sizes were recorded and blue stars indicate locations where both group size and behaviour were recorded. Behavioural data of chital (*Axis axis*) was collected through video recording of herds or individuals observed near the National Highway 44 (bottom right).

4.2.2. Analytical methods

4.2.2.1. Chital group size

I compared group sizes between roadside (2-lane and 4-lane) and control habitat using Wilcoxon rank sum test at 95% significance. Further I tested for variation of group size with increasing distance from the road and site (road type and control) using a linear model.

4.2.2.2. Chital behaviour

From the recorded behavioural data, I carried out focal sampling of as many individuals in a herd as possible (at least 80% of the herd) to assess individual behaviour and vigilance (Hirschler et al., 2016). The time spent by chital involved in different behaviours was coded using the software Cowlog 3.0.2 (Pastell, 2016). The software records the time spent on different behaviours and behaviour classes, that is then transferred to a .csv file that is used for further analysis. As a reference of chital behaviour, I used the 32 categories of behaviour (Table 4.1 *(b)*) in the ethogram constructed by Ghuman (2009) for chital in PTR, Madhya Pradesh. For the purpose of the study, I categorised all chital behaviour into three broad classes: 1. Vigilance behaviour, 2. Individual behaviour (non-vigilant), and 3. Social behaviour between interacting chital individuals (Table 4.1 *(a)*), and combined certain behaviours

Table 4.1. Chital behaviours (b) defined by (Ghuman, 2009), and their categorisation (a) and combinations (c) used for the present study.

(a) Behaviour class	*(b) Behaviour*	*(c) Behaviours combined as*
1. Vigilance behaviour	Scan, alert, smelling when alert, alarm calling	Vigilant
2. Individual (non-vigilant) behaviour	Feeding, drinking, looking for food, masticating	Feeding
	Grooming	Grooming
	Thrashing	Thrashing
	Play	Play
	Traveling, disturbed	Travel
	Resting	Rest

3. Social behaviour	Groomer, groomee	Allogrooming
	Aggressor, aggresse, physical aggression, harassed	Aggression
	Display, courtship	Courtship
	Rutting, vocalising	Vocalising
	Interacting, look at conspecific	Interaction
	Nursing	Nurse
	Spar	Spar

I estimated chital group vigilance through scan sampling of the recorded individuals every 5 minutes. Proportional group vigilance was calculated as the number of vigilant individuals divided by the total number of visible individuals:

$$Proportional\ group\ vigilance = \frac{Number\ of\ vigilant\ individuals}{Total\ visible\ individuals} \tag{1}$$

I then calculated the proportion time spent in different behavioural categories (vigilance, individual non-vigilant and social) as

$$Proportion\ time\ spent\ in\ activity = \frac{Total\ time\ spent\ in\ activity\ (s)}{Total\ time\ observed\ (s)} \tag{2}$$

This was calculated for all age-sex classes and cumulatively for chital herds in control and roadsides.

For assessing differences in chital vigilance and feeding at the two sites, I calculated the following metrics:

(a) Proportion time vigilant and feeding (equation 2).

(b) Average duration of vigilance and feeding bout:

$$Average\ duration\ of\ bout\ (s) = \frac{Time\ spent\ in\ activity\ (s)}{Number\ of\ activity\ bouts} \tag{3}$$

(c) Vigilance and feeding frequency:

$$Frequency\ of\ activity = \frac{Number\ of\ bouts}{Total\ time\ observed\ (s)} \tag{4}$$

I also calculated the frequency of vigilance events per sum of all behavioural events per observation. Finally, I assessed the influence of group size, vegetation density, time of day, proportional time feeding, average duration of feeding bout and frequency of feeding events on roadside vigilance metrics (a, b and c) using generalised linear models, assessed using AIC values. All analyses were carried out in Rstudio (RStudio Team, 2020).

4.3. Results

4.3.1. Chital group size

I observed a total of 267 chital groups within PTR (n=85) and along NH 44 (2-lane n=41, 4-lane n=141). The mean group size of chital herds in control habitat was 7.94 (5.79-10.1). The mean group size of chital herds on the roadside habitat was 6.07 (5.28-6.85), with a mean of 6.38 (5.43-7.33) near 4-lane road and 5.00 (3.79-6.21) near 2-lane (Fig. 4.2 (a) and (b)).

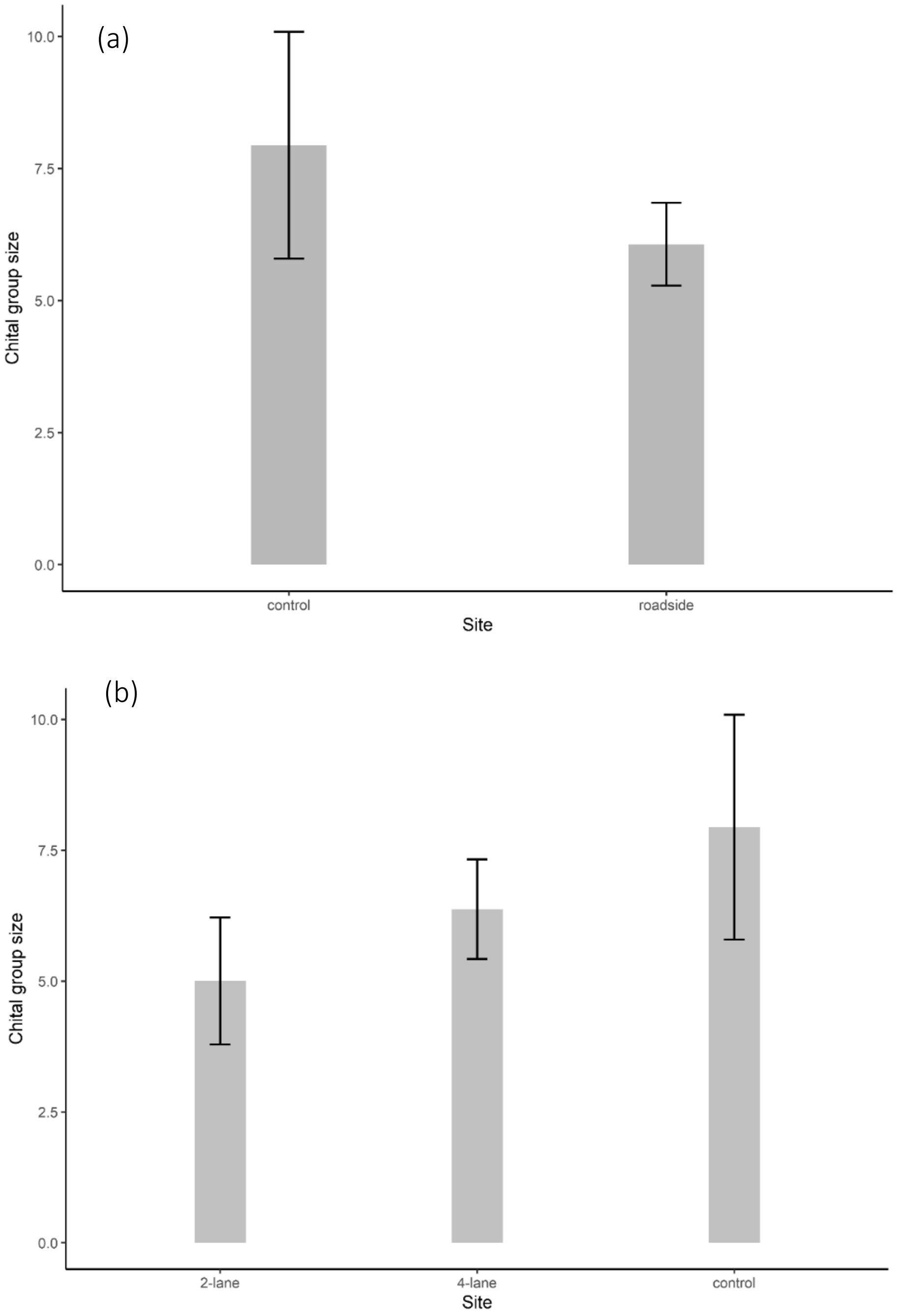

Figure 4.2. Observed chital group sizes (a) between roadside and control, and (b) 2-lane and 4-lane segments of National Highway 44 passing through Pench Tiger Reserves, Madhya Pradesh and Maharashtra. Error bars represent 95% upper and lower confidence intervals.

I found no significant difference between group sizes near roadsides (2-lane and 4-lane combined) and control habitat (Wilcoxon rank sum test p = 0.612). Consequently, the linear model did not show variation in group size with site. I found that though there was a statistically significant increase in chital group size with increasing distance to the highway (β=0.00035, SE=0.00011, p=0.0028; Fig. 4.3), distance to highway did not significantly explain this variation ($R^2 = 0.029$).

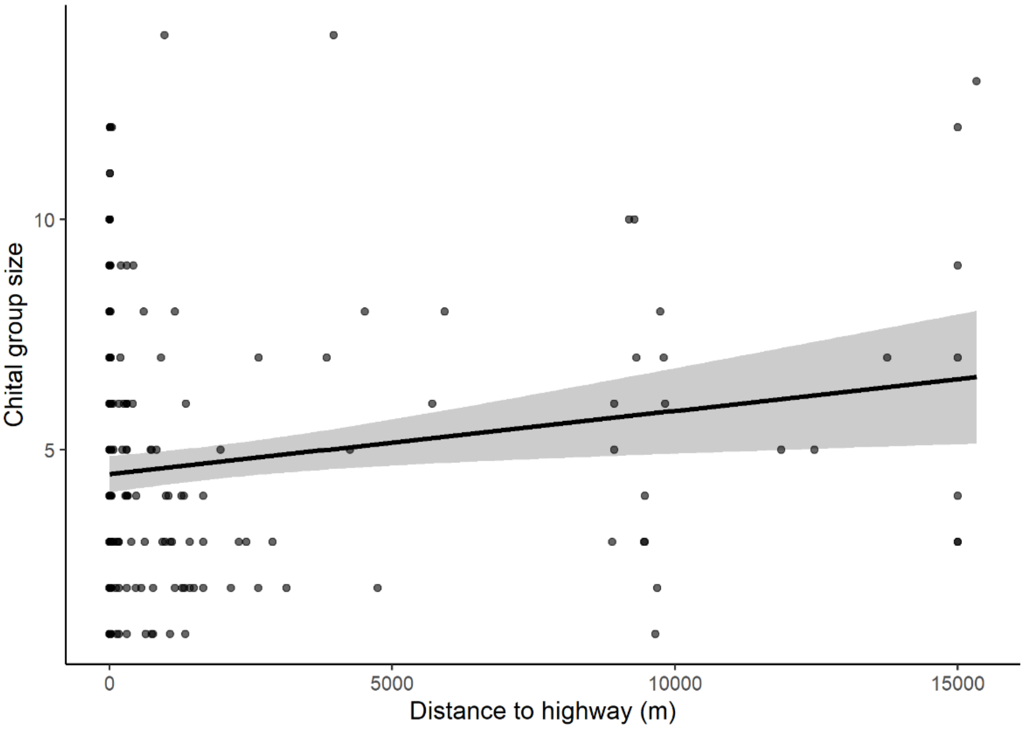

Figure 4.3. Variation in chital group size with distance to NH 44 as predicted by linear model. Solid dots represent observation data points.

4.3.2. Chital behaviour

I recorded a total of 2092.48 minutes of chital behaviour (1017.38 minutes in control and 1075.1 minutes in roadside) among 78 herds. Chital herds near the highway were observed between 1 and 150 m from the highway. Chital individuals in both sites spent a greater proportion of time in individual behaviours, followed by vigilance and social behaviours (Fig. 4.4).

Group vigilance between control and roadside site were not significantly different (Wilcoxon rank sum test p=0.687), with a mean of 0.21 and 0.23 respectively (Fig. 4.5).

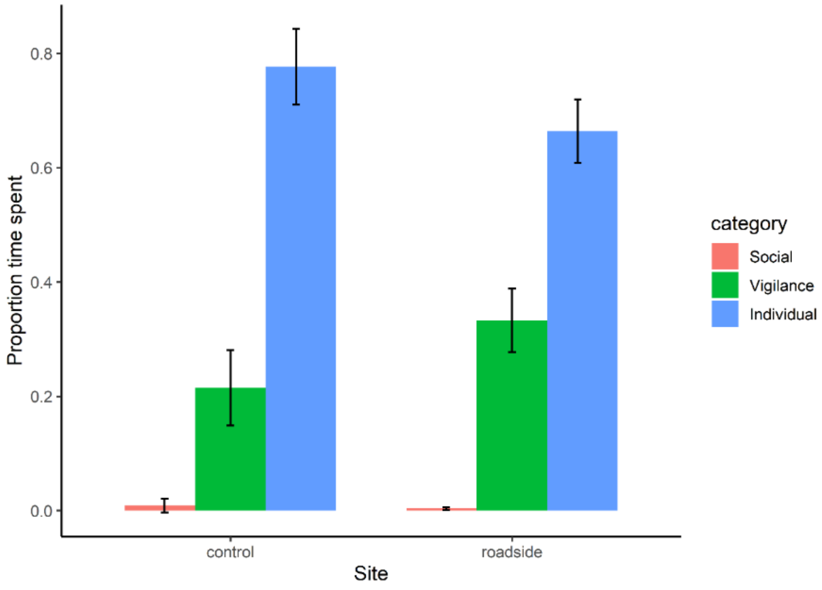

Figure 4.4. Proportion time spent in social, vigilant and individual (non-vigilant) behaviours in chital herds near National Highway 44 and inside Pench Tiger Reserve, Madhya Pradesh and Maharashtra (control). Error bars represent 95% upper and lower confidence intervals.

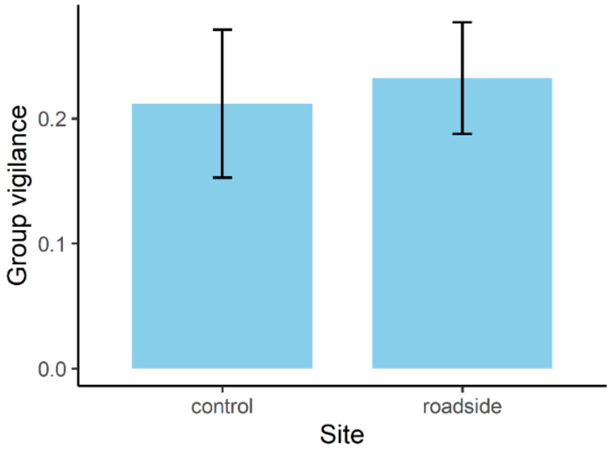

Figure 4.5. Proportional chital group vigilance between control (park) and roadside habitat (near National Highway 44). Error bars represent 95% upper and lower confidence intervals.

Adult female chital individuals near roadside spent less time in individual non-vigilant activities as compared with control (Wilcoxon rank sum test p = 0.02), while there was no significant difference between the time spent on non-vigilant behaviours within the two sites among other age-sex classes (Wilcoxon rank sum test p > 0.05). Moreover, there was no significant difference in the proportional time spent in social behaviour among any of the age-sex classes between the two sites (Wilcoxon rank sum test p > 0.05). Adult female chital were significantly more vigilant near roadside than control (Wilcoxon rank sum test p = 0.008), while proportion time being vigilant among other age-sex class individuals did not vary significantly between the two sites (Wilcoxon rank sum test p > 0.05; Fig. 4.6).

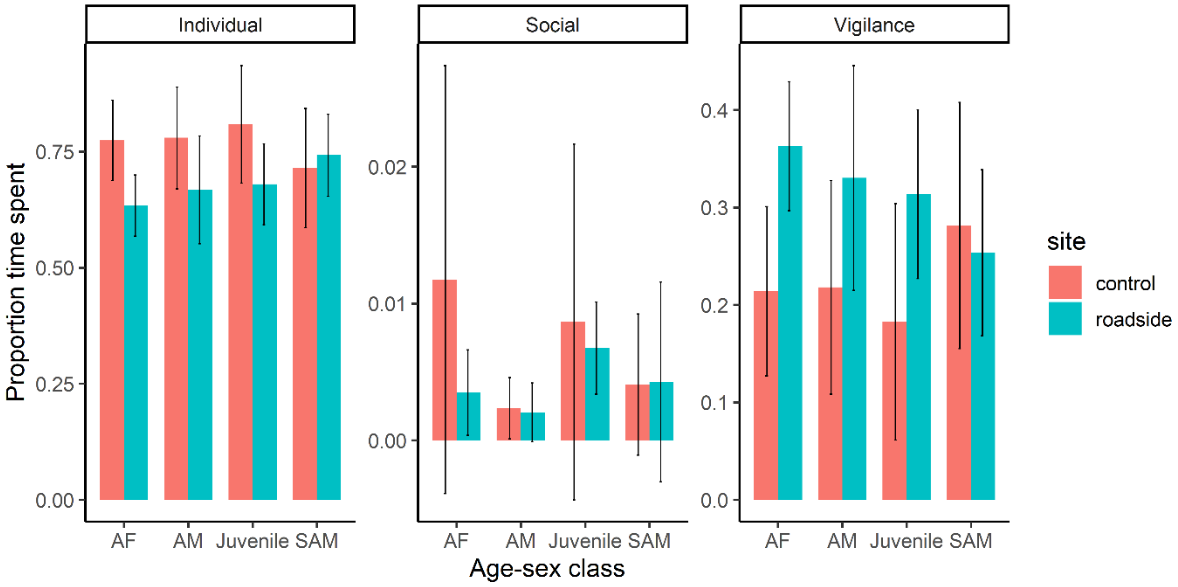

Figure 4.6. Proportion time spent in social, vigilant and individual (non-vigilant) behaviours by chital individuals belonging to different age-sex categories near National Highway 44 and inside Pench Tiger Reserve, Madhya Pradesh and Maharashtra (control). Error bars represent 95% upper and lower confidence intervals.

Within the individual non-vigilant behavioural category, I found no significant difference in proportion time spent in play, thrash, travel and feeding behaviours between the two sites (Wilcoxon rank sum test p > 0.05; Fig. 4.7). Proportion time spent grooming near roadside was significantly less than that in control (Wilcoxon rank sum test p = 0.005). Resting as an activity was not observed among chital individuals near the highway.

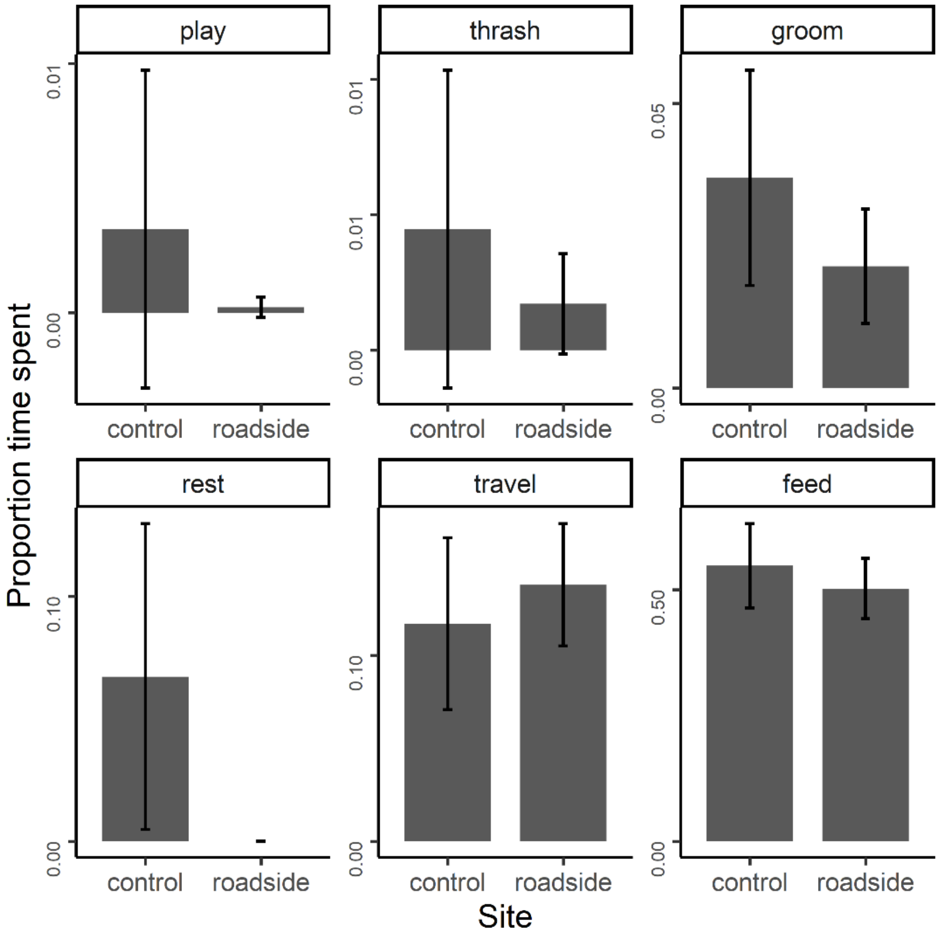

Figure 4.7. Proportion time spent by chital on different non-vigilant individual behaviours near NH 44 (roadside) and within Pench Tiger Reserves, Madhya Pradesh and Maharashtra (control). Error bars indicate 95% upper and lower confidence intervals.

Within the social behavioural category, I found no significant difference in proportion of time spent in courtship, interaction, aggression and allogrooming between the two sites (Wilcoxon rank sum test p>0.05; Fig. 4.8). No observations of chital individuals engaged in vocalisation and nursing were observed near the highway, while no observation of chital individuals sparring was observed in control.

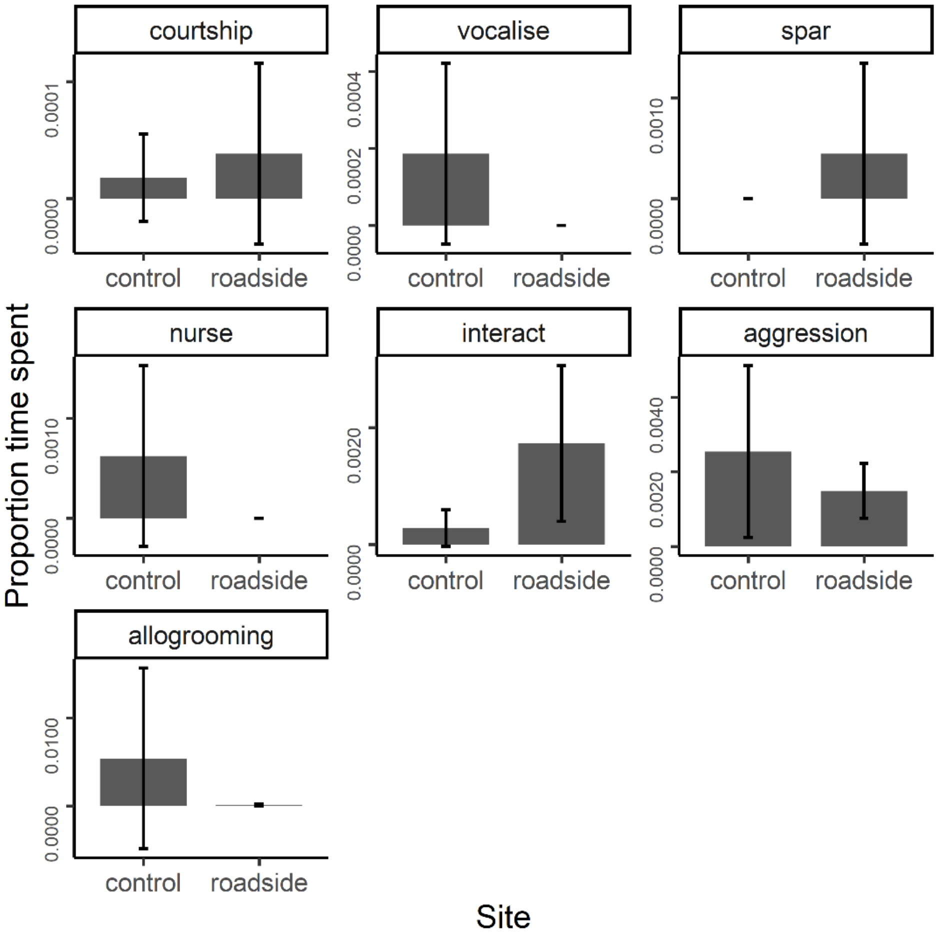

Figure 4.8. Proportion time spent by chital on different social behaviours near NH 44 (roadside) and within Pench Tiger Reserves, Madhya Pradesh and Maharashtra (control). Error bars represent 95% upper and lower confidence intervals.

Vigilance and feeding

While greater time spent being vigilant was only observed among adult female chital (Fig. 4.9), there was no significant difference in time spent feeding among any of the age-sex classes between the two sites (Wilcoxon rank sum test $p > 0.05$).

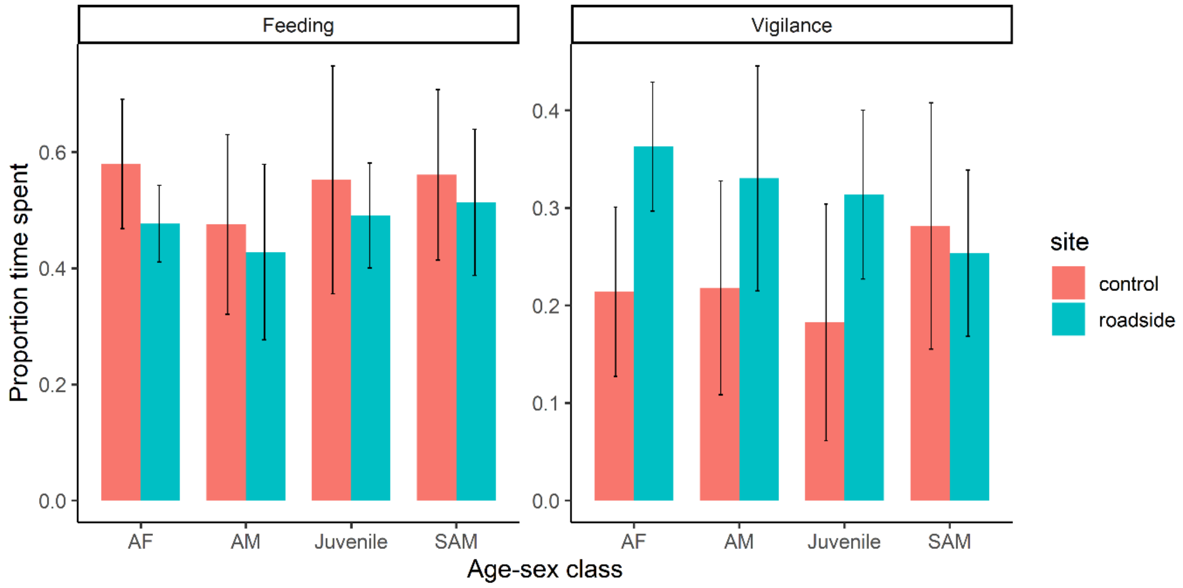

Figure 4.9. Proportion time spent in feeding and vigilance activities by different age-sex classes of chital near NH 44 (roadside) and within Pench Tiger Reserve, Madhya Pradesh and Maharashtra (control). Error bars represent 95% upper and lower confidence intervals.

Chital individuals observed in both sites did not differ in the proportion of time spent feeding (Wilcoxon rank sum test p = 0.43). However, proportion time spent by chital near the highway being vigilant was significantly greater as compared with chital in control (Wilcoxon rank sum test p = 0.006; Fig. 4.10 (a)).

Average duration of a feeding bout in control was significantly higher (19.45 s 14.82-24.08) as compared with that near the highway (11.34 s 9.58-13.11) (Wilcoxon rank sum test p=0.0009), with similar average vigilance durations (Wilcoxon rank sum test p=0.28; Fig. 4.10 (b)).

Both frequency of feeding and vigilance by chital near the highway were significantly higher than that in control (Wilcoxon rank sum test p < 0.05; Fig. 4.10 (c)). Moreover, the number of vigilance events per sum of all other events per observation were significantly higher in the roadside (Wilcoxon rank sum test p = 0.002; Fig. 4.10 (d)).

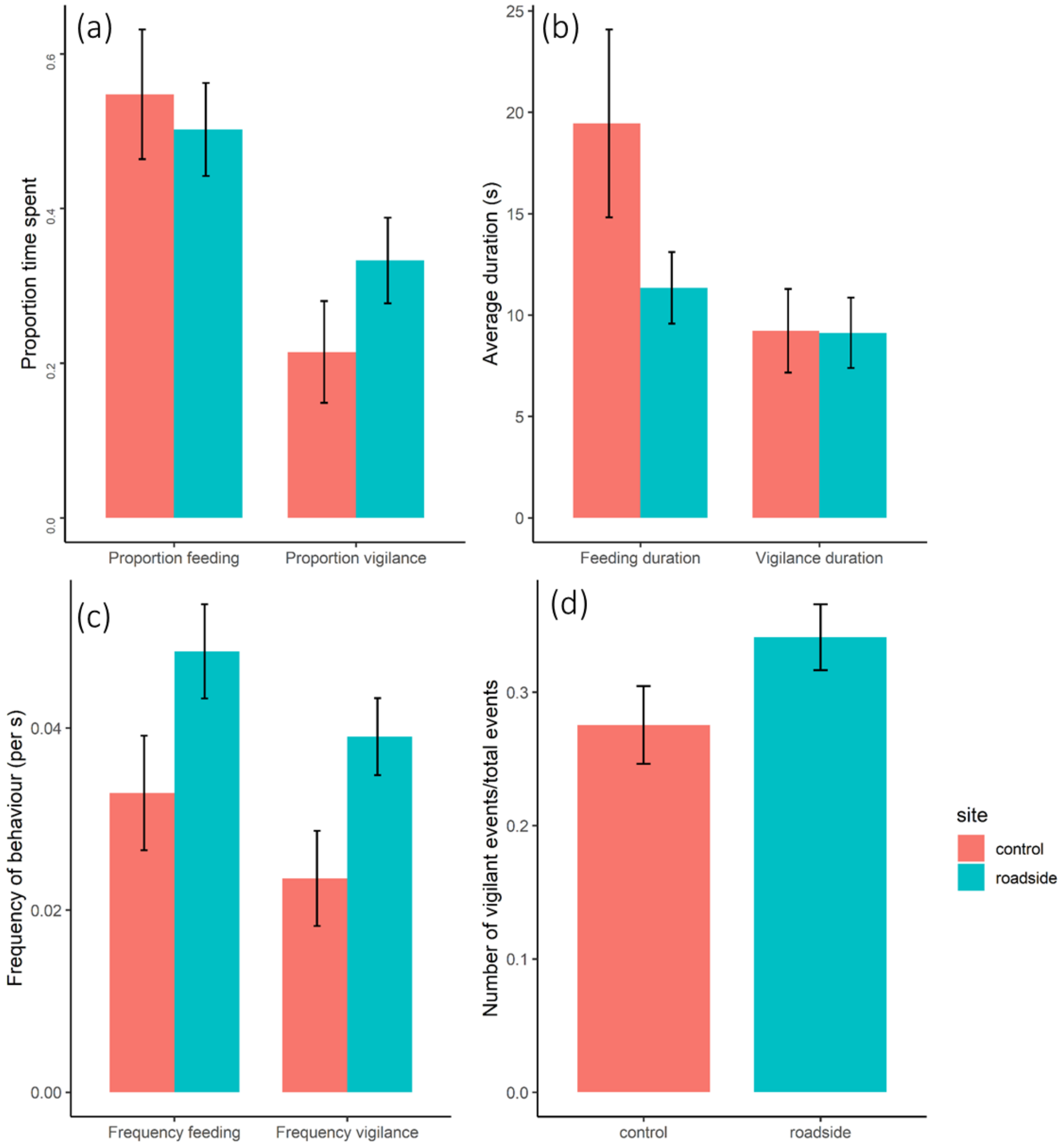

Figure 4.10. Different metrics calculated to estimate vigilance and feeding behaviour of chital near NH 44 (roadside) and within Pench Tiger Reserves, Madhya Pradesh and Maharashtra (control): (a) Proportional time spent feeding and being vigilant, (b) Average duration (in s) of feeding and vigilance bouts, (c) Frequency (per s) of feeding and vigilance bouts, and (d) Frequency of vigilance events among all behavioural events. Error bars represent 95% upper and lower confidence intervals.

Factors affecting vigilance metrics

None of the vigilance metrics (Fig. 4.10 (a-c)) were influenced by time of the day, month or season, but were highly influenced by proportion of time spent feeding and frequency of feeding events (Table 4.2). Proportion time spent being vigilant decreased with increasing chital group size, increasing proportion of feeding time and increasing frequency of feeding events. It was the lowest in low vegetation density (Fig. 4.11 (a-d)). Similarly, the average duration of a vigilance event decreased with increasing distance to the highway, chital group size, frequency of feeding events and proportion of time spent feeding (Fig. 4.12 (a-d)). Lastly, the frequency of vigilance events increased with increasing frequency of feeding events, but decreased with increasing proportion of time spent feeding. The frequency of vigilance events was lowest in low vegetation density (Figs. 4.13 (a-c)).

Table 4.2. Generalised linear model coefficients of factors influencing proportion of time vigilant, average duration of vigilance event and frequency of vigilance events for chital near National Highway 44.

	Proportion of time vigilant		**Average duration of vigilance event**		**Frequency of vigilance events**	
Predictors	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*
Intercept	**0.89** ***	**0.06**	**27.46** ***	**1.92**	**0.03** ***	**0.01**
Distance to highway (m)			**-0.04** *	**0.02**		
Group size	-0.0047$^{\cdot}$	0.0025	**-0.22** *	**0.09**		
Proportion of time feeding	**-0.73** ***	**0.06**	**-12.04** ***	**2.47**	**-0.04** ***	**0.01**
Frequency of feeding events	**-2.40** **	**0.73**	**-181.96** ***	**28.08**	**0.58** ***	**0.08**
Vegetation density: high	*Reference*		*Reference*		*Reference*	
Vegetation density: medium	-0.04	0.03			-0.0012	0.0034

Vegetation density: low	**-0.10** *	**0.04**			**-0.01** *	**0.00**
R^2	0.795		0.686		0.603	

$\cdot\ p<0.1 \quad {*}\ p<0.05 \quad {**}\ p<0.01 \quad {***}\ p<0.001$

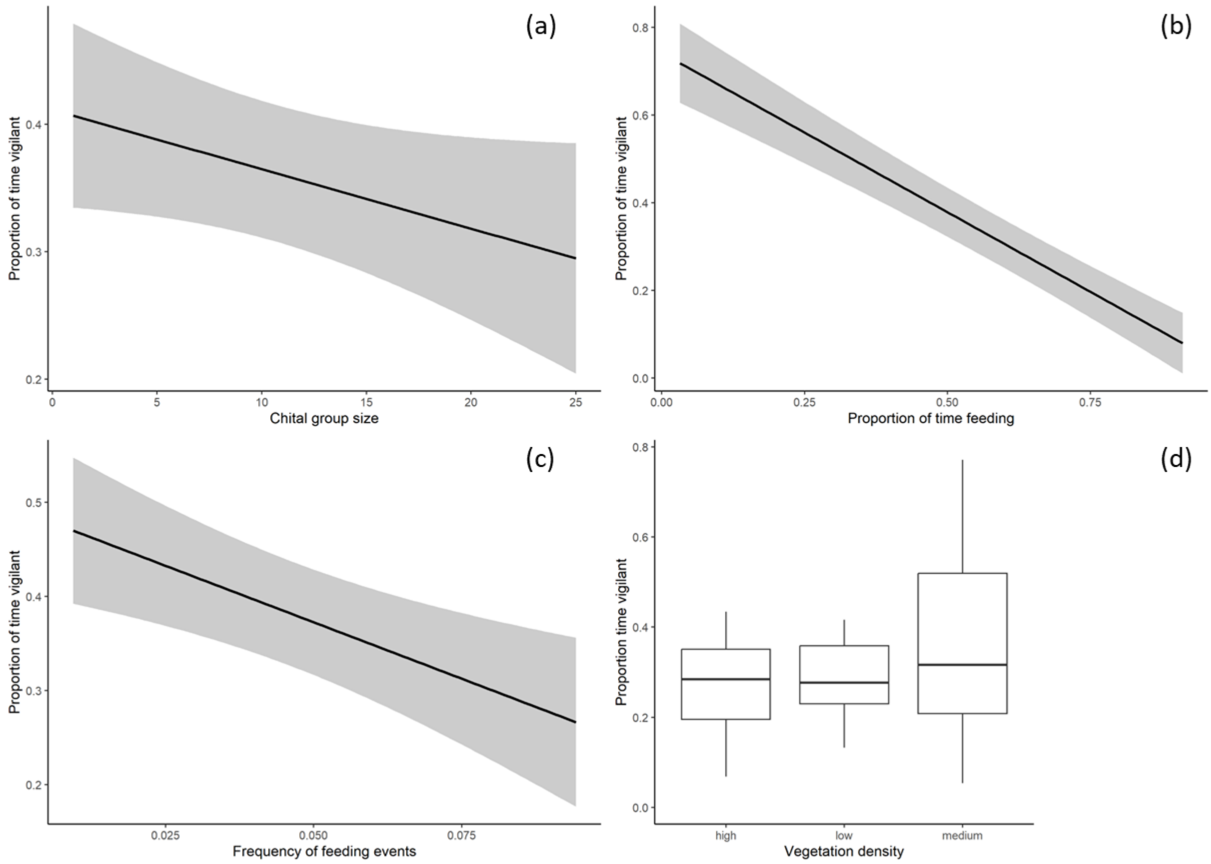

Figure 4.11. Model-derived effect plots predicting influence of (a) chital group size, (b) proportion time feeding, (c) frequency of feeding events, and (d) vegetation density on proportion of time spent by chital being vigilant near National Highway 44.

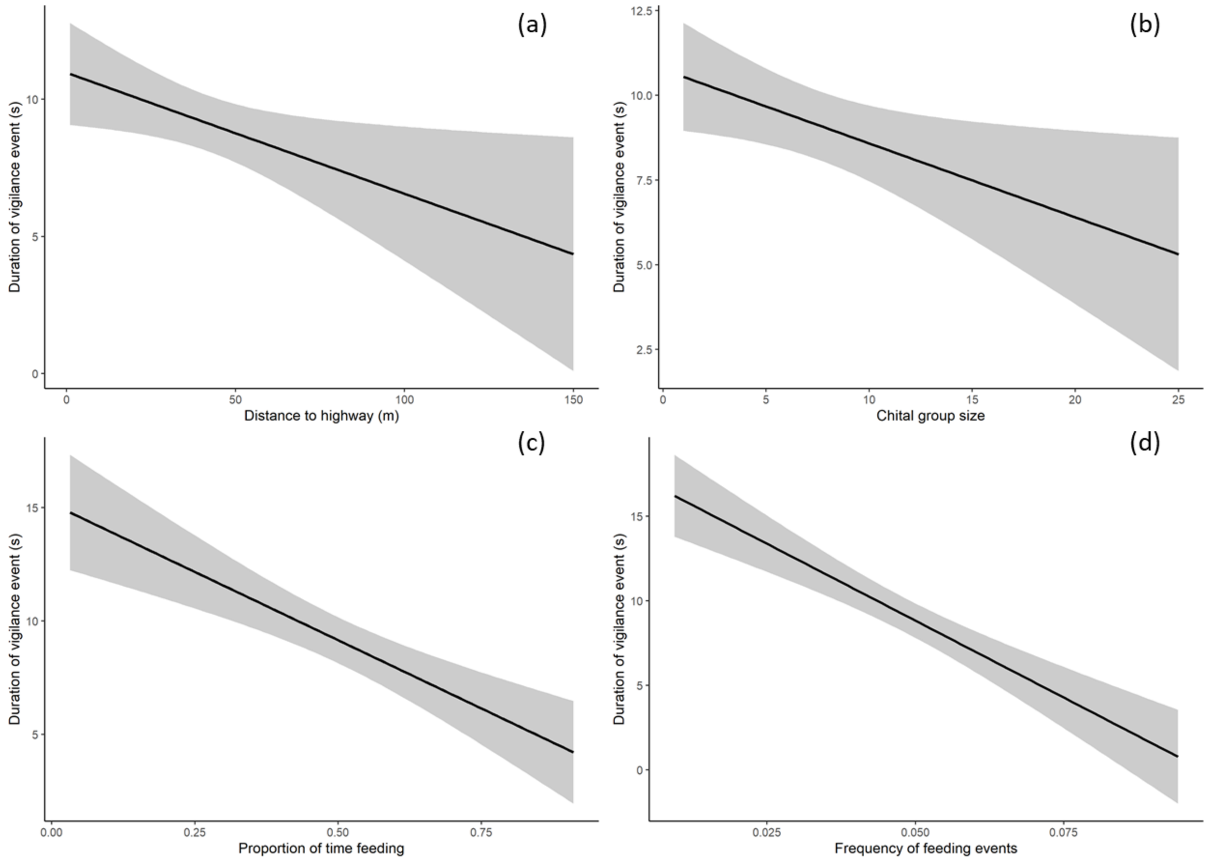

Figure 4.12. Model-derived effect plots predicting influence of (a) distance to highway (m), (b) chital group size, (c) proportion of time spent feeding, and (d) frequency of feeding events on average duration of vigilance events of chital near National Highway 44.

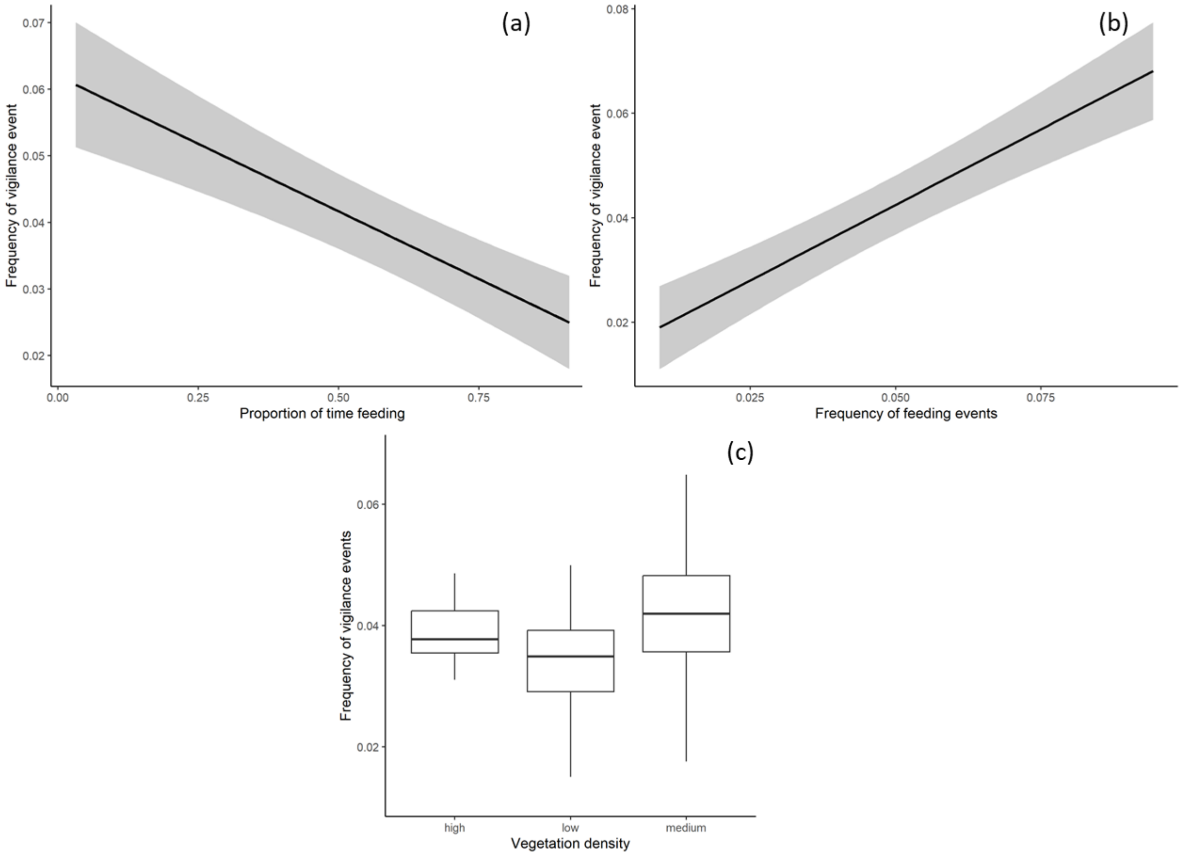

Figure 4.13. Model-derived effect plots predicting influence of (a) proportion of time spent feeding, (b) frequency of feeding events, and (c) vegetation density on frequency of vigilance events by chital near National Highway 44.

4.4. Discussion

Human infrastructure such as roads impact wildlife through multiple pathways. Of particular concern are impacts that may have long-term deleterious consequences for populations and ecosystems. While changes in animal behaviour may presently not appear lethal compared to other impacts such as roadkill, these may have population level consequences that could be evident in the long-term. Findings from such studies may lend clues to mitigate adverse impacts and help us understand the costs borne by generalists in exploiting habitats in the vicinity of human-dominated infrastructure.

Among significant findings from the roadside chital behavioural observations were the absence of resting and less proportion of time (though insignificant) spent in allogrooming as compared to control habitat. Moreover benign social interactions such nursing and vocalising (rutting calls) were absent from roadside chital observations. St. Clair and Forrest (2009) similarly reported reduced time spent by male elk exhibiting reproductive behaviour viz., sparring near roads. Decreased social interactions and social communication while trying to maximally exploit resources in human-dominated landscapes can have adverse consequences for individual fitness of social and group-living animals (Gil et al., 2017; Manor and Saltz, 2003). Further such behaviours may also decrease vigilance and increase vulnerability to predation (Loehr et al., 2005). Moreover absence of resting behaviour among animals in disturbed habitats (Naylor et al., 2009) has a direct implications for animal health.

I coded all vigilance behaviours (scan, alert, alarm calling) as one category of vigilance since it was difficult to hear alarm calls near the roadside. However, it is worth noting that alarm calls are usually associated with foot stomping, and no such event was observed among roadside chital while this was a fairly common vigilance behaviour inside PTR.

Variations between chital age-sex classes were largely insignificant with the exception of adult females allocating proportionally more time to vigilance and less time to individual non-vigilant behaviour. Similar findings have been reported in other studies, wherein females or groups with more young ones showed greater vigilance and flight responses (Ghuman, 2009; Stankowich, 2008). The female biased chital population of PTR (Majumder et al., 2013) possibly also translated to high cumulative proportional vigilance in my study. However, given the fact that the study was carried out for one year (April – December), I could not test for the effect of season, and consequently influence of breeding or calving periods, on behaviour and vigilance levels specific to age-sex categories.

Differences in perception of threats

While it is proposed that humans are perceived by wild prey in the same way as their natural predators (Frid and Dill, 2002), some variation in the anti-predator strategies directed at natural predators and humans is expected (Ciuti et al., 2012b; Proudman et al., 2020). Similar proportional feeding times and average vigilance event durations were observed between chital individuals at control and roadsides. However, both proportional vigilance time and frequency of vigilance events were higher among chital observed at the roadsides. Considered together with absence of activities such as resting, nursing, vocalising and reduced allogrooming, high proportion of vigilance behaviour could indicate that chital on the roadside possibly trade-off such activities to allocate more time to being vigilant. Lower average feeding duration and more frequent feeding and vigilance events among roadside chital further indicate a state of frequent vigilant behavioural state in response to frequently passing vehicles and associated noise (Nojoumi et al., 2022).

Ydenberg and Dill (1986) proposed an economic hypothesis of fleeing from predators in contrast to the perpetual limit hypothesis (which states that prey flee as soon as a predator is detected i.e., flight is a function of predator detection) to underline the difference between detection and response. From an economic point of view, prey would not flee as soon as a threat/predator is detected, but the flight response would be evaluated on the basis of the costs and benefits of fleeing versus remaining. This decision could also be based on the perceived lethality of the threat. Consequently, there seemed to be a difference in perception by chital of different threats posed by humans and vehicles. On the roadsides, perceived threat from passing vehicles is omnipresent given the continuous flow of traffic and percolation of traffic noise into the surrounding habitat. On the other hand, chital herds at roadsides were occasionally observed to flee when vehicles stopped in their vicinity on the highway, or when humans alighted from their vehicles on the highway. This could be because humans on foot are perceived as a greater threat than other stimuli like vehicular noise (Brown et al., 2012; Stankowich, 2008), leading chital to abandon feeding grounds at roadsides in response to humans on foot as compared to being vigilant in response to passing vehicles. This behaviour could hold solutions for mitigating roadkill of habituated or tolerant animals, for example by utilising human cues to deter animals from approaching the road surface.

Group size and vigilance

Group size is a proactive anti-predation response to use of dangerous habitats among prey species (Creel et al., 2014), with small group sizes recorded in the vicinity of roads (Gavin and Komers, 2006). I found no significant difference in group sizes between roadside sites and control, indicating that chital perceive roadsides as potentially dangerous as the control habitat. While I observed increasing group sizes with increasing distance from the highway, the increase was not significantly explained by distance from the highway, indicating other factors influencing group sizes, especially >150 m away from the highway. However at the roadside, group size was a determining factor for vigilance levels, in that larger groups showed lesser proportional time vigilant and shorter average durations of vigilance events (Puig et al., 2021). The same was observed among chital groups inside PTR, Madhya Pradesh (Ghuman, 2009). Moreover, contrary to the findings of Manor and Saltz (2003) who found no effect of large group sizes on vigilance near highly disturbed areas, I found lower proportional time vigilant and lower average duration of vigilance events in larger groups. Therefore, at present road-related disturbance levels, group size is a determining factor in chital anti-predation strategy. High frequency of vigilance and feeding bouts among roadside chital were observed. This effect was independent of group size, contrary to the findings of Berger (1978), who found that smaller groups experienced greater interruptions in foraging to scan surroundings for predators.

The trade-off between feeding and being vigilant on roadsides

Feeding (control 65%, roadside 52%) and vigilance (control 15%, roadside 29%) were the behaviours to which most time was allocated both in control and roadside respectively. While vigilance helps decrease the risk of mortality (Creel et al., 2014), it also involves forgoing other fitness enhancing activities such as foraging. All three vigilance metrics viz., proportional vigilance time, average duration of vigilance events, and frequency of vigilant behaviour, increased with decreasing proportional time feeding. A direct implication of this finding is that the cost of remaining vigilant near roadsides directly translated to loss of feeding opportunity, i.e., within a limited time budget, chital on the roadside have to continually choose between feeding more or being more vigilant. This is contrary to the findings of Shannon et al. (2014) who found higher feeding and lower vigilance levels near high traffic roads.

Why do chital use roadsides despite high vigilance costs?

A possible reason behind the use of roadside habitat by chital despite the aforementioned costs of being vigilant could be disturbance-induced absence of predators from such areas (Kuijper et al., 2016), that can cause prey species such as chital to exploit these predator-free areas (Laurian et al., 2015). Thus, greater presence of ungulates in disturbed habitats can be an indicator of the absence of disturbance-sensitive predators. While predator presence did increase after construction of mitigation measures on NH 44, it was still relatively less than that in the absence of road-related disturbance within PTR (Chapter 3). Moreover, chital foraging on roadsides could also be explained by the reduced presence of other members of the herbivore guild that may compete for foraging resources (Chapter 3). Overall, chital increase their vigilance levels and modify their activity levels near roadsides, but do not significantly alter space use patterns (St. Clair and Forrest, 2009). However I did not assess vegetation or forage quality during the study, which may also have a bearing on the use of roadside habitat by chital (Benhaiem et al., 2008).

Implications of roadside habitat by chital

The most direct management relevance of chital behaviour near roadsides can be increased vulnerability to chital-vehicle collisions because of apparent non-flight response to moving vehicles. Chital management at the roadsides may include fencing to reduce occurrence of roadkill, and the use of human cues to dissuade individuals from accessing the road corridor. On the other hand, habituation/tolerance of road-related disturbance by chital is the probable reason why chital were among the first mammals to start using wildlife crossing structures on the highway, and also among the most frequent users (Saxena and Habib, 2022). Consequently adaptation of chital to human-disturbance could also enable ecosystem processes like movement and gene flow to persist (Wilson et al., 2020).

The long-term ecological consequences of human-induced behavioural changes in wildlife may not be evident or realised, or translate to detectable change (Wilson et al., 2020). While chital use of roadside habitat, albeit with highly costly vigilance behaviour, could be a consequence of predation release, it could also be a maladaptive strategy with long-term deleterious consequences (Courbin et al., 2022). According to a review by Blumstein (2016), habituation is defined as the decreased responsiveness to stimulus, making it unlikely that individuals will respond to harmless stimulus. In contrast, sensitisation is the increased responsiveness to stimulus that may be adaptive and help animals avoid potentially risky or costly situations. Consequently, tolerance to human presence may be exhibited by some animals that are habituated i.e., they allow close approach by humans. Apparent tolerance to human disturbance may not always be a consequence of habituation, such as in cases where resources are limited forcing sensitised animals to approach disturbed areas. Heightened responses to disturbance may thus be recorded among such individuals. Considering these factors, chital on the roadsides may be tolerant of apparently non-lethal human disturbance (vehicular traffic), but with sensitisation of human approach (humans on foot) which may be the reason behind heightened vigilance responses i.e., flight (Stankowich, 2008).

Presently, the most probable consequences of altered behaviour of chital near roadsides include behavioural, social and fitness costs in terms of lack of resting, inter-group interaction and foraging opportunities. 'Noise-masking' or loss of communication among wildlife because of anthropogenic noise (through absence of rutting call behaviour near roadside) is a potential mechanism of species loss. This could also interfere with anti-predator strategies near roadsides (Grade and Sieving, 2016), although the effect on large mammals has not been studied (Duquette et al., 2021). Non-expression of behaviours such as vocalising (rutting calls by males) not only indicates chital forgoing such activities for allocating more time to vigilance, it also points to decreased vocal communication between and among herds. However empirical pathways through which these impacts may have ecological consequences remain unstudied (Wilson et al., 2020).

The study was carried out in the vicinity of a protected area, i.e., a relatively large intact and unfragmented habitat patch. Moreover, considering no obstruction to chital movement between the roadside and undisturbed habitat, effects such as population declines caused by road mortality, excessive loss of vegetation because of increased foraging and loss of sociality, and interspecific interactions can be buffered. However, the consequences of long-term impacts of such behavioural change can be greater in fragmented landscapes with greater spatial extent of roads and without large habitat patches to buffer or offset these impacts. Further studies linking behaviourally-mediated impacts of human presence in natural areas on wildlife are required to assess long-term population scale consequences for wildlife, if any (Wilson et al., 2020).

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Chapter 5

Ungulate use of habitat near roads in the central Indian landscape and species-specific road-effect zones under different road and traffic scenarios

5.1. Introduction

Large mammals are most vulnerable to negative effects of roads owing to biological and ecological traits like large body size and movement rates, and low reproductive rates and natural densities (Fahrig and Rytwinski, 2009; Rytwinski and Fahrig, 2012). High daily movement rates increase the probability of individuals encountering roads, while low natural densities and reproductive rates make it difficult for such populations to recover from barrier and mortality effects (Rytwinski and Fahrig, 2011). In addition, behavioural responses such as avoidance of roads and roadside habitat at spatial and temporal scales lead to loss of habitat, and impede daily activity and movement of animals between habitat patches (D’Amico et al., 2015; de Oliveira, 2018; Dyer et al., 2002; Wattles et al., 2018) – leading to the road acting as a barrier. The consequent barrier effect could be a result of avoidance of the physical road surface, avoidance of traffic emissions such as noise, and avoidance of cars and vehicular traffic (D’Amico et al., 2015; Jaeger et al., 2005a). Thus, varying perception of risk from different road related variables defines wildlife responses to roads and traffic, creating varied levels of barrier effect. Additionally, roads can decrease prey persistence by increasing access by humans, and consequently affect large carnivore conservation (Espinosa et al., 2018; Li et al., 2017; Xiao et al., 2018). Other factors influencing variations in responses to roads include road width and surface types (Cappa et al., 2019; Loosen et al., 2021; Schroeder et al., 2018), and human activity (hunting, harassment; (Marino et al., 2012)).

At the same time, some ungulates have been found to exhibit tolerance or habituation over a period of time to road-related disturbance (Boyle et al., 2020; Munro et al., 2012). Such effect of roads and traffic has been theorised to be the result of a combination of factors, including attraction to roadside habitat for forage, cognitive ability to avoid vehicles and tolerate non-lethal ‘predictable human behaviour’ on roads (Jacobson et al., 2016; Shannon et al., 2014), tolerance of traffic emissions and disturbance, and the negative effect of roads on the preys’ primary predators , leading to a ‘predator release’ situation (Berger, 2007; Kuijper et al., 2016). Greater tolerance of human presence and footprint by ungulates is attributed to the perceived role of humans in regulating predator presence, or providing a shelter from carnivores (Brown et al., 2012; Shannon et al., 2014; Stankowich, 2008). Moreover, differential responses to roads at the same site among different species in mammal communities have also been observed (Boyle et al., 2020; Newmark et al., 1996). The spatial extent of the spread of significant ecological impacts of roads that extend beyond the physical road infrastructure, such as avoidance and habitat use alterations, is termed the ‘road effect zone’ (hereafter REZ) (Forman and Deblinger, 2000). The concept has gained recognition worldwide as a means to quantify the effect of roads on ecosystems, floral and faunal species and communities (Boarman and Sazaki, 2006; He et al., 2019; Jones et al., 2016; Torres et al., 2016). Variation in species REZ estimates for different species has been attributed to species-specific responses to these disturbances with respect to animal behaviour and ecology, and landscape and road characteristics (Boarman and Sazaki, 2006; Eigenbrod et al., 2009; He et al., 2019; Jacobson et al., 2016; Jaeger et al., 2005b; Shanley and Pyare, 2011). The REZ has also been found to vary with road density and season (Wattles et al., 2018), and human activity and traffic load on roads (Polfus et al., 2011). The earliest estimates of the extent of the REZ were made by (Forman, 2000), wherein he expected the REZ to further increase through the inclusion of effects of roads on wildlife corridors, small fragmented habitats and animal populations, and human access to remote areas. Recently, REZ have been estimated for endangered and critically endangered mammals using modelled species densities (Andrasi et al., 2021), and coefficients of the effect of distance to roads on predominantly North American and European mammals (Benítez-López et al., 2010; Carter et al., 2020).

I aimed to determine the effect of road-related factors on presence of four ungulate species in habitats near roads, and subsequently determine species-specific REZ for these species in the central Indian landscape. I selected four common ungulates that are among the prey species of the tiger and other large predators in the Central Indian landscape (Ghaskadbi et al., 2022; Majumder et al., 2013) – chital or spotted deer *Axis axis*, gaur *Bos gaurus*, sambar *Rusa unicolor* and wild pig *Sus scrofa*. I expected varied responses to different road types among the study species, reduced road effects away from roads and in the vicinity of protected areas, and decreased habitat use near wide roads. I postulate that in addition to representing the negative impacts of roads on mammals, quantifying the REZ for prey species positively affected by roads is important for managing consequences of roadside habitat exploitation viz., increased roadkill risk and long-term trophic cascades.

5.2. Methodology

5.2.1. Field methods

I selected 10 forest sites near different road types within and outside PAs/TRs in CIL (Table 5.1) to sample for ungulate presence in the forested habitat on both sides of the roads (Fig. 5.1). I walked 2 km long transects spaced 500 m apart perpendicular to the roads (Fig. 5.1 [inset]). I collected ungulate presence data from circular pellet plots of 10 m radius spaced 250 m apart on the transects. On each pellet plot, I noted down presence or absence of ungulates based on their pellets/droppings, the GPS location of the plot and location of the plot in terms of protection status of the forest viz., ‘core’ and ‘buffer’ zones in TRs, and ‘other’ forests that were outside the TRs.

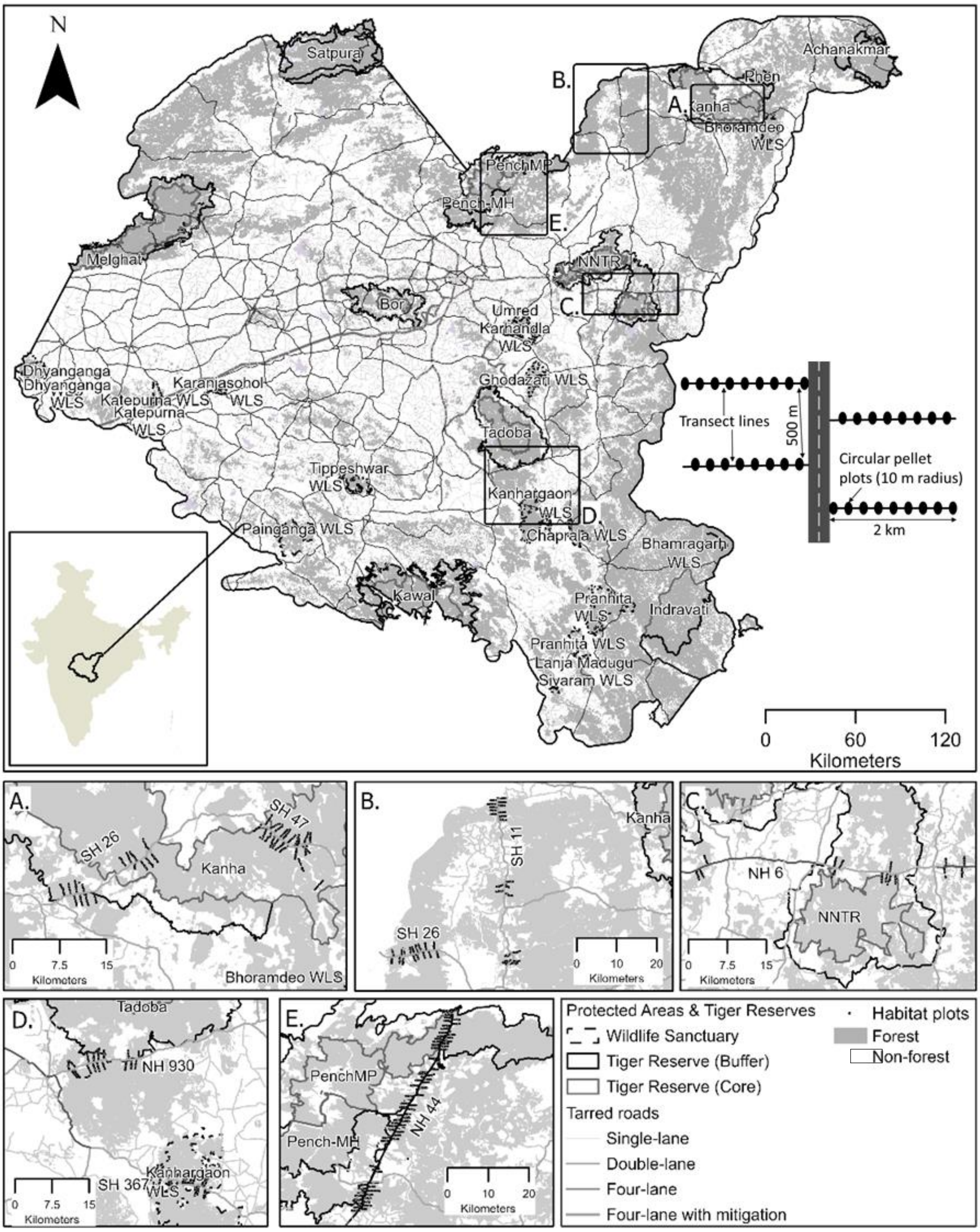

Figure 5.1. Study area in the central Indian landscape and sampling design (Top), and intensive study sites where ungulate presence near roads were sampled: (A) State Highway 26 passing through Khapa, Mukki, and Supkhar ranges of Kanha Tiger Reserve, (B) State Highway 26 and State Highway 11 passing through the Pench-Kanha corridor (Balaghat and Barghat Forest Divisions), (C) National Highway 6 passing through the

Navegaon-Nagzira Tiger Reserve, (D) National Highway 930 passing through the Tadoba-Andhari Tiger Reserve, and State Highway 367 passing through Kanhargaon Wildlife Sanctuary (present), both intersecting the Tadoba-Indravati corridor, and (E) National Highway 44 (earlier NH 7) passing near the Pench Tiger Reserves, Madhya Pradesh and Maharashtra states and intersecting the Pench-Kanha (Madhya Pradesh side) and the Pench-Navegaon-Nagzira (Maharashtra) corridors.

Table 5.1. Details of sites near roads surveyed in Central India. Site ID refers to site represented in Figure 5.1.

Site ID (in map)	***Location***	***Site ID***	***Name of highway***	***Road type***	***Traffic level***	***Number of plots surveyed***
A	Kanha Tiger Reserve	Khapa	State Highway 26	2-lane	Medium	65
		Mukki	State Highway 26	2-lane	Low	63
		Supkhar	State Highway 47	1-lane	Low	172
B	Balaghat and Barghat Forest Divisions, Pench-Kanha corridor, Madhya Pradesh	Balaghat	State Highway 11	2-lane	Medium	175
		Nainpur	State Highway 26	2-lane	Medium	139
C	Navegaon-Nagzira Tiger Reserve	NNTR	National Highway 6	2-lane	High	94
		NNTR	National Highway 6	4-lane	High	29
D	Tadoba-Andhari Tiger Reserve	Tadoba	National Highway 930	2-lane	High	147
	Kanhargaon Wildlife Sanctuary*	Kanhargaon	State Highway 367	2-lane	Medium	169
E	Pench Tiger Reserve, Madhya Pradesh	Pench_MP	National Highway 44	2-lane	High	336
	Pench Tiger Reserve, Maharashtra	Pench_MH	National Highway 44	4-lane (before mitigation)	High	277
	Pench Tiger Reserve, Maharashtra	Pench_MH	National Highway 44	4-lane with mitigation	High	169

*at the time of the study (2018), Kanhargaon Wildlife Sanctuary was under the Forest Development Corporation of Maharashtra involved in forestry activities for timber and other forest products.

5.2.2. Analytical methods

5.2.2.1. Factors affecting habitat use by ungulates near roads

For each pellet plot, I extracted forest type (open forest, moderately dense and dense forest type, ("Bhuvan | ISRO's Geoportal | Gateway to Indian Earth Observation," 2016)), terrain roughness (calculated from the Digital Elevation Model ("Bhuvan | ISRO's Geoportal | Gateway to Indian Earth Observation," 2016)), Euclidean distances (in m) to nearest PA/TR, human settlement, and water body using ArcGIS Pro (ESRI Inc., 2021), Normalised Differential Vegetation Index (NDVI, (Didan, 2021)), mean annual precipitation (MAP), mean annual temperature (MAT) (Fick and Hijmans, 2017), and evapotranspiration rate (ET, (Running et al., 2021)). Protection level of forests in which pellet plots were surveyed were assigned as: 'core' and 'buffer' zones within TRs, PAs as 'buffer', and all other forests as 'other'. Road related variables included road type (number of lanes), distance to reference road, distance to nearest tarred road and density of tarred roads (m/km^2), extracted using the Open Street Map dataset of roads ("OpenStreetMap").

I assessed correlation between continuous independent variables using function *chart.Correlation* in R package PerformanceAnalytics (Peterson and Carl, 2020) and dropped highly correlated variables (>|0.7|) from further analysis. Then, for each species, I tested for the effect of the environmental and road-related variables on the presence or absence of the species' signs in the plot (response variable) using generalised linear mixed models in R package glmmTMB (Magnusson et al., 2020) with binomial error distribution and a logit link function. I used site ID as a random variable to account for inter-site variation. Interactions between road type and protection level with distance to tarred road were also used as independent variables. Model performance was assessed using AIC and

ΔAIC values. I averaged models with ΔAIC < 2 using function *modelaverage* in package MuMIn in R (Barton, 2020).

5.2.2.2. Estimation of species-specific road effect zones (REZ)

I predicted ungulate presence probabilities from the best performing models for the study area at 500 x 500 m pixel resolution under four scenarios:

(a) *Present scenario*: ungulate presence probabilities under present road conditions.

(b) *No road scenario*: the potential presence probabilities in the absence of roads in the landscape were calculated by substituting the value of road-related variables with values with the least impact on species presence. For example, the value for distance to road for different species in this scenario was set as the distance at which the species presence probability was the highest (from (a)).

(c) *Road up-gradation to 4-lane without mitigation measures*: presence probabilities were calculated by assuming up-gradation of all 2-lane roads in the landscape to 4-lane road without any mitigation measures.

(d) *Road up-gradation to 4-lane with mitigation measures on all roads*: presence probabilities were calculated by assuming up-gradation of all 2-lane roads in the landscape to 4-lane road with mitigation measures.

For each road development scenarios (a, c and d), I subtracted the potential presence probabilities (from b) to estimate ungulate habitat potentially lost. I defined the REZ as the area near the road up to which the presence probabilities of individual ungulate species declined between 40 and 60% compared to the no-roads scenario. Potential habitat lost under different road development scenarios was thus calculated as the area (in %) in the landscape where presence probabilities declined by 40-60% compared to no-roads scenario. All analyses were done in R-Studio (“RStudio | Open source & professional software for data science teams - RStudio,” 2020), Microsoft Excel and ArcGIS Pro (ESRI Inc., 2021).

5.3. Results

I surveyed 1835 pellet plots within 10 study sites. I detected chital (896), sambar (559), wild pig (138) and gaur (128) signs in 52%, 32.5, 8% and 7.4% of the surveyed plots respectively. I observed high negative correlation between distance to nearest tarred road and density of tarred roads (-0.75), therefore density of tarred roads was not used as an explanatory variable.

5.3.1. Factors affecting habitat use by ungulates near roads

I found differential influences of environmental and road-related variables on ungulate presence probabilities near roads (Table 5.2 and Fig. 5.2). Inclusion of traffic volume (categorical independent variable) in the models led to model non-convergence, and therefore were not found in any of the top models. Interactive effects between road and environmental covariates better explained the presence probabilities of chital and gaur.

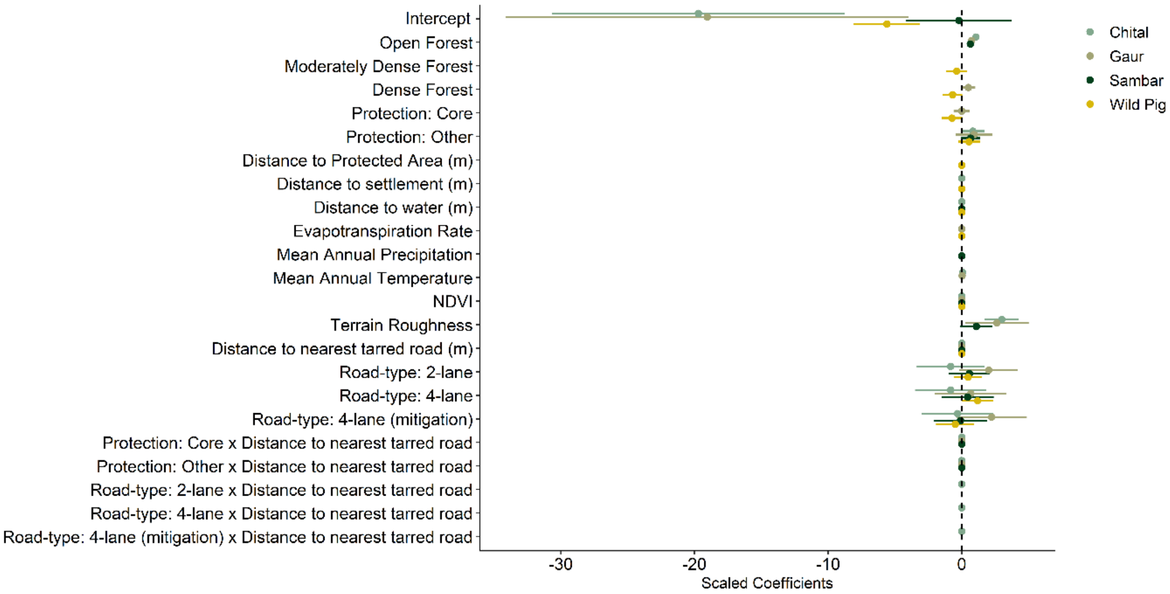

Figure 5.2. Scaled coefficients showing effect of road and environmental variables on presence probabilities of four common ungulates (chital, gaur, sambar and wild pig) in the central Indian landscape.

Table 5.2. Model averaged coefficients explaining presence of four ungulate species near roads in the central Indian landscape.

	Chital		Gaur		Sambar		Wild pig	
Predictors	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*	*Estimate*	*SE*
(Intercept)	-19.71113 ***	5.58121	-19.05702 *	7.68295	-0.20413	1.97232	-5.61641 ***	1.25499
Open forest							-0.39243	0.39705
Moderately dense forest			0.48424	0.26857			-0.68976	0.37172
Dense forest			-0.01810	0.30321			-0.73487	0.39585
Protection: Buffer	*Reference*		*Reference*		*Reference*		*Reference*	
Protection: Core	0.82914	0.42984	0.91815	0.70537	**0.93223** **	**0.32175**	0.53448	0.41660
Protection: Other	-0.41374	0.25497	**-1.56644** ***	**0.47577**	-0.34294	0.21104	**0.54334** *	**0.25347**
Evapotranspiration rate			**0.00035** **	**0.00012**			-0.00019	0.00010
Mean Annual Temperature	**0.06580** **	**0.02061**	0.02995	0.02790				
NDVI	**0.00047** ***	**0.00010**	0.00047	0.00024	**0.00073** ***	**0.00012**	**0.00057** ***	**0.00016**
Mean Annual Precipitation					**-0.00516** ***	**0.00145**		
Distance to PA							**-0.00002** *	**0.00001**
Distance to settlement	**-0.00012** **	**0.00004**					-0.00006	0.00004
Distance to water	-0.00008	0.00004			-0.00005	0.00004	0.00008	0.00004
Terrain roughness	**2.98857** ***	**0.64617**	**2.62289** *	**1.21964**	1.06981	0.61331		
Distance to nearest road	**-0.00110** *	**0.00049**	-0.00036	0.00035	0.00021	0.00016	**0.00032** *	**0.00016**
Road type: 1-lane	*Reference*		*Reference*		*Reference*		*Reference*	
Road type: 2-lane	-0.83956	1.28985	2.01454	1.11681	0.52144	0.77982	0.46159	0.52617
Road type: 4-lane	-0.83829	1.35403	0.66166	1.36362	0.37266	1.00501	**1.17794** *	**0.60006**

Road type: 4-lane_mitigated	-0.32954	1.37772	2.22646	1.34747	-0.16575	1.01570	-0.49452	0.73318
Protection: Core x distance to nearest road	**0.00099** *	**0.00041**	-0.00005	0.00053	0.00042	0.00029		
Protection: Other x distance to nearest road	0.00019	0.00025	**0.00144** ***	**0.00043**	0.00029	0.00025		
Road type: 2-lane x distance to nearest road	**0.00092** *	**0.00045**						
Road type: 4-lane x distance to nearest road	**0.00137** *	**0.00055**						
Road type: 4-lane_mitigated x distance to nearest road	**0.00134** *	**0.00062**						
Random Effects								
σ^2	3.29		3.29					
τ_{00}	1.11 $_{\text{siteID}}$		0.52 $_{\text{siteID}}$					
ICC	0.25		0.14					
N	10 $_{\text{siteID}}$		10 $_{\text{siteID}}$		10 $_{\text{siteID}}$			
Observations	1835		1705		1835		1835	
Marginal R^2 / Conditional R^2	0.159 / 0.371		0.256 / 0.358		0.194/0.282		0.104 / 0.379	

** p<0.05   ** p<0.01   *** p<0.001*

Chital

Chital presence probability was positively influenced by NDVI, mean annual temperature and terrain roughness, and negatively influenced by distance to human settlement. While increasing distance to road generally decreased chital presence probabilities, interaction between distance to road and protection type of roadside forest, and that between distance to road and road type better explained chital presence probabilities near roads. Chital presence probability near buffer and other forest protection type significantly declined with increasing distance to roads, and was highest near core roadside habitats. Moreover, while chital presence probabilities declined with increasing distance to 1- and 2-lane roads, it increased with increasing distance to 4-lane roads with and without crossing structures.

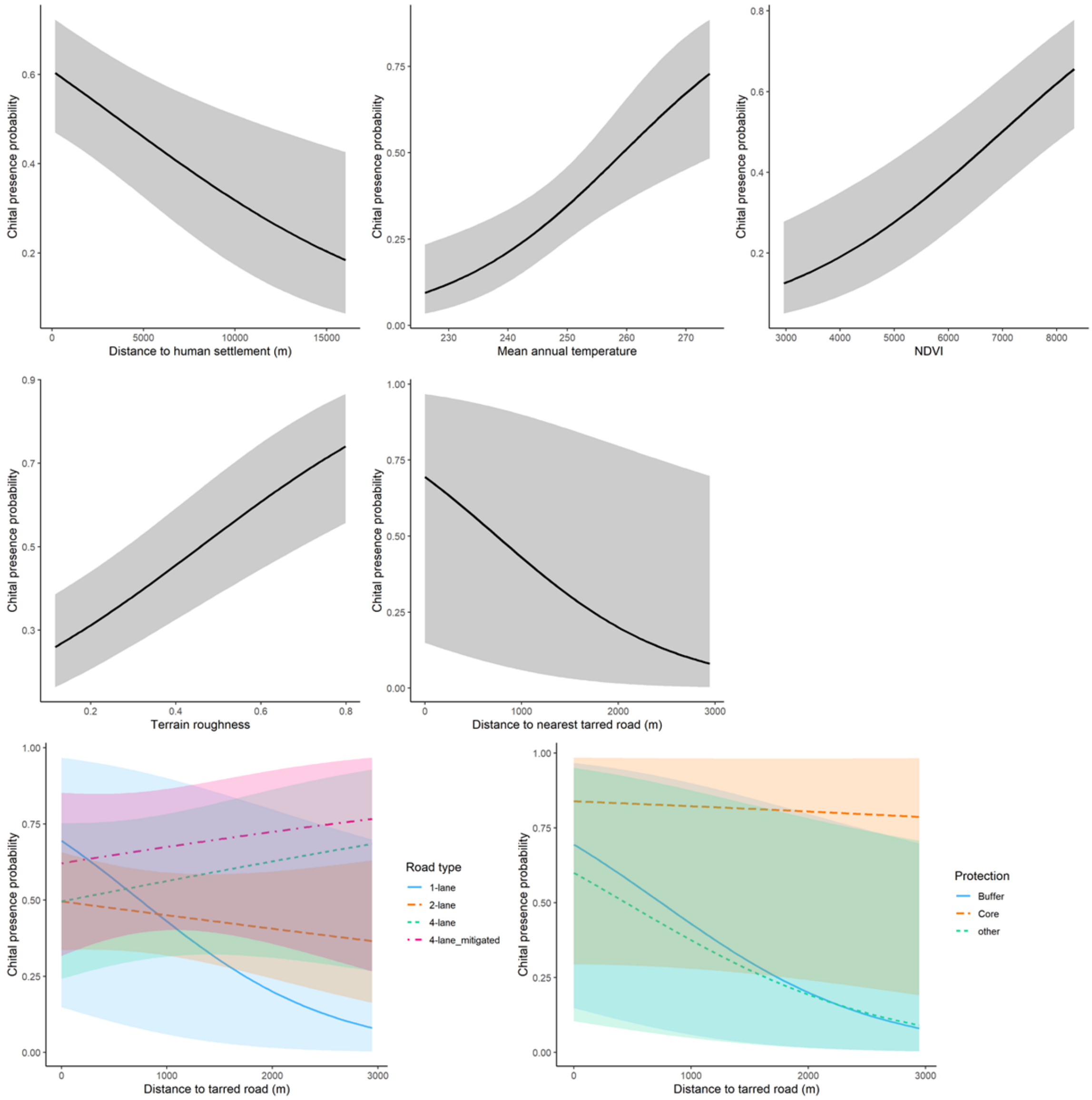

Figure 5.3. Effect plots showing significant relationships between model-predicted chital presence probabilities with environmental and road-related variables.

Gaur

Gaur presence was significantly positively influenced by evapotranspiration rate and terrain roughness. While gaur presence near protected (core and buffer) forests decreased with increasing distance to road, it was least near other forest protection types and increased at greater distances to the road (Fig. 5.4).

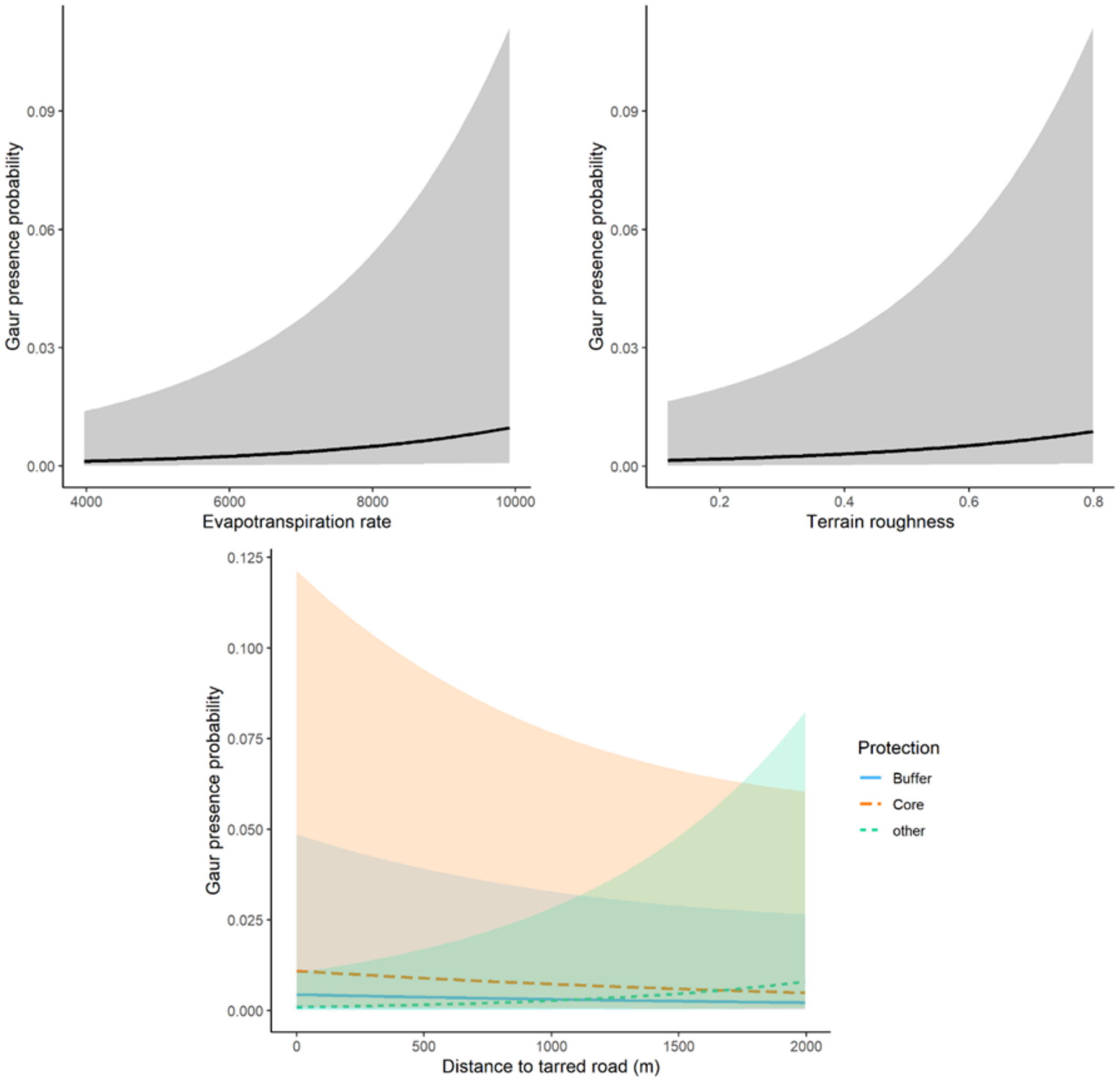

Figure 5.4. Effect plots showing significant relationships between model-predicted gaur presence probabilities with environmental and road-related variables.

Sambar

Sambar presence was positively influenced by NDVI and negatively by mean annual precipitation. Sambar presence was significantly high in core and buffer roadside habitats as compared with other forest protection types (Fig. 5.5). None of the road-related variables significantly explained variation in sambar presence probabilities, but addition of road-related variables (distance to road and road type) improved model fit (ΔAIC 5.65).

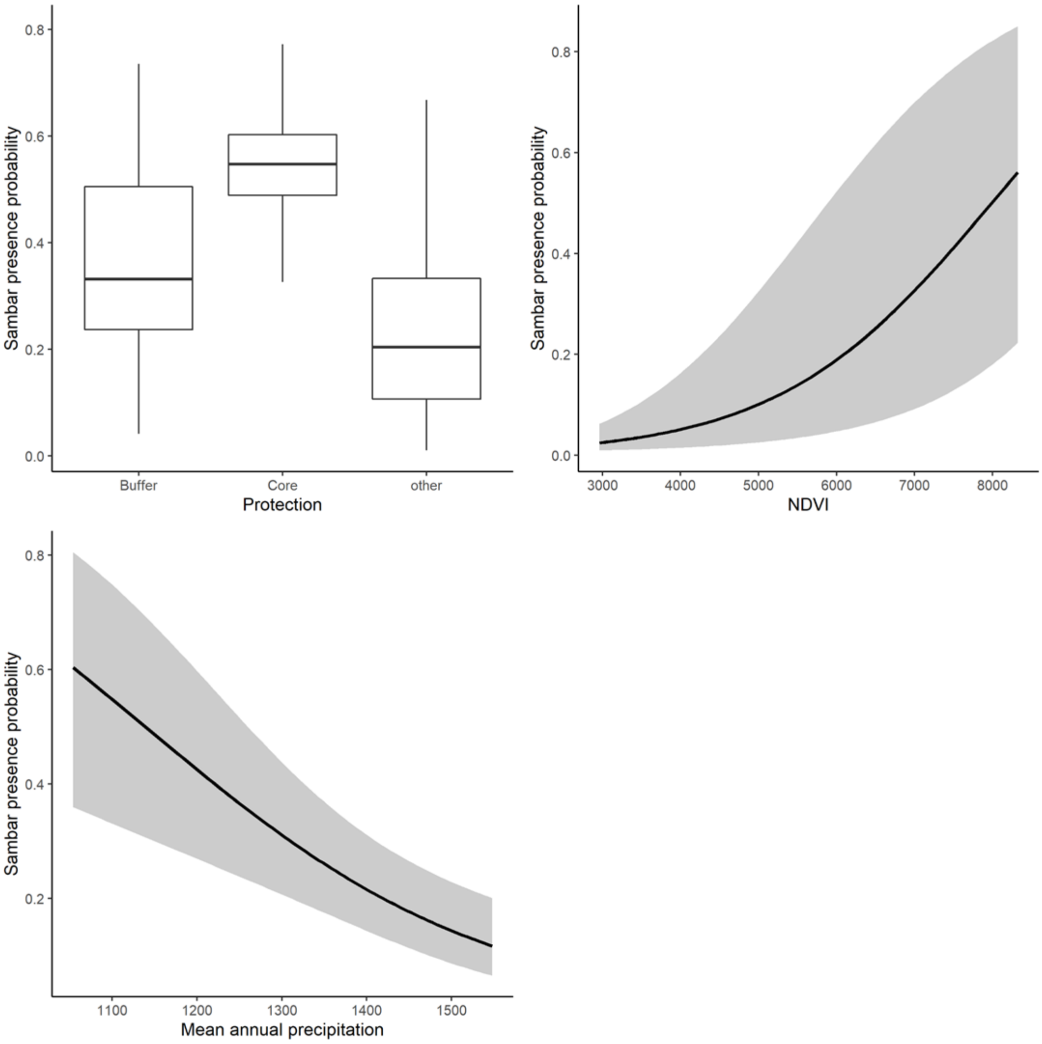

Figure 5.5. Effect plots showing significant relationships between model-predicted sambar presence probabilities with environmental and road-related variables.

Wild pig

Wild pig presence probability was higher in non-core roadside forests, positively influenced by NDVI and negatively by distance to protected area. Wild pig showed a weak positive relationship with increasing distance to road, highest presence probabilities near 4-lane roads, and significantly reduced presence near 4-lane road after construction of crossing structures (Fig. 5.6).

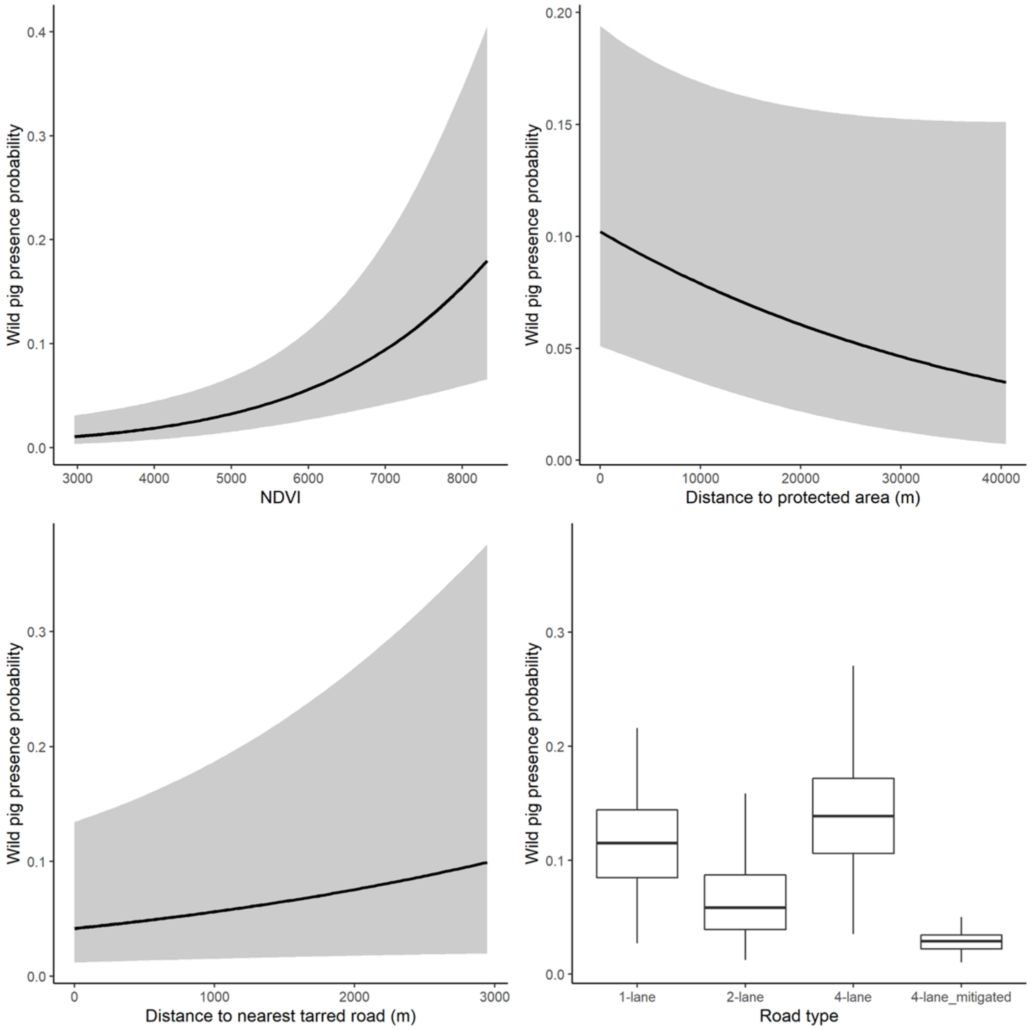

Figure 5.6. Effect plots showing significant relationships between model predicted wild pig presence probabilities with environmental and road-related variables.

5.3.2. Estimation of species-specific road effect zones (REZ)

Chital

Chital are attracted to roadside habitat, resulting in less reduction in roadside presence probabilities near the roads. As a result of the apparent attraction, the reduction in presence probabilities increased as distance to road increased. Hence the REZ for chital can be described as the extent up to which chital presence probabilities experience reduction < 40 – 60% as a consequence of attraction to the effect zone. Consequently, the distance at which 40-60% reduction in chital presence probabilities occurs under present and future road development scenarios was found to be similar (less than 1163 m) (Fig. 5.7).

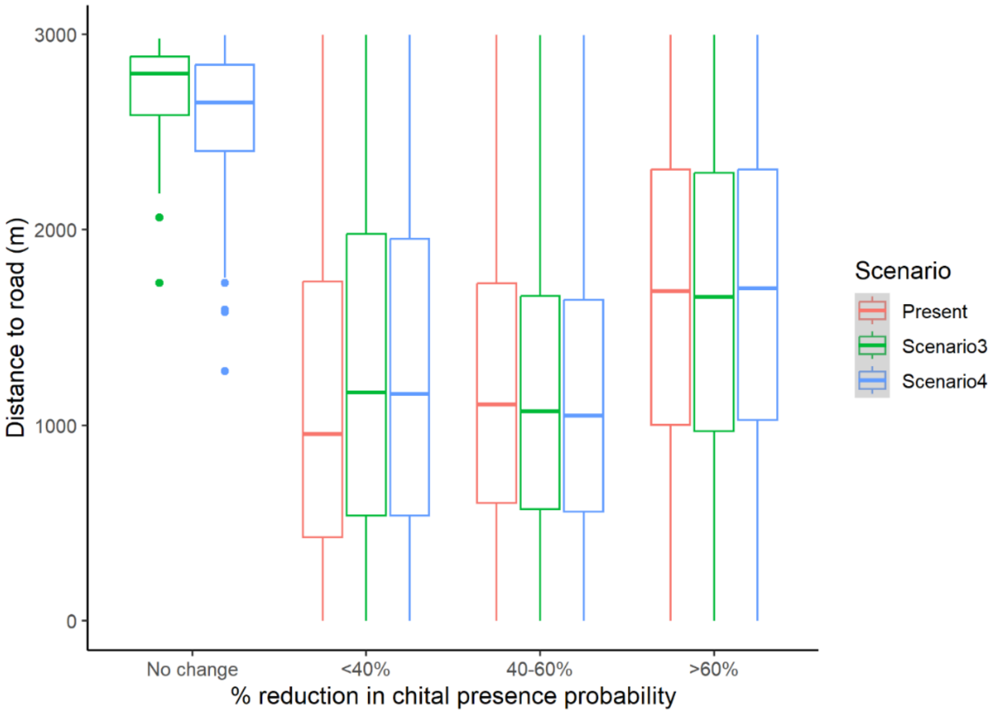

Figure 5.7. Road effect zone (40-60% reduction in presence probabilities) estimates for chital under different road development scenarios in the central Indian landscape.

Considering the interactive effect of roadside habitat protection with distance to road, chital REZ were significantly wider near core and buffer zones of roadsides habitat (1243 m), as compared with that in other forest protection zones. Similar trends in REZ were seen under future road development scenarios (3 and 4), with the exception of widest REZ near core roadside habitats (1290 m) under road development scenario 4 (Fig. 5.8 (a)).

The REZ presently near 2-lane and 4-lane roads are the widest (>1322 m), and least near 4-lane roads with crossing structures (1000 m). Similar REZ values were predicted under road development scenario 3, while under road development scenario 4, the REZ was widest near 4-lane roads with crossing structures (1215 m) (Fig. 5.8 (b)). Variation in chital REZ with roadside forest protection levels, road types and road development scenarios is depicted in Fig. 5.9.

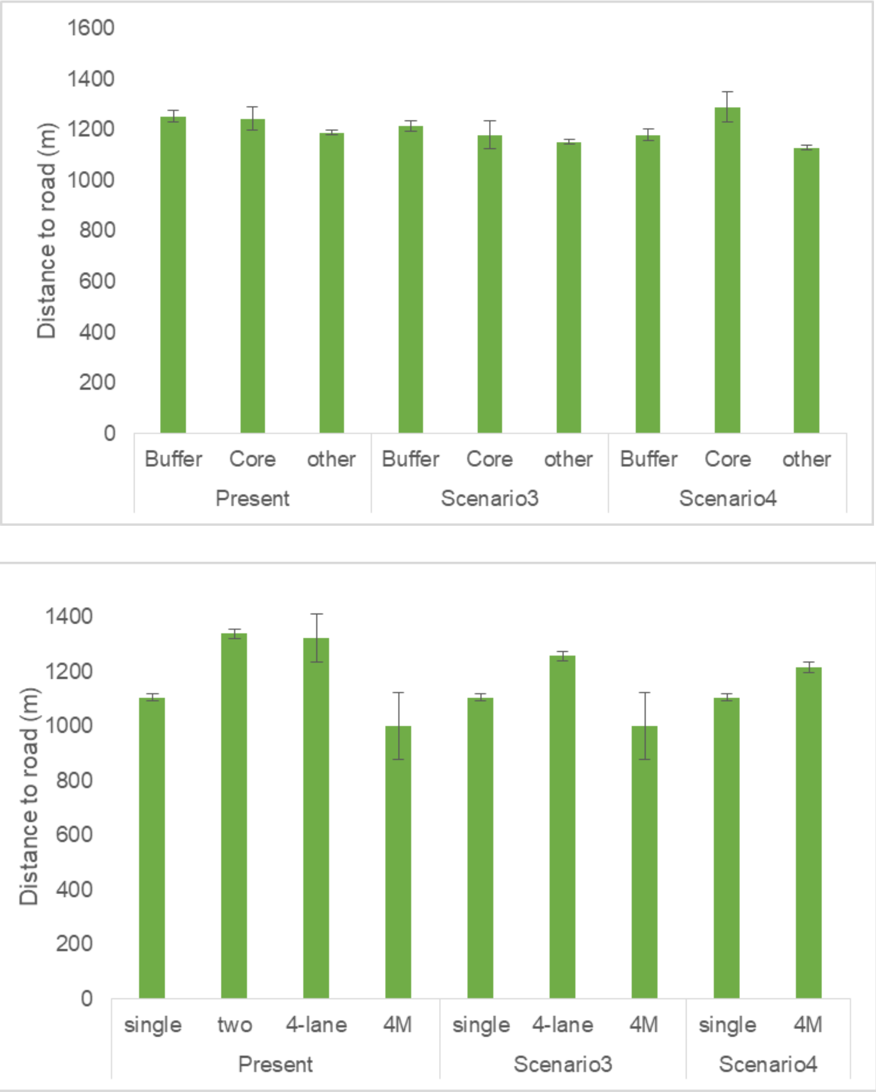

Figure 5.8. Road effect zone estimates for chital under different road development scenarios near (a) different roadside forest protection types, and (b) different road types.

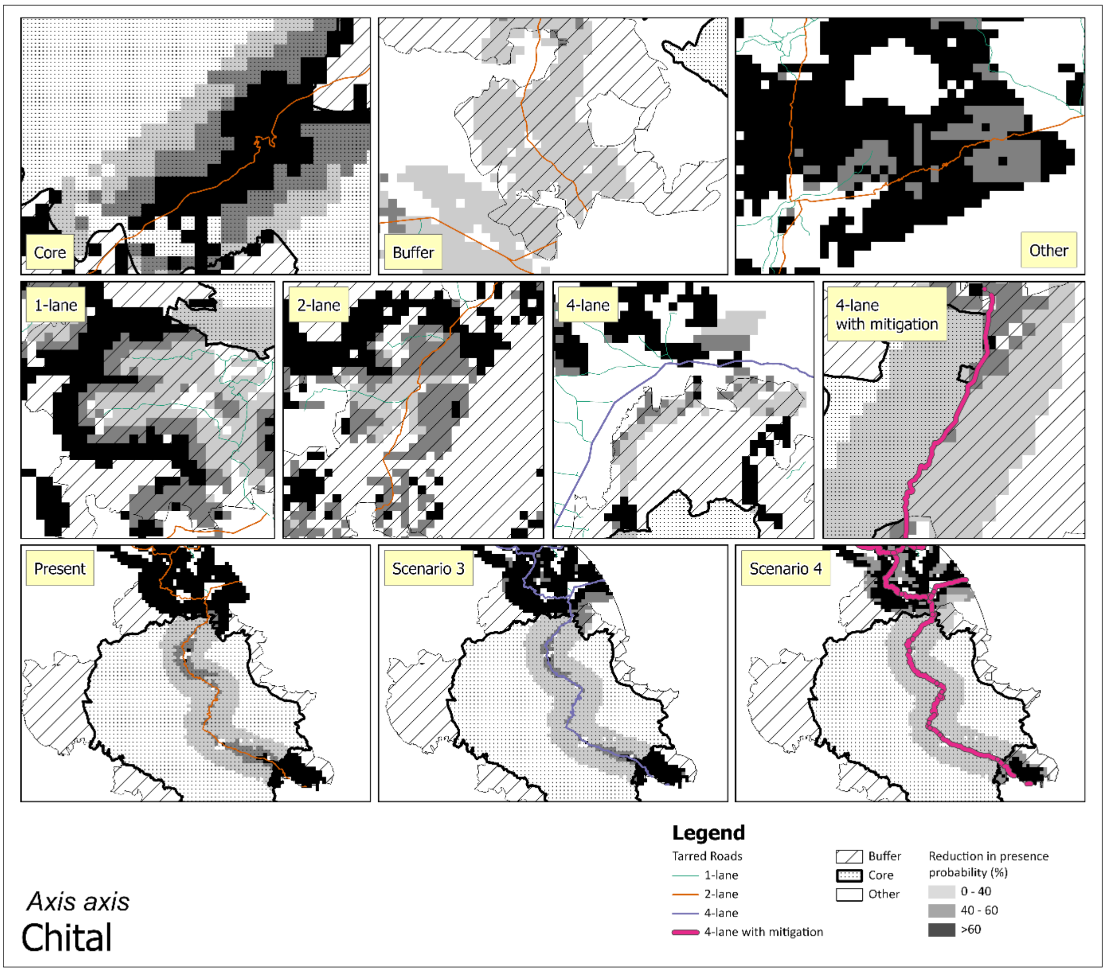

Figure 5.9. Examples of chital road effect zones under different roadside forest protection levels, road types and road development scenarios in the central Indian landscape.

Gaur

REZ for gaur under present road scenario was estimated at 1345 m away from the road. This zone decreased to 1049 m and 1097 m under future road development scenarios 3 and 4 respectively (Fig. 5.10).

Gaur showed some attraction to roadside habitat in protected (core and buffer) roadside forests (Fig. 5.4). Consequently, the REZ defined as the area up to which gaur experienced attraction in core and buffer zones was estimated at 1573 and 1658 m respectively (Fig. 5.11). Conversely, in non-protected roadside forests, gaur presence probabilities declined to more than 40-60% at 1227 m from the road. In the event of road up-gradation to 4-lane without implementation of crossing structures (scenario 3), significantly narrower REZ near roadside core and buffer forests were estimated (667 m and 411 m respectively). Under the road development scenario involving road up-gradation with crossing structures, REZ for gaur near core and buffer roadside habitats were wider (1835 m and 1657 m respectively) as compared with narrower REZ in non-protected roadside forests (1037 m). Variation in gaur REZ with roadside forest protection levels, road types and road development scenarios are depicted in Fig. 5.12.

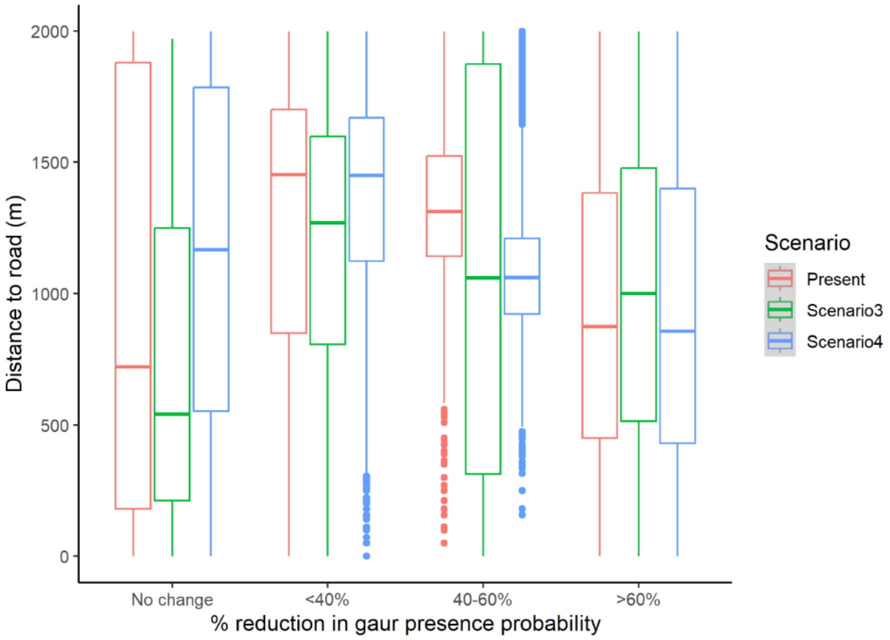

Figure 5.10. Road effect zone (40-60% reduction in presence probabilities) estimates for gaur under different road development scenarios in the central Indian landscape.

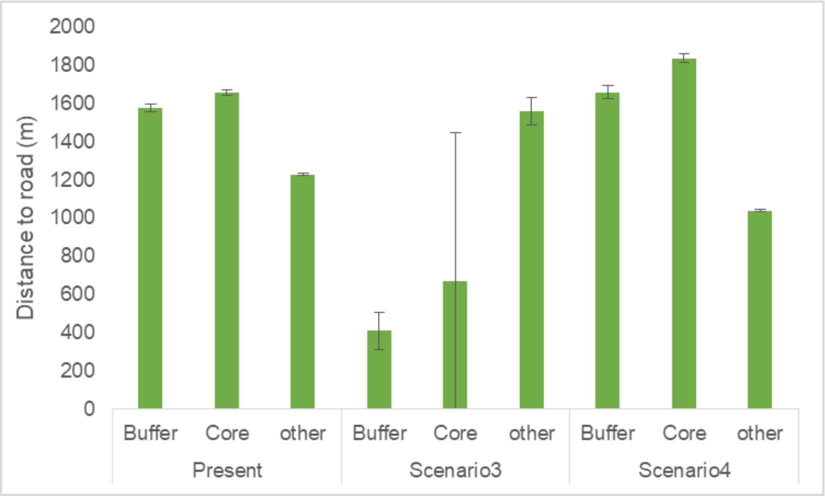

Figure 5.11. Road effect zone estimates for gaur under different road development scenarios near different roadside forest protection types.

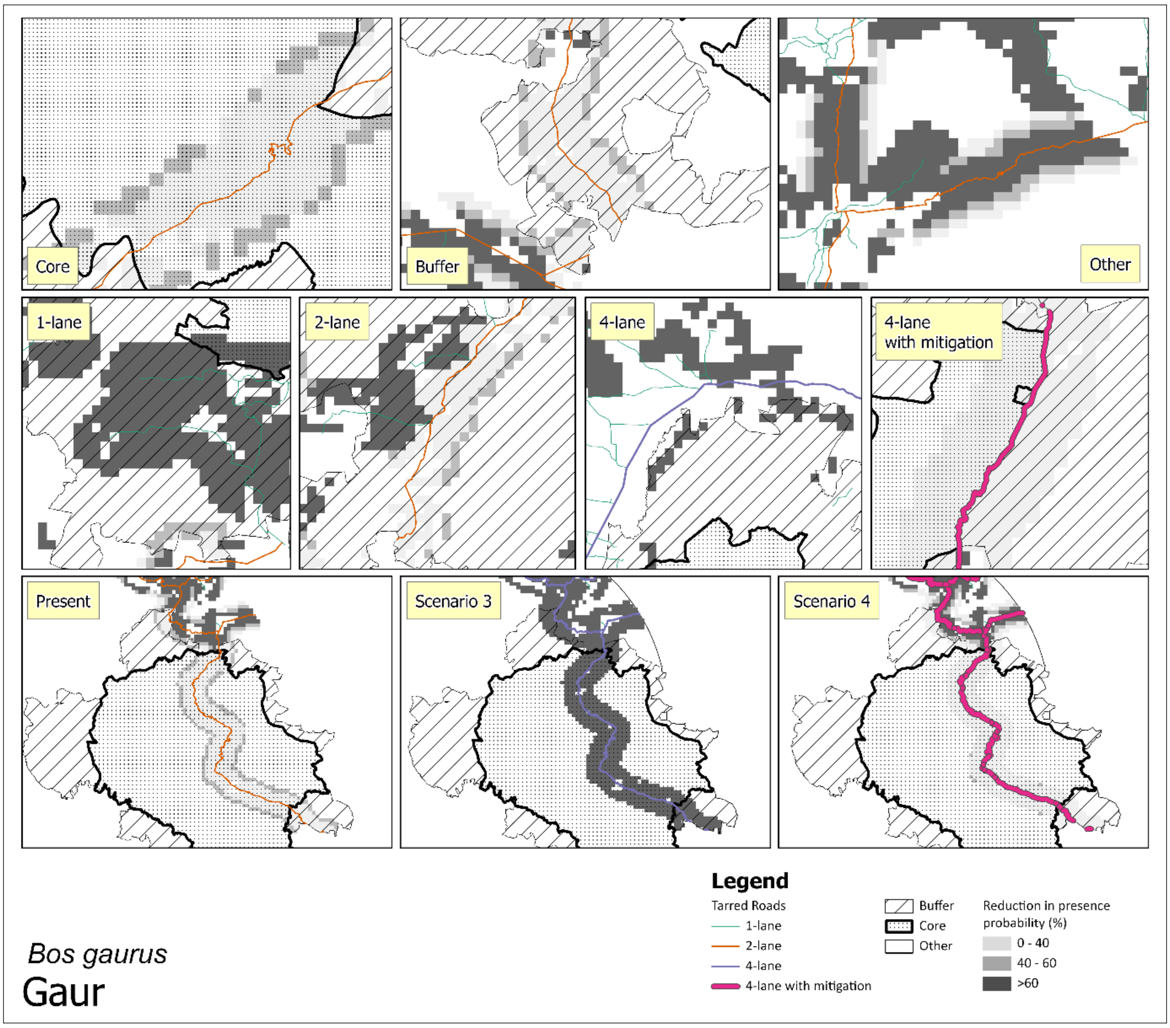

Figure 5.12. Examples of gaur road effect zones under different roadside forest protection levels, road types and road development scenarios in the central Indian landscape.

Sambar

Similar estimates of REZ for sambar under all three road development scenarios were found (1692 – 1731 m) (Fig. 5.13).

Similar trends in sambar REZ widths were observed between the three road development scenarios, with the narrowest effect zone being near the core roadside habitat, followed by that near the buffer and non-protected roadside forest (Fig. 5.14). Variation in sambar REZ with roadside forest protection levels, road types and road development scenarios are depicted in Fig. 5.15.

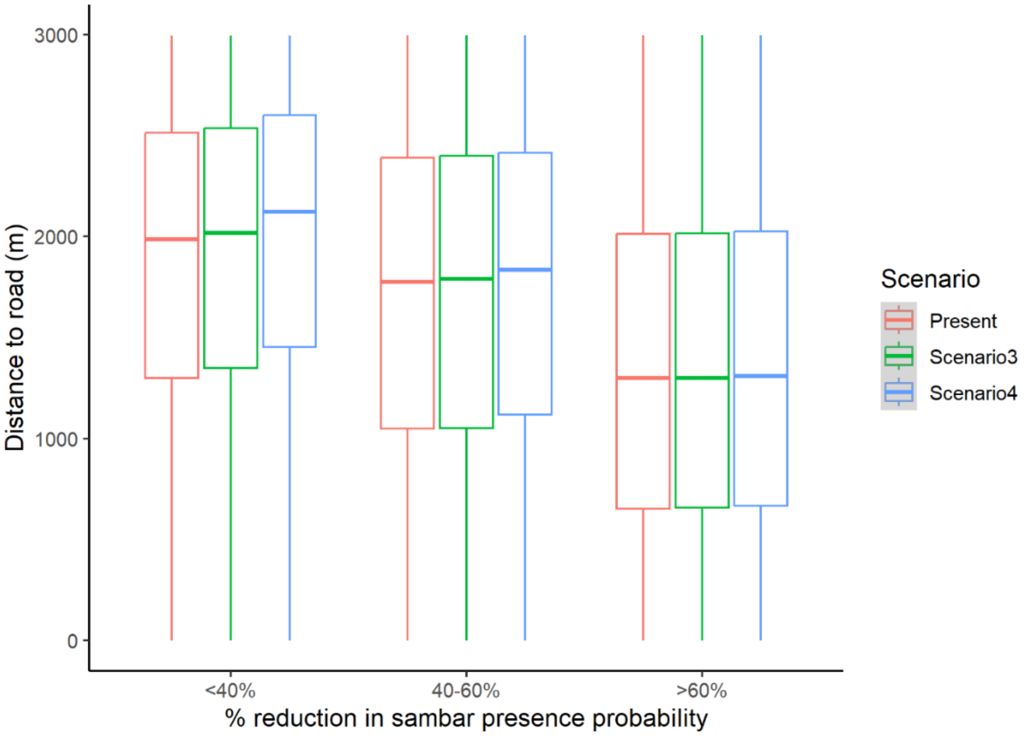

Figure 5.13. Road effect zone (40-60% reduction in presence probabilities) estimates for sambar under different road development scenarios in the central Indian landscape.

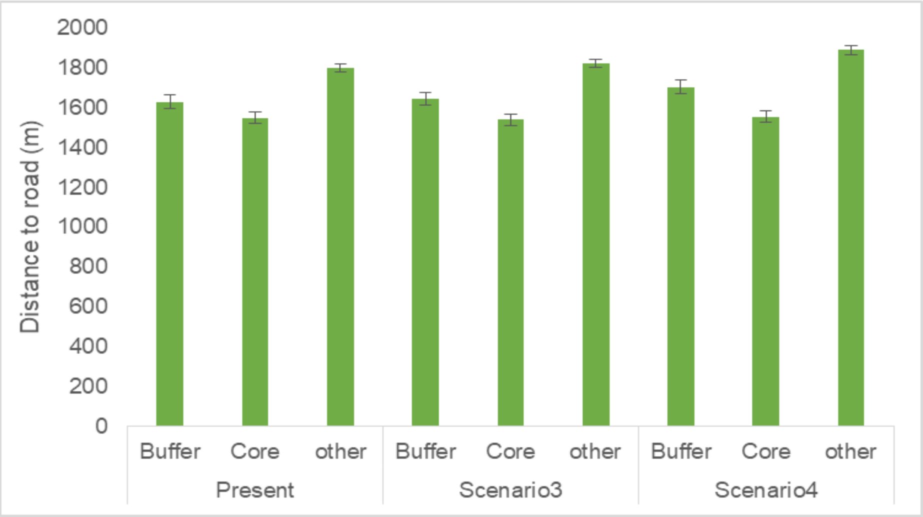

Figure 5.14. Road effect zone estimates for sambar under different road development scenarios near different roadside forest protection types.

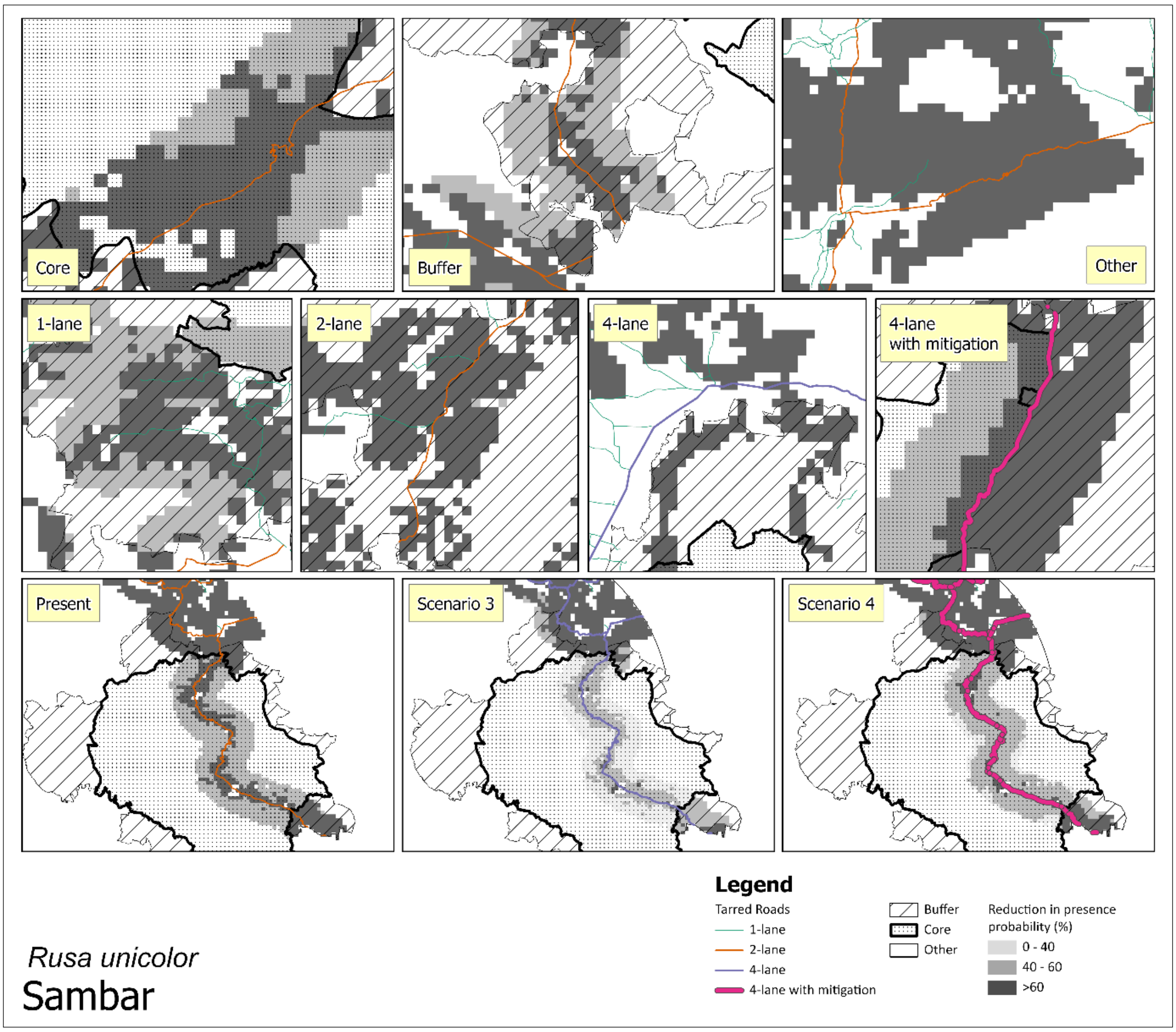

Figure 5.15. Examples of sambar road effect zones under different roadside forest protection levels, road types and road development scenarios in the central Indian landscape.

Wild pig

Similar REZ estimates were obtained for wild pig under present and future road development scenarios (2406 and 2319 m respectively) (Fig. 5.16). Under road development scenario 4, reduction in wild pig presence was greater than 60%, thus the REZ would be greater than 3000 m. Variation in wild pig REZ with roadside forest protection levels, road types and road development scenarios is depicted in Fig. 5.17.

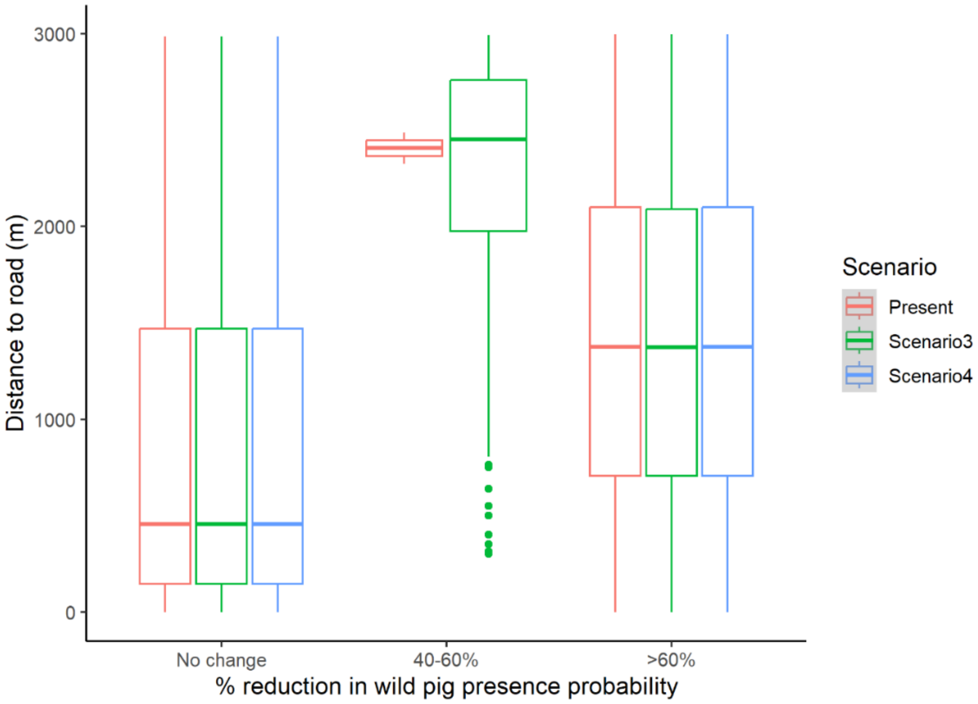

Figure 5.16. Road effect zone (40-60% reduction in presence probabilities) estimates for wild pig under different road development scenarios in the central Indian landscape.

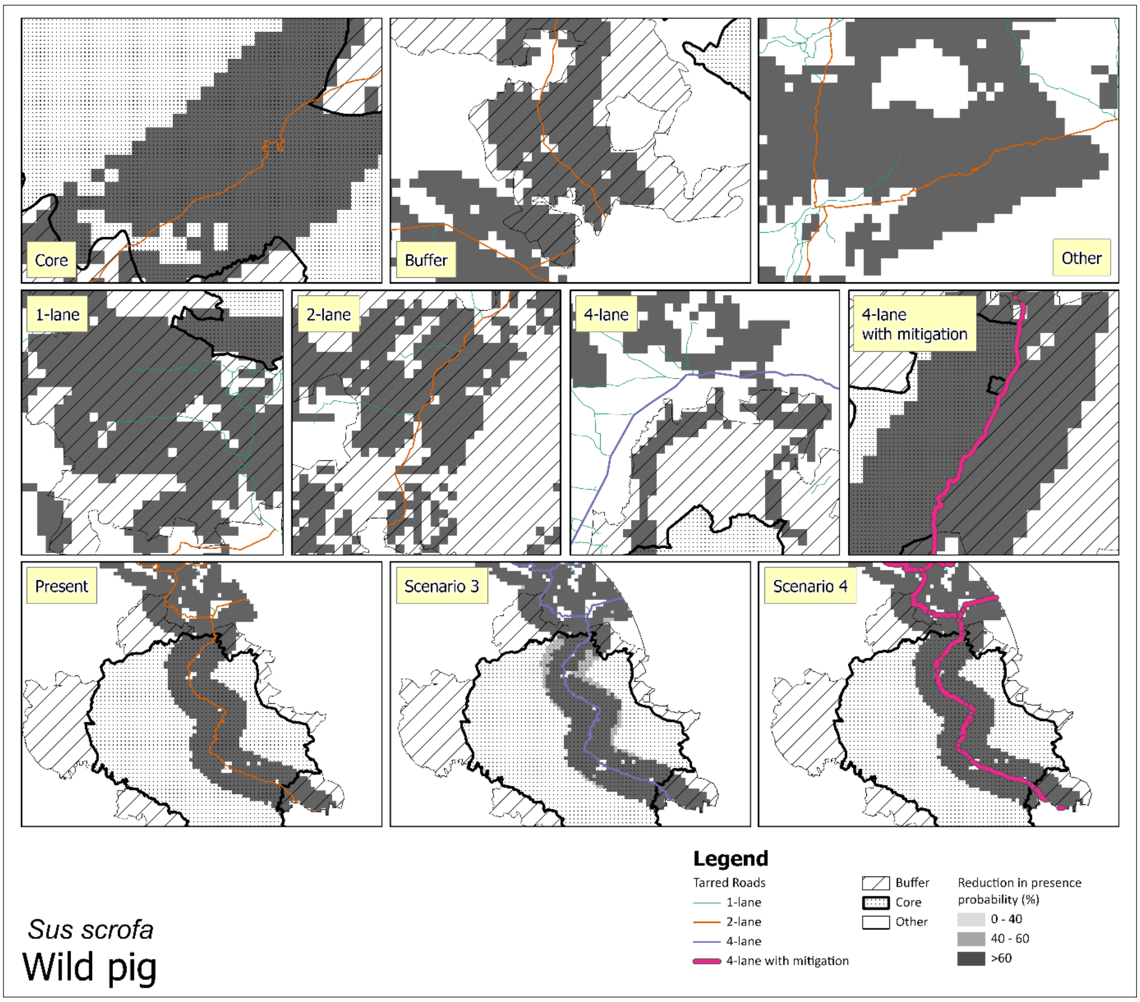

Figure 5.17. Examples of wild pig road effect zones under different roadside forest protection levels, road types and road development scenarios in the central Indian landscape.

Potential loss in available habitat because of roads

Road effects because of the present road network in the landscape account for 79.1% loss of total potential forested habitat in the landscape, and 64% reduction in potential protected habitat of chital, gaur, sambar and wild pig. Of this, 49.6% loss in core habitats, 72.6% in buffer habitats and PAs, and 83.3% in habitats outside PA and TR network was estimated.

5.4. Discussion

Roads cause indirect loss of habitat through impacts such as noise and traffic emissions (D’Amico et al., 2015). These effects can percolate up to a few kilometres inside the forests near roads that seem otherwise structurally intact. While different environmental and road related factors can influence the degree to which such effects percolate (He et al., 2019), species behaviour and tolerance to disturbance (Jacobson et al., 2016) also affect the extent of the species-specific REZ. I found similar variations in the influence of environmental and road related variables among the four ungulates studied.

Protected areas can act to cushion road impacts such as disturbance due to road and traffic emissions (Sangiwa et al., 2019). This could also be because of the role of protected areas in regulating ancillary human activities associated with road incursions into pristine areas (Burson et al., 2000; Laurance et al., 2009). I found evidence that protection of roadside habitat was an important factor determining the use of roadside habitat by different ungulates. While sambar showed a clear preference for protected roadside habitats, wild pig presence was highest in core and other roadside forest type. Chital, a habitat generalist tolerant of human disturbance, was found to exploit roadside habitat near all forest protection types, with the highest presence being near core zones. Gaur which is a disturbance averse species preferring forested tracts with good forage away from human habitations (Ashokkumar et al., 2011), was found to exploit roadside habitat but only in the vicinity of protected roadside forests. This could be because road-related disturbance is presently below threshold of tolerance by gaur (Schroeder et al., 2018). Near non-protected roadside forests, the expected trend of decline in gaur presence probabilities was observed. Large body size and home ranges coupled with avoidance of habitats near roads in presence of human disturbance could drastically reduce the habitat available for gaur conservation. Thus, it can be said that the consequences of roads outside the purview of protected areas can be drastic for species like gaur.

Road-related variables also influence the intensity of road effects and consequently the percolation of effects into the surrounding habitats (Eldegard et al., 2012). While chital presence probabilities decreased with increasing distance to road, the opposite was true for wild pig. This is contrary to the expectation of a habitat generalist and disturbance tolerant ungulate with high behavioural plasticity like wild pig. This could be a consequence of less preference for open habitats (Khan et al., 2019) near roadsides. Moreover it is likely that wild pigs preferred more natural habitat types than roadside habitat (Stillfried et al., 2017). Despite this, wild pig remains the most encountered roadkill in the study area, given its high local abundance.

The effect of road type was important in explaining chital and wild pig presence probabilities. A notable result is the decrease in wild pig presence probabilities near 4-lane roads with crossing structures and non-significant increase in chital presence at increasing distances from such roads. This could be attributed to the increase in predator activity near roadsides after construction of crossing structures (Saxena and Habib, 2022) that has possibly reduced the exploitation of such areas by chital and wild pig. This exploitation of roadside habitat prior to construction of crossing structures by chital and wild pig expectedly because of the ‘predator release’ effect could be an indicator of the degree of absence of or reduced predation by top predators (Berger, 2007; Espinosa et al., 2018; Kerley et al., 2002) near the road, since chital and wild pig are among the primary tiger and co-predator prey in the landscape.

Unlike the adaptations to road related effects in different protection regimes adopted by other ungulates, sambar response to road-related disturbance was found to be negative, notwithstanding the type of protection level of roadside forest or the road type. This indicates preference of undisturbed forests by sambar. Chital and sambar, both cervids and with similar reproductive rates, show extremely opposite responses to roads. This is because even though both cervids are taxonomically close, responses to road related disturbance are largely driven by behaviour (Jacobson et al., 2016).

Jacobson et al. (2016)) proposed a behavioural framework that could explain the differential responses to traffic. Under the framework, sambar and gaur can be categorised as ‘avoiders’, that experience moderate mortality levels at lower traffic volumes that declines steadily with increased avoidance of roadside habitat, resulting in an early onset of barrier effect. Low mortality and avoidance of roadside habitat leads to the road becoming a barrier as a combined effect of mortality and avoidance for such species at higher traffic volumes. An exception to this theory for the present study is the exploitation of protected roadside habitat by gaur. Thus, among the ‘avoiders’ in my study, gaur can be said to have a slightly greater tolerance to road-related disturbance as compared with sambar.

On the other hand, chital and wild pig can be called ‘speeders’ that have high mortality rates at traffic volumes till such time gaps in traffic allow for road crossing. The barrier effect in case of speeders is majorly caused by high mortality rates at medium traffic volumes and avoidance at high traffic volumes (Jacobson et al., 2016). In the absence of crossing structures, chital and wild pig in the landscape use roadside habitats in the absence of top predators, whilst tolerating non-lethal road-related disturbance on roadside habitats. While habituation or tolerance of wildlife to human disturbance may seem beneficial or positive through increased foraging opportunities, it may have overall negative consequences for the population (Bejder et al., 2009) via increased exposure to humans and vulnerability to mortality.

Overall, all species exhibited comparatively lesser use of non-protected roadside habitat. While human presence is related with increased predation risk by some animals (Frid and Dill, 2002), some animals perceive areas of moderate human disturbance as free of their natural predators (Kuijper et al., 2016) to some extent. Moreover, considering greater negative effects outside PAs, we can conclude that road effects interacting with other anthropogenic disturbances that are absent inside PAs amplify the negative effects of roads on wildlife. Moreover, while positive responses were observed, the overall negative effects of roads outweigh the positive effects, and priority should be accorded to mitigate them (Fahrig and Rytwinski, 2009).

REZ has been described as the extent up to which significant road effects percolate into the adjacent habitat (Forman et al., 1997). It is expected that this zone would be characterised by a reduction in overall species abundances. However, I found exceptions to this characterisation of REZ. I found the reverse i.e., less decline near the road as a result of attraction to roadside habitat for chital and gaur (in protected roadside habitat). REZ can thus be defined for these two ungulates as the distance near the road up to which less than expected reduction in presence probabilities occurs. This can be said to be the zone in which attraction to roadside habitat causes a reverse effect.

Both chital and gaur REZ were wide near core and buffer roadside habitats (up to 1660 m), with no significant change in chital REZ observed under any of the present and future road development scenarios. For gaur, the REZ got narrower under future road development scenarios. Moreover, gaur REZ in non-protected roadside habitats reduced significantly under road development scenario involving construction of mitigation measures. This implies that gaur would benefit from the construction of crossing structures, especially in forests outside protected areas.

The widest REZ were observed for sambar and wild pig. While sambar experienced narrower effect zones within protected roadside forests, there was no significant reduction in REZ under the road development scenario involving construction of crossing structures. This could be because at the time of collection of information on use of roadside habitat after construction of crossing structures, sambar were found to be sparingly using the crossing structures (Saxena and Habib, 2022). This use could increase in the future, thereby indicating that disturbance averse species like sambar would take time to use mitigation measures, particularly crossing structures. Thus, early identification of priority mitigation road segments would reduce long-term adverse impacts on such species.

High declines in wild pig presence probabilities under all road development scenarios was found. This could be because the no-roads scenario predicted high wild pig occurrence across the study area owing to its generalist nature. Moreover, wild pig presence probabilities after construction of crossing structures declined more than 70%. The REZ for wild pig under future road development scenario thus could be greater than 3 km.

Understanding such differential patterns in habitat use by wildlife near roads is the first step towards understanding wildlife responses to roads in rapidly changing anthropogenic landscapes. Behavioural changes have repercussions for mitigation planning and understanding patterns of use of mitigation structures by wildlife (Kintsch et al., 2015; Saxena and Habib, 2022). The present study has demonstrated that REZ can vary among ungulates in their responses to road related disturbances. The results can help in better understanding animal responses, and consequently help design suitable mitigation plans for the most adversely impacted species. I found that chital and wild pig responded similarly to road development scenarios involving crossing structures. More importantly, construction of crossing structures for gaur and sambar (particularly in non-protected forests intersected by roads) is essential to offset the long-term deleterious impacts of roads on these populations. We can conclude that gaur and sambar are the species most affected by indirect loss of habitat, and road development especially in non-protected corridor areas may have the most drastic consequences for population connectivity for these species. Gaur distribution in India, found in three disjunct populations, is already threatened and disconnected, and behaviourally induced population fragmentation because of linear infrastructure can further aggravate this problem (Choudhury, 2002). Additionally this estimate can also act a proxy for the REZ for predators, whose presence is limited by the roads (Espinosa et al., 2018) leading to the increased use of roadside habitats by prey species.

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Chapter 6

Identification and prioritisation of crossing zones to mitigate barrier and collision likelihood in the central Indian landscape

6.1. Introduction

Across the world, road networks cause fragmentation of contiguous wildlife by creating barriers to movement and through animal-vehicle collisions. Avoidance of the road corridor because of behavioural aversion and road-related mortality at the local scale can have landscape scale effects on wildlife populations, communities and ecosystems (Jones, 2000; Riley et al., 2006). Moreover, the interactive effect of barrier and mortality effects in highly fragmented landscapes and populations can have detrimental effects on long-term species persistence (Cullen et al., 2016) by causing species isolation (Ceia-Hasse et al., 2018). Carnivores avoid using habitat patches outside their activity centres that are surrounded by roads (Bischof et al., 2017), reinforcing the barrier effect and restricting access to resources. Moreover, impedance of movement because of roads also hampers gene flow required for recolonisation (Epps et al., 2005). Animal-vehicle collisions involving animals with large body sizes can also endanger human safety and lead to high economic costs (Abra et al., 2019; Ascensão et al., 2021).

In view of the impacts of roads on animal persistence and human safety, measures such as wildlife crossing structures and animal-proof fencing have been deployed around the world. In order to decide the appropriate sites for installing such measures, animal movement data from telemetry studies and roadkill data have been extensively used for modelling and delineating critical road segments (Coitiño et al., 2021; Colchero et al., 2011; Ford et al., 2011; Lin et al., 2019), along with species distribution and habitat use models, often complemented with roadkill information (Balčiauskas et al., 2020; Clevenger et al., 2002; Russo et al., 2020). Moreover in the absence of such information, literature-based information on species use of habitat, environmental and landscape variables have been additionally utilised to generate information on potential corridors and consequent bottlenecks on road networks (Loro et al., 2015). While most of these studies have focussed on single species, multi-species models have been also been used to delineate priority mitigation sites for mammal communities (Balčiauskas et al., 2020; Coitiño et al., 2021; Fedorca et al., 2021). Thus a combination of available data on animal movement, mortality and habitat suitability, and road and traffic characteristics have been used to identify and prioritise road segments for mitigation across the world. Visintin et al. (2016) used a hazard-exposure framework by combining animal presence and presence and movement of vehicles to delineate high risk eastern grey kangaroo *Macropus giganteus* mortality sites across a road network in Australia.

The central Indian tiger population is genetically the most diverse, but shows the greatest signs of genetic structuring caused by human-induced habitat fragmentation (Kolipakam et al., 2019). Road networks have been identified among the land uses that could decrease genetic diversity and increase extinction probabilities in the landscape (Thatte et al., 2020, 2018). Moreover, the road network in central India has been growing at a rapid pace. Consequently, it is important to generate information in a timely manner to adequately inform mitigation measures on such road up-gradation and development plans. Maintaining landscape level connectivity for tigers and associated wildlife requires planning of mitigation measures at the strategic level, instead of singular road projects (Saxena et al., 2016). Given the fact that road infrastructure development involves high financial costs, timely interventions to integrate mitigation measures to ensure maintenance of landscape connectivity and long-term viable conservation in the landscape is essential. Consequently, alternative approaches to predict priority zones for preventing collision and barrier effects caused by roads are required utilising available datasets of animal presence and road characteristics for extrapolation to larger landscapes.

In this study, I attempted to map road segments in corridors and protected areas of the central Indian landscape with varying levels of collision and barrier likelihood for four ungulates and two large carnivores. I used a simple rule-based metric under an exposure-hazard framework (adapted from Visintin et al. (2016)) to calculate species collision and barrier likelihood using road-related factors viz., predicted traffic volumes, road types, speeds and density of linear infrastructure, in addition to environmental variables like species habitat suitability, movement corridors, presence of forests and protected areas. I adopted the methodology used by Visintin et al. (2016) to calculate traffic volume, since this information for the entire road network in the landscape is missing. Finally, I weighted these variables according to different criteria to produce priority cumulative barrier and collision road segment maps across the landscape. The methodology used is simple and easily reproducible for other fauna and can help highway agencies and conservation professionals make decisions on construction of mitigation measures.

6.2. Analytical methods

I used a combination of variables that have been found to influence occurrence of roadkill and barrier effect for mammals to identify vulnerable road segments. The description of road-related, environmental, and animal presence data used, and the scoring criteria is given as under. All analyses were done using ArcGIS Pro (ESRI Inc., 2021) and R (RStudio Team, 2020).

6.2.1. Preparation of variables

Road related variables

Only tarred roads (fclass = trunk, primary, secondary, tertiary) from the OpenStreetMap road database were used.

Density of linear infrastructure

Density of transportation infrastructure has been found to affect mortality of wildlife (Morelle et al., 2013), and creating barriers to animal movement (Basille et al., 2013). Linear infrastructure density (km/km^2) including the roads and railways layers for the study area was estimated using the line density tool in ArcGIS Pro within a 3 km search radius to include all linear infrastructure within this distance. Linear infrastructure density was further classified as low, medium and high based on natural breaks (Jenks classification in ArcGIS Pro) (Supplementary Fig. A6.1).

Road type, speed and median

Road type, in terms of the number of lanes, indicates the exposure time of an animal to getting hit by a vehicle (Saxena et al., 2020), and also the barrier to be navigated (Chen and Koprowski, 2016; Thatte et al., 2018). High traffic speeds and volumes are indicative of high probability of an animal getting hit, while it also indicates low barrier to animal movement (Gagnon et al., 2007; Valero et al., 2015) since high speed traffic flows are possible under low traffic volume conditions (Saxena et al., 2020). Additionally, medians on wide roads present a possible barrier to animal movement.

"Road type" was assigned as: trunk and primary roads – 4-lane, secondary roads – 2-lane, tertiary roads – 1-lane. I also verified the lane status of trunk and primary roads using Google Earth. Additionally, National Highway 44 was categorised as '4-lane mitigated' as this is the only highway in the landscape with mitigation measures in the form of crossing structures, and the Nagpur-Mumbai Maharashtra Samruddhi Expressway was categorised as 4-lane mitigated with fences. Further, trunk roads were designated as high speed, primary and secondary roads as medium speed, and tertiary roads as low speed. All 4-lane roads were further assumed to have a median (divider).

Traffic volume estimation

I extracted traffic data in daily PCU (Passenger Car Units) from various sources ("NHAI Toll Information System," 2022) for different road types for Maharashtra and Madhya Pradesh states. PCU data was available for trunk and primary roads through the toll booths, while traffic data for secondary roads was extracted from project documents. I only used traffic data <5-7 years old.

The resulting traffic volume data was classified into six categories based on specifications of the Indian Roads Congress (*Four-laning of highways through public-private partnership: Manual of specifications & standards*, 2010; *IRC SP 073: Manual of standards and specifications for two-laning of state highways*, 2007) (Table 6.1).

Table 6.1. Categorisation of traffic volumes in PCU (Passenger Car Units) based on specifications of the Indian Roads Congress.

Road type/traffic	PCU	Code	Lanes
Minor	<2500	I	
Very low	2500 – 5000	II	1
Low	5000 – 10000	III	Intermediate
Moderate	10000 – 25000	IV	2-lane
High	25000 – 55000	V	4-lane
Very high	>55000	VI	6-lane

I created segments of all roads divided at intersections, and for each segment I extracted variables such as distance to nearest city, town, village, trunk and primary road, population density (people/km^2), tarred road density in km/km^2 (calculated using line density tool in ArcGIS Pro), and the road type ("fclass") as independent variables to predict traffic volume. All the variables were then tested for correlation. The data was partitioned into a training and testing subset (75:25). I then ran a Random Forest regression on the training data. After searching for the best values of model iterations, nodes and trees, the accuracy of the model was evaluated using the testing data subset. The model was subsequently used to predict PCU categories for all tarred roads in the study area.

Scores for road-related variables (road type, traffic volume and speed) were assigned based on the findings of Saxena et al. (2020). Following the traversability model (Saxena et al., 2020) species-specific collision and barrier risk (Fig. 6.1), traffic volume score was assigned as below:

i. at traffic volume corresponding to <20% probability of hit, low animal mortality and low levels of barrier to movement are expected to occur,

ii. at traffic volume corresponding to 20-50% probability of hit, high animal mortality and moderate levels of barrier to animal movement is expected to occur, and

iii. at traffic volume corresponding to >50% probability of hit, medium animal mortality is expected to occur (since mortality rate would plateau) but with high level of barrier to animal movement.

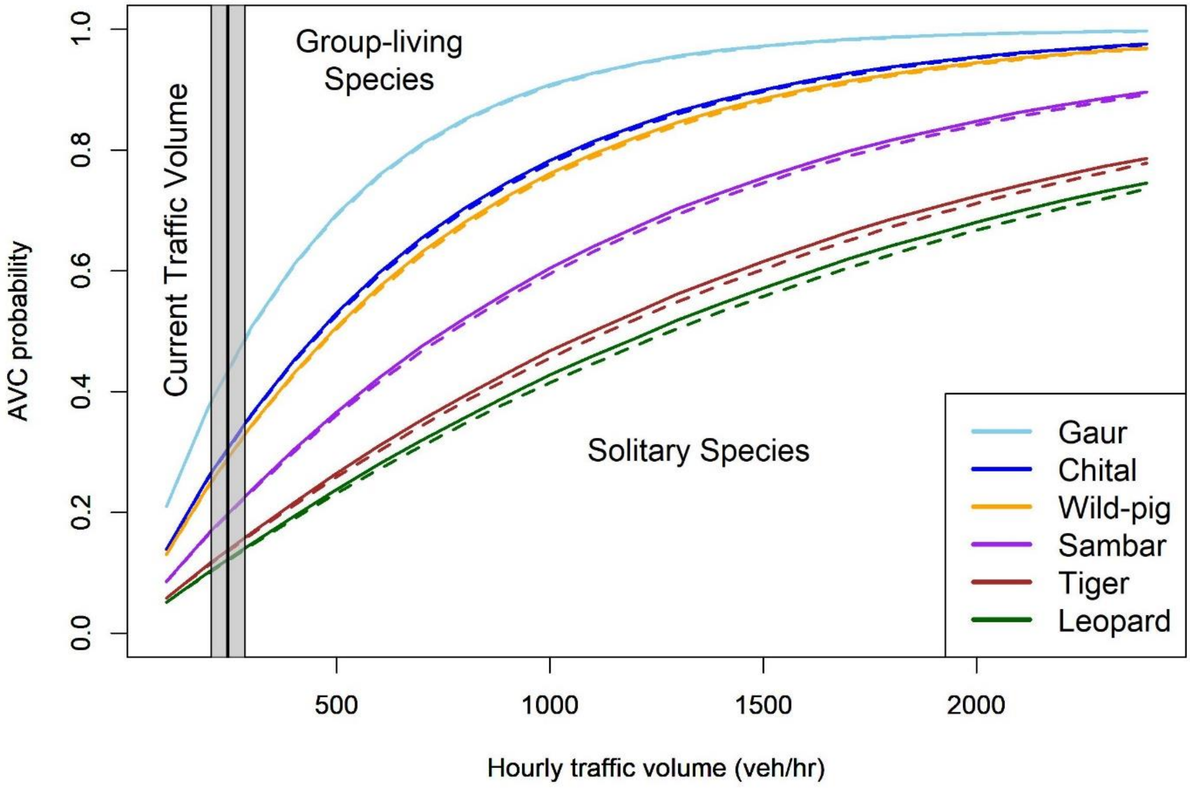


Figure 6.1. Trends of species-specific animal-vehicle collision (AVC) probability with changing traffic volume as calculated by Saxena et al. (2020) through the traversability model.

Further I converted hourly traffic volumes (in vehicles per hour) from Saxena et al. (2020) to daily traffic volume in PCU using vehicle-wise PCU values given by Bains et al. (2012) at the current V/C (volume/capacity) ratio on NH 44 that is 0.29 (PCU values of car: 1.87, bus/truck: 4.0, MAV: 5.07). Consequently, I calculated the proportions of different vehicle types in the traffic flow and multiplied it with the PCU values to get the daily PCU values.

Environmental variables

I used the forest type layer (“Bhuvan | ISRO’s Geoportal | Gateway to Indian Earth Observation,” 2016) of the study area (Supplementary Fig. A6.2) and distance to nearest PA (protected area) and TR (tiger reserve) (Supplementary Fig. A6.3). Distance to nearest PA and TR was further classified as low, medium, and high based on natural breaks (Jenks classification).

Species presence probabilities

For the four ungulates, I used the presence probability maps generated through habitat use analysis under present scenario (chapter 5), which were then classified as low, medium and high using natural breaks (Jenks classification). I used PA and TR layer, forest class layer, and telemetry-based corridor map prepared by Habib et al. (2021) to assign probability of tiger and leopard presence (Supplementary Fig. A6.4).

6.2.2. Species-specific collision and barrier likelihood index

I assigned numerical values to the variables according to the relative contribution to barrier or collision risk (Tables 6.2 and 6.3).

Table 6.2. Scores assigned to different levels of road, environmental and species variables with explanation of scoring criteria for calculation of barrier likelihood for four ungulates and two carnivores in the central Indian landscape.

S. no.	*Variable*	*Level*	*Score*	*Scoring justification*
1.	Road type (lanes)	4	3	Road width in increasing order would increase barrier to movement
		2	2	
		1	1	
		4 (mitigation)	0	Roads with crossing structures and fencing would enable animal movement, and thus pose no barrier
		4 (mitigation with fences)	0	
2.	Median	Present (4lane & above)	2	Presence of median would pose a barrier to movement
		Absent	0	
3.	Traffic volume	High	3	High traffic volumes would pose barrier to movement.
		Medium	2	
		Low	1	
4.	Speed	High	1	Low traffic speeds indicate high traffic volume, which would pose a barrier to movement
		Medium	2	
		Low	3	
5.	Linear infrastructure density	High	3	High linear infrastructure density areas pose barriers to animal movement
		Medium	2	
		Low	1	
6.	Distance to PA	High	3	Roads away from PAs pose greater barriers to animal movement
		Medium	2	
		Low	1	
7.	Forest type	Non-forest (1,2)	3	Roads in non-forest areas pose greatest barrier to movement
		Open (3,4)	2	Intermediate and high probability of animal movement in roads passing through forested areas
		Dense and very dense (5,6)	1	
8.	Species presence	Low	3	Roads in areas with low animal presence pose greater barrier to movement
		Medium	2	
		High	1	
		None	0	
	Tiger presence	PA/TR, corridor	3	Highest tiger presence and movement probability assumed within PA/TRs and in corridors, followed by other forests.
		Other forests	1	
		Non-forest	0	
	Leopard presence	PAs/TR, forests and corridors	3	Being widespread, leopard presence was assumed to be high in PAs/TRs, forests and corridors
		Non-forest	0	
	Presence of corridor	Yes	2	

9.		No	0	Presence of corridor indicates high movement probability and consequently high barrier risk

Table 6.3. Scores assigned to different levels of road, environmental and species variables with explanation of scoring criteria for calculation of collision likelihood for four ungulates and two carnivores in the central Indian landscape.

S. no.	*Variable*	*Level*	*Value*	*Scoring justification*
1.	Road type (number of lanes)	4	3	Wider roads would have highest risk of collision
		2	2	
		4 (mitigation)	2	Unfenced with crossing structures may have moderate risk of collision
		1	1	Narrow roads would have least collision risk
		4 (mitigation with fences)	0	Completely fenced highways with crossing structures would have no collision risk
2.	Traffic volume (PCU)	High	2	Categorised according to traversability model: High: 20 – 50%; medium: >50%; Low: <20%
		Medium	3	
		Low	1	
3.	Traffic speed	High	3	Highest traffic speeds would pose high risk of collision.
		Medium	2	
		Low	1	
4.	Linear infrastructure density	High	3	High linear infrastructure density would increase collision likelihood
		Medium	2	
		Low	1	
5.	Forest type	6, 5, 4	2	Scored according to probability of animal presence in different forest classes
		3	1	
		2, 1	0	
6.	Distance to PA	Low	3	Areas near PAs would have highest risk of wildlife mortality because of high local animal abundance
		Medium	2	
		High	1	
7.	Species presence (ungulates)	High	3	High animal abundance near roads would indicate high probability of road mortality
		Medium	2	
		Low	1	
		None	0	
	Tiger presence	Within PA/TR and corridors	3	Highest tiger presence and movement probability assumed within PA/TRs and
		Non-PA forests	1	

		Non-forest	0	in corridors, followed by other forests.
	Leopard presence	PAs/TRs, Forests and corridors	3	Being widespread, leopard presence was assumed to be high in PAs/TRs, forests and corridors
		Non-forest	0	

For each road segment in the study area, species-specific barrier and collision likelihood index using scores for different variables were calculated as under:

$$\begin{aligned} \mathit{Barrier\ likelihood\ index} &= (\mathit{Median} + \mathit{PCU} + \mathit{Speed} + \mathit{LI\ density} + \mathit{Distance\ to\ PA} \\ &+ \mathit{Presence\ of\ corridor}) * \mathit{Species\ presence} * \mathit{Road\ type} \\ &* \mathit{Forest\ type} \end{aligned} \tag{1}$$

$$\begin{aligned} \mathit{Collision\ likelihood\ index} &= (\mathit{PCU} + \mathit{Speed} + \mathit{LI\ density} + \mathit{Distance\ to\ PA}) * \mathit{Species\ presence} \\ &* \mathit{Forest\ type} * \mathit{Road\ type} \end{aligned} \tag{2}$$

6.2.3. Multi-species priority barrier and collision mitigation zones

Natural breaks (Jenks classification) were used to categorise species-specific barrier and collision likelihood indices to high, medium, and low. I then combined all species-specific barrier and collision likelihood indices on each road segment using a priority matrix, wherein I assigned higher priority scores to the higher barrier and collision likelihood indices (Equation 3), and to species in order of conservation priority (Table 6.4).

Table 6.4. Criteria used to assign priority to species and road segments for delineating road segments vulnerable to barrier and collision effects in the central Indian landscape.

Species (in order of conservation priority)	***Collision/barrier likelihood index***		
	Low (2)	*Medium (3)*	*High (4)*
Leopard Tiger (4)	16	64	256
Gaur Sambar (3)	9	27	81
Chital Wild pig (2)	4	8	16

I multiplied the resulting value with the number of species (n_species) found vulnerable to either barrier or collision at that road segment using the formula:

$$Priority\ score = \Sigma\left(Species\ weight^{Likelihood\ score}\right) * n\_species \quad (3)$$

6.3. Results

6.3.1. Preparation of variables

Road related variables

In the study area, a total of 32,500 km of tarred roads of different types are present, with 5800 km of trunk (high speed), 4971 km of primary (high speed), 5343 km of secondary (medium speed) and 15,896 km tertiary roads (low speed) (Supplementary Fig. A6.5). Of these, 1823 km are 4-lane, 14,587 km are 2-lane and 116,088 km are single lane roads (Supplementary Fig. A6.6). Thus, single lane (49.5%) and 2-lane roads (44.8%) make up the majority types of tarred roads in the landscape.

Traffic volume estimation

No significant correlation between the continuous variables used to predict traffic volume was observed (Supplementary Fig. A6.7). Different variables had differential influence over the six PCU categories (Supplementary Fig. A6.8), with tarred road density, distance to city, town and village and population density being among the top variables influencing most PCU classes. The best random forest regression model utilised 7 *mtry's* (with 77.9% accuracy), 260 *maxnodes* (with 81.3% accuracy), and 1000 *ntrees* (with 54.3% accuracy). 10-fold cross-validated resampling of the training dataset yielded an accuracy of 75.2% (kappa = 68.6%). Further using the best model on testing dataset yielded 74.15% (95% CI: 72.05 – 76.16%) accuracy (Supplementary Table A6.1), with a no information rate of 29.82%.

According to the random forest model for traffic volume prediction, most tarred roads in the landscape belonged to PCU category III (daily volume = 5000-10000 PCUs) with 59.8% of tarred roads, followed by PCU category II (daily volume = 2500-5000 PCUs) (Table 6.5 and Fig. 6.2).

Table 6.5. Length (in km) of tarred roads in the central Indian landscape belonging to different categories of traffic volumes (in PCU) as predicted by the random forest model.

PCU categories	Length (in km)	% of total road length
I	3447.148	10.60
II	6231.959	19.17
III	19437.33	59.80
IV	2033.73	6.26
V	602.2872	1.85
VI	747.7523	2.30

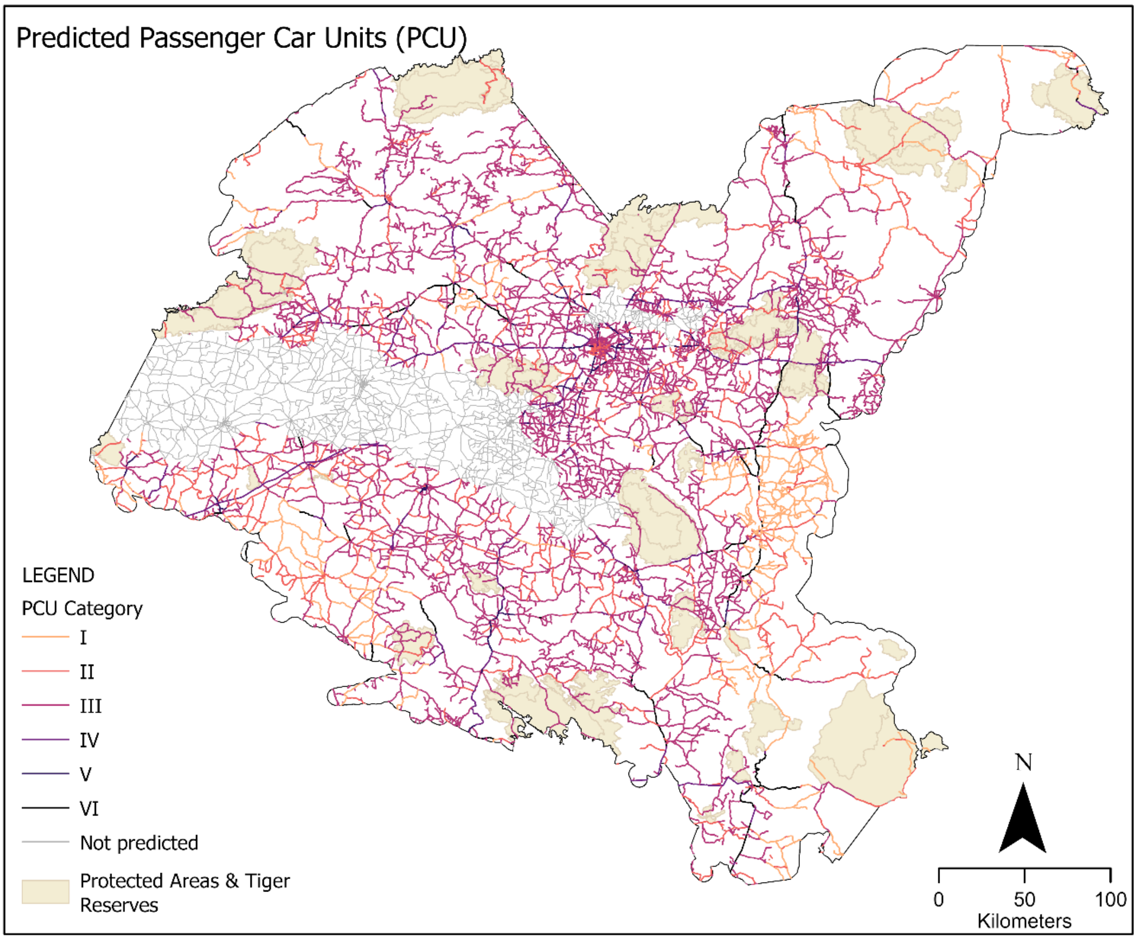


Figure 6.2. Traffic volume in daily PCU divided into six categories predicted for the study area in central Indian landscape.

Species presence probabilities

Presence probabilities as predicted by the habitat use analysis near a 3 km buffer of roads in the study area revealed generally high presence for all four ungulate species within protected areas and corridor areas with good forest cover (Figs. 6.3 – 6.6).

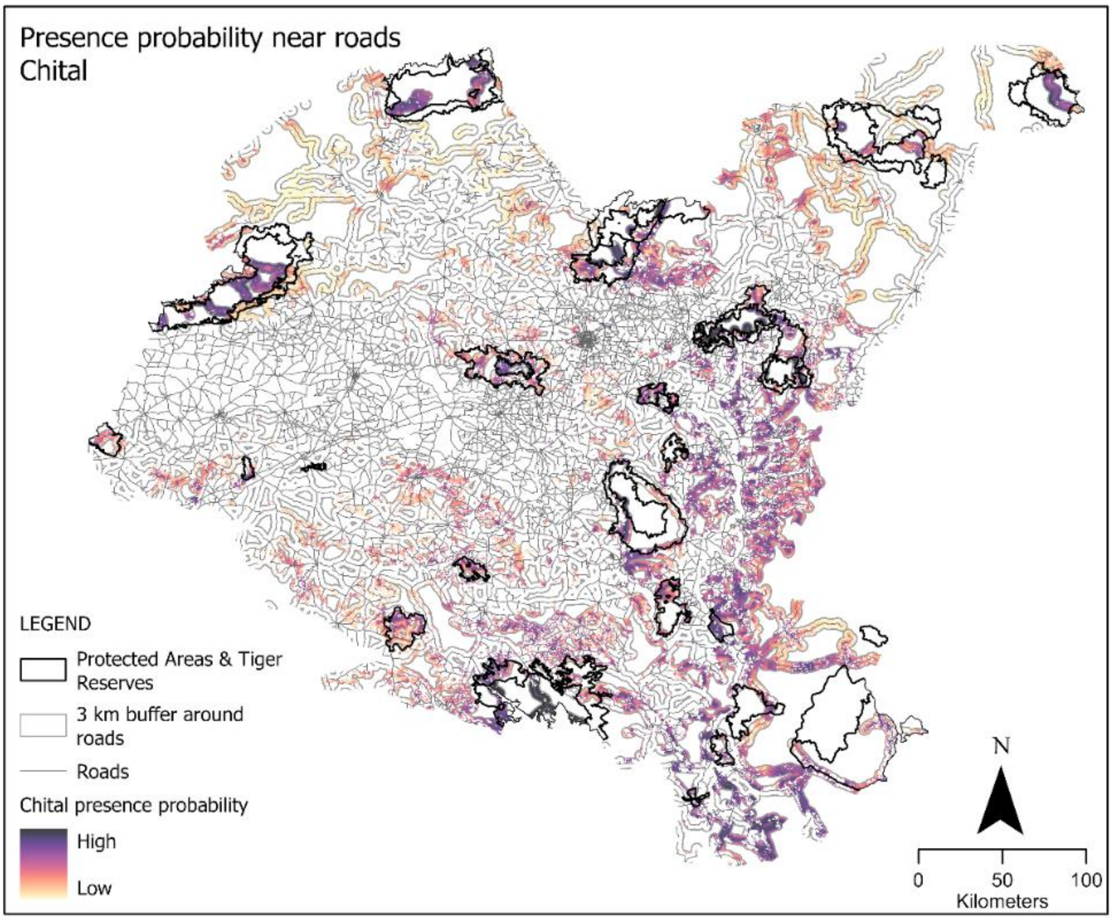


Figure 6.3. Presence probability map of chital within a 3 km buffer around roads in the central Indian landscape as predicted by habitat use analysis.

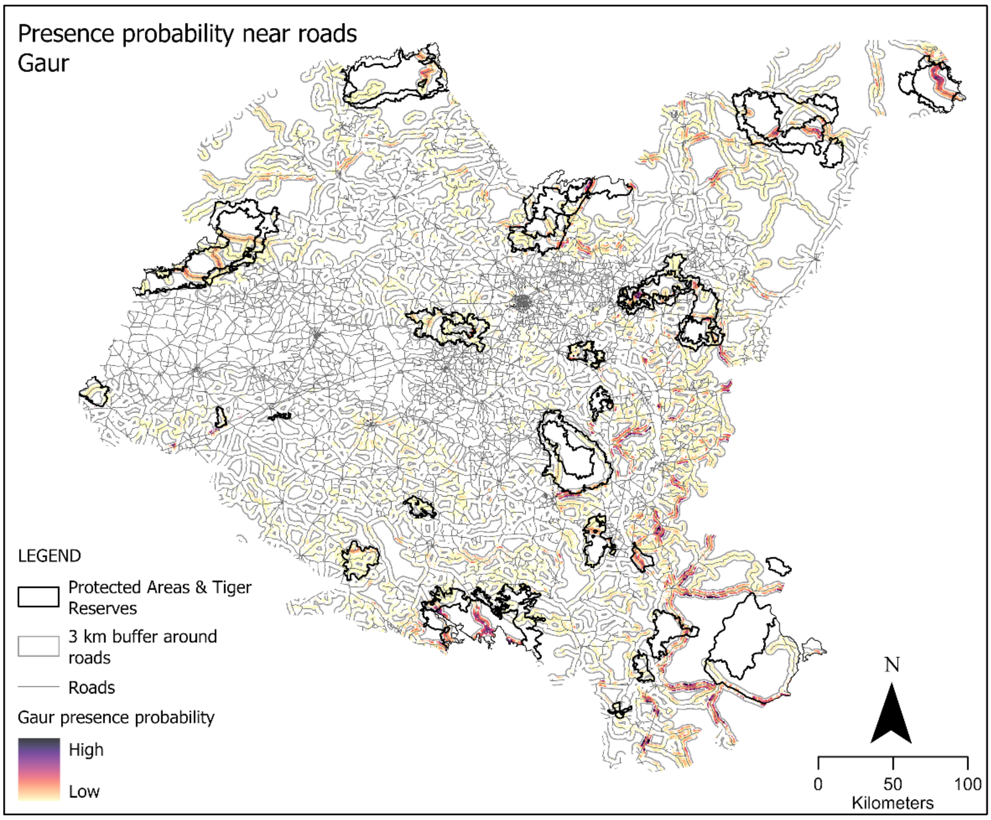


Figure 6.4. Presence probability map of gaur within a 3 km buffer around roads in the central Indian landscape as predicted by habitat use analysis.

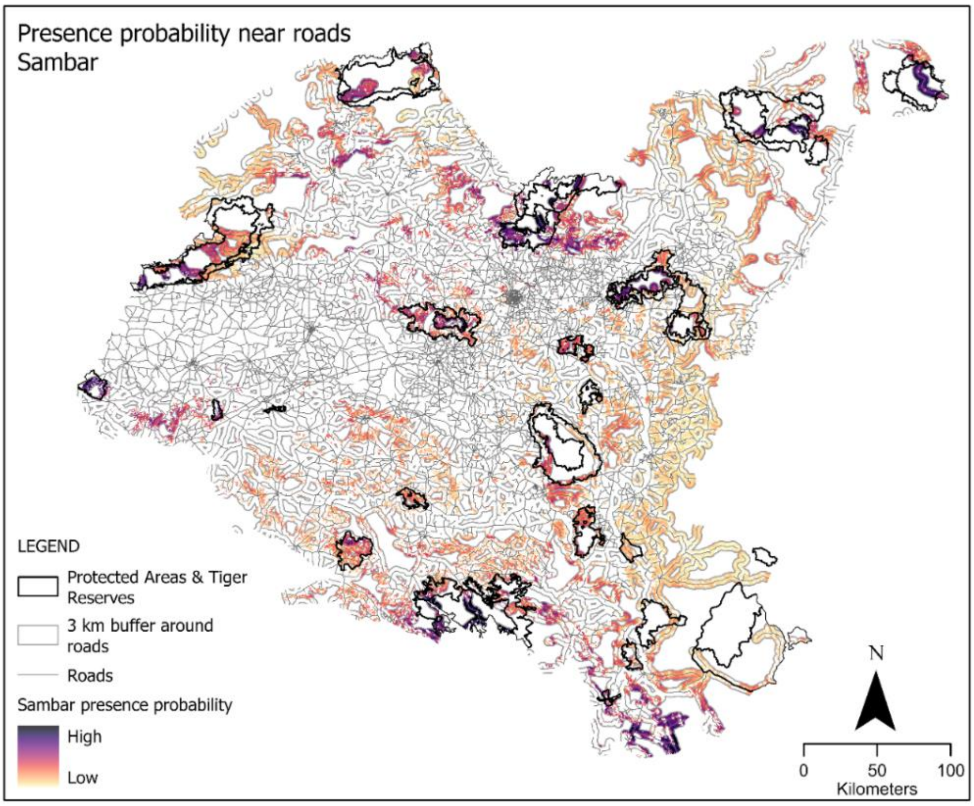


Figure 6.5. Presence probability map of sambar within a 3 km buffer around roads in the central Indian landscape as predicted by habitat use analysis.

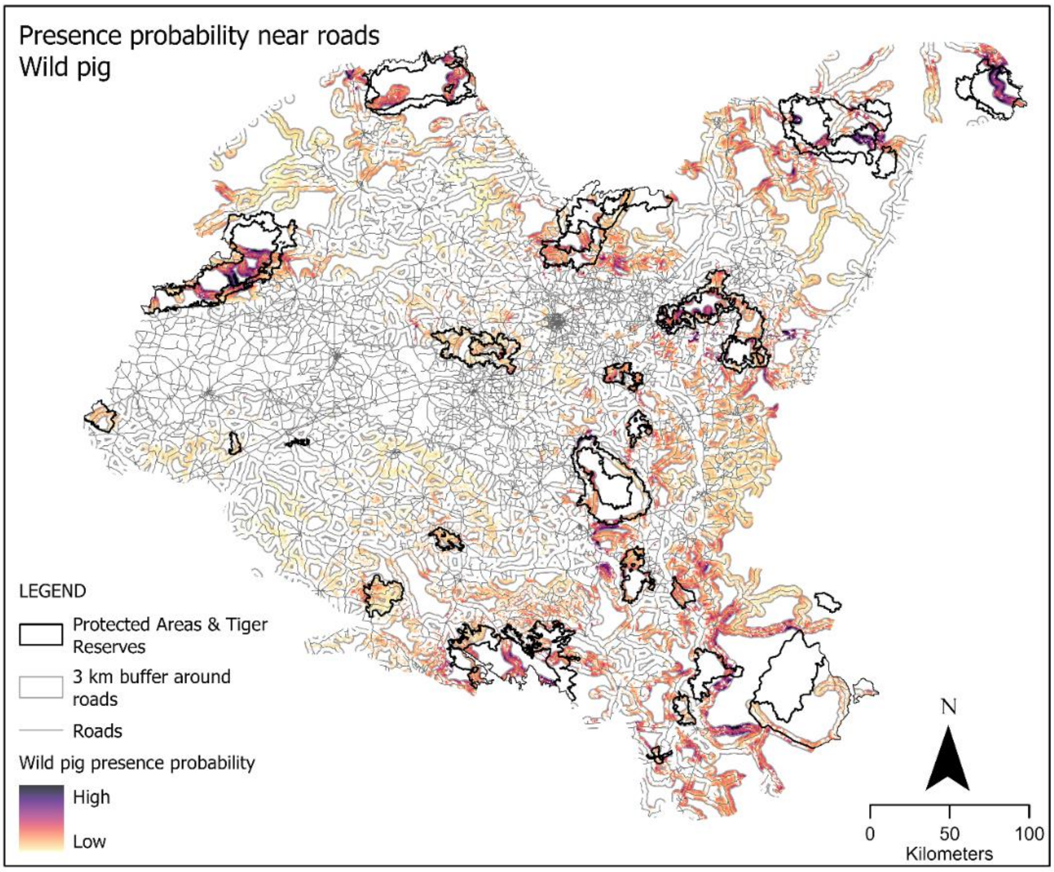


Figure 6.6. Presence probability map of wild pig within a 3 km buffer around roads in the central Indian landscape as predicted by habitat use analysis.

6.3.2. Species-specific barrier and collision likelihood index

For the six study species, more roads in the landscape presented a high-medium likelihood of barrier to movement than a collision risk (Supplementary Figs. A6.9 (a-f) and A6.10 (a-f)). More than 25% of the tarred roads in the landscape posed a high-medium barrier likelihood for chital, gaur, sambar and wild pig, while more than 40% of the roads in the landscape posed a high-medium barrier likelihood for leopard and tiger. Moreover, less than 10% of tarred roads in the landscape posed a high-medium collision risk for gaur, sambar and wild pig, while >10% of roads were of high-medium collision risk for chital, leopard and tiger. More roads posed high-medium barrier likelihood for leopard and tiger (19023.75 km), compared to equivalent collision likelihood (8404.5 km) (Table 6.6).

Table 6.6. Lengths of tarred roads in central Indian landscape under different barrier and collision likelihood categories for six species.

Species	***Length (in km) of tarred roads under collision and barrier likelihood categories***							
	High		**Medium**		**Low**		**None**	
	Barrier	**Collision**	**Barrier**	**Collision**	**Barrier**	**Collision**	**Barrier**	**Collision**
Chital	758.22	1383.07	2486.48	2874.72	5448.20	2122.77	23807.32	26119.65
Gaur	1063.02	396.45	3039.97	1635.37	4589.91	4348.73	23807.32	26119.65
Sambar	975.52	703.96	4279.82	2050.04	3437.55	3626.56	23807.32	26119.65
Wild pig	929.07	728.82	3855.24	1519.80	3821.28	4086.27	23894.63	26165.32
Leopard	2311.17	1835.76	6990.23	2044.13	4969.05	2761.27	18229.77	25859.05
Tiger	2296.81	1621.28	7425.54	2903.35	4548.09	2116.53	18229.77	25859.05

6.3.3. Multi-species priority barrier and collision mitigation zones

At least 10% of the roads in all corridors posed a high-medium multi-species barrier likelihood, the highest percentage being in the Tadoba-Indravati and NNTR-Bor-TATR corridor. Most TRs in the landscape have tarred road lengths > 100 km, with the exception of Achanakmar and Pench-MP. About 103.4 km of tarred roads within Navegaon-Nagzira posed a high-medium barrier to animal movement, followed by Indravati (62.7 km) and Kanha (40 km). Among non-TR PAs, Painganga has the longest length of tarred roads (97 km), while all others have road lengths < 30 km. Consequently, Paingana and Dhyanganga WLS have the largest proportion of roads that pose high-medium barrier likelihood in the landscape (Fig. 6.7, Supplementary Table A6.2).

About 3735.5 km of tarred roads in the landscape pose a high-medium multi-species collision risk to wildlife (Fig. 6.8). In corridor areas outside PAs, 2656.5 km of roads pose a high-medium collision risk to wildlife, with the highest length of such roads intersecting the Tadoba-Indravati corridor (915 km), and the NNTR-Bor-TATR corridor (500.8 km). Within TRs, 117 km of tarred roads inside Melghat and 102.7 km within Satpura pose high-medium collision risk. Most WLS in the landscape have road lengths <20 km that pose high-medium collision risk, with the exception of Painganga WLS (60 km).

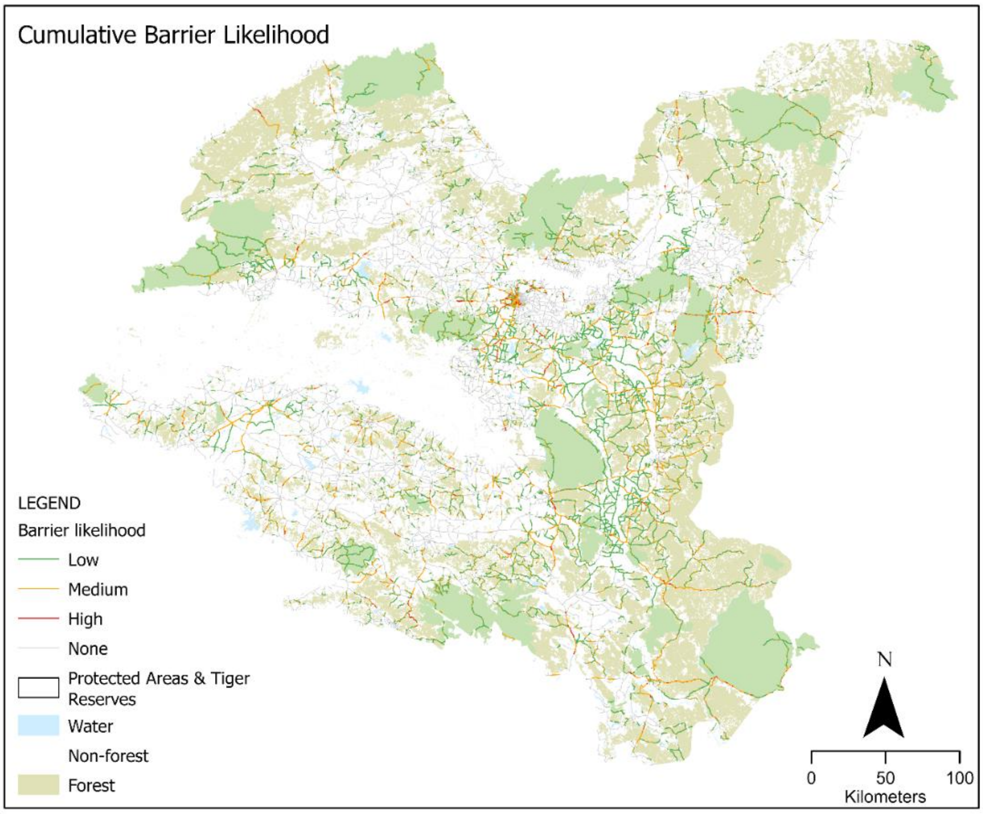


Figure 6.7. Cumulative or multi-species barrier likelihood map for the central Indian landscape.

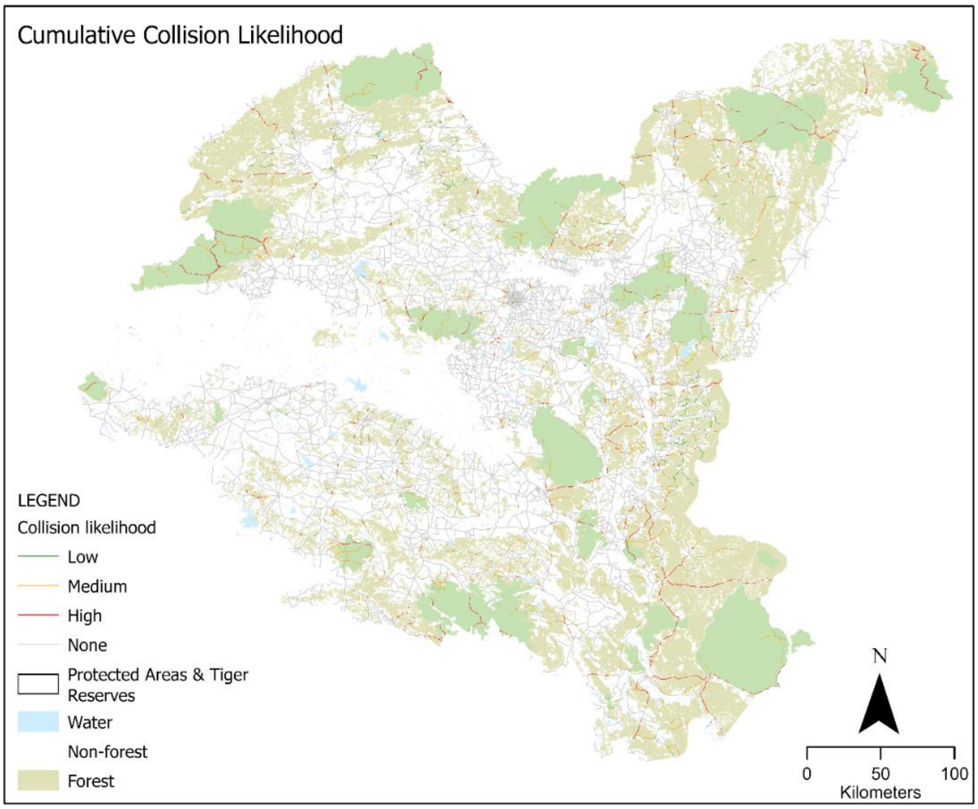


Figure 6.8. Cumulative or multi-species collision likelihood map for the central Indian landscape.

Corridor-wise barrier and collision priority mitigation zones

A. Kanha-Achanakmar Corridor

The Kanha-Achanakmar corridor connecting Kanha (with Phen WLS) and Achanakmar TRs, along with Bhoramdeo WLS has about 564 km of roads, of which 83 km roads pose a high-medium barrier to animal movement. These include 46.4 km of roads within PAs and 36.8 km of roads in forests outside PAs (Fig. 6.9 and Table 6.7). Most of the roads posing high-medium barrier likelihood are 2-lane roads (73 km).

Outside PAs 110 km of roads in the corridor pose high-medium collision risk (Fig. 6.10). Within TRs, Kanha (69.6 km) and Achanakmar (40.6 km) pose high-medium collision risk. 2-lane roads (213.6 km) pose the most collision risk in the corridor, including areas within and outside PAs.

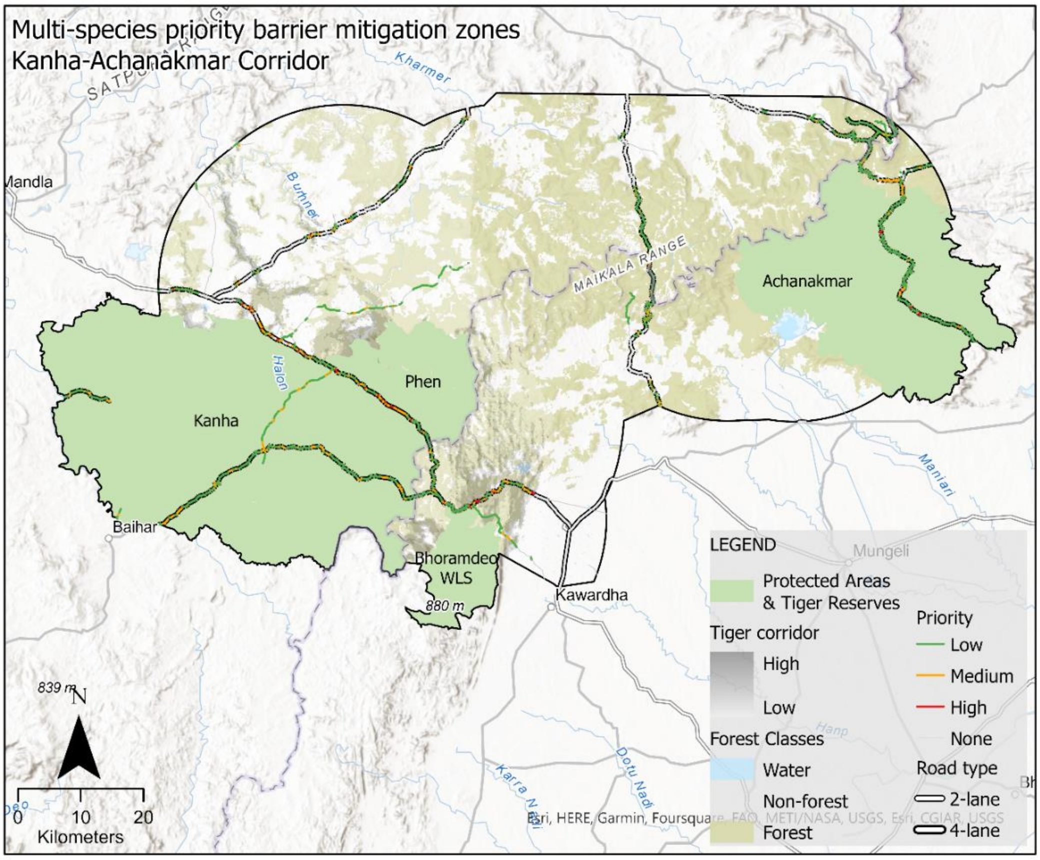


Figure 6.9. Multi-species priority barrier mitigation zones for the Kanha-Achanakmar Corridor in the central Indian landscape.

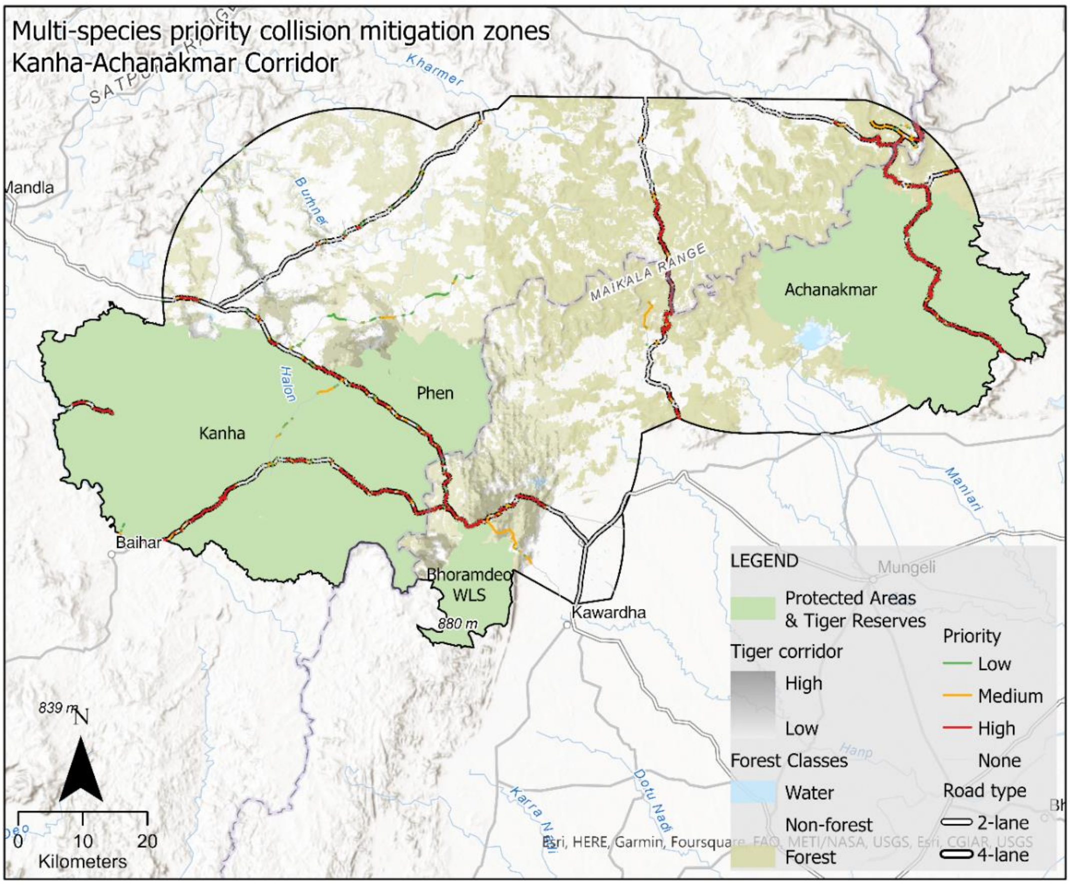


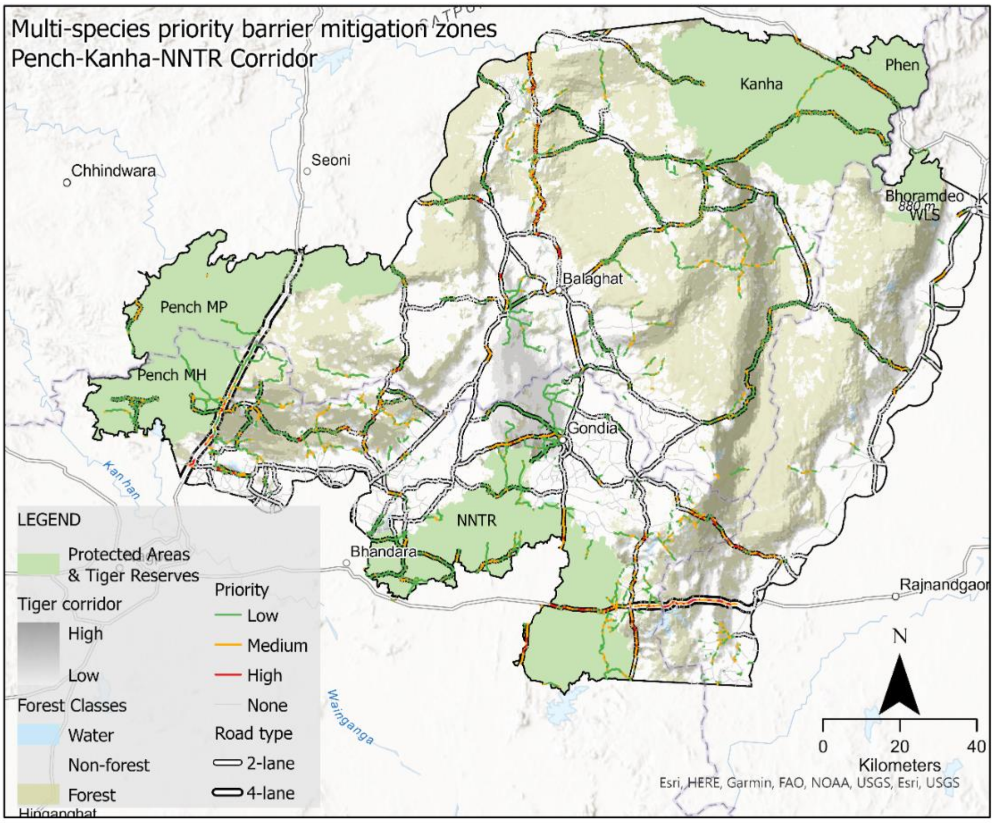
Figure 6.10. Multi-species priority collision mitigation zones for the Kanha-Achanakmar Corridor in the central Indian landscape.

Table 6.7. Sums of road lengths under different categories of multi-species priority barrier and collision mitigation zones in the Kanha-Achanakmar Corridor in the central Indian landscape.

Area	***Length of roads posing barrier (km)***			***Length of roads posing collision risk (km)***		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
Bhoramdeo WLS	0.37	0.29	5.94	4.79	1.47	
Achanakmar	1.99	3.63	37.59	39.51	1.17	
Kanha	4.55	35.58	78.82	57.71	11.88	6.74
Outside PAs	3.97	32.86	154.20	63.76	46.41	37.63

B. Pench-Kanha-NNTR Corridor

The Pench-Kanha-NNTR Corridor between Pench (MP and Maharashtra), Kanha and Navegaon-Nagzira TRs and intervening forests have about 4515 km of roads. Within TRs, >30% of roads within the Navegaon-Nagzira TR pose high-medium barrier to animal movement. In the intervening forests, about 490 km of roads pose high-medium barrier to animal movement (Table 6.8). High-medium barrier roads comprise of around 351 km of 2-lane roads and 73 km of 4-lane roads, including roads within and outside PAs (Fig. 6.11). A total of 637.7 km of tarred roads pose a high-medium collision risk within the corridor (Fig. 6.12 and Table 6.8). About 268 km of roads within PAs and TRs, and 369.4 km of roads outside PAs and TRs pose a high-medium collision risk. 2-lane roads pose the greatest collision threat (435 km), followed by single-lane roads (145 km). 4-lane roads measuring 57 km pose a high-medium collision risk.



Esri, HERE, Garmin, FAO, NOAA, USGS, Esri, USGS

Figure 6.11. Multi-species priority barrier mitigation zones for the Pench-Kanha-NNTR Corridor in the central Indian landscape.

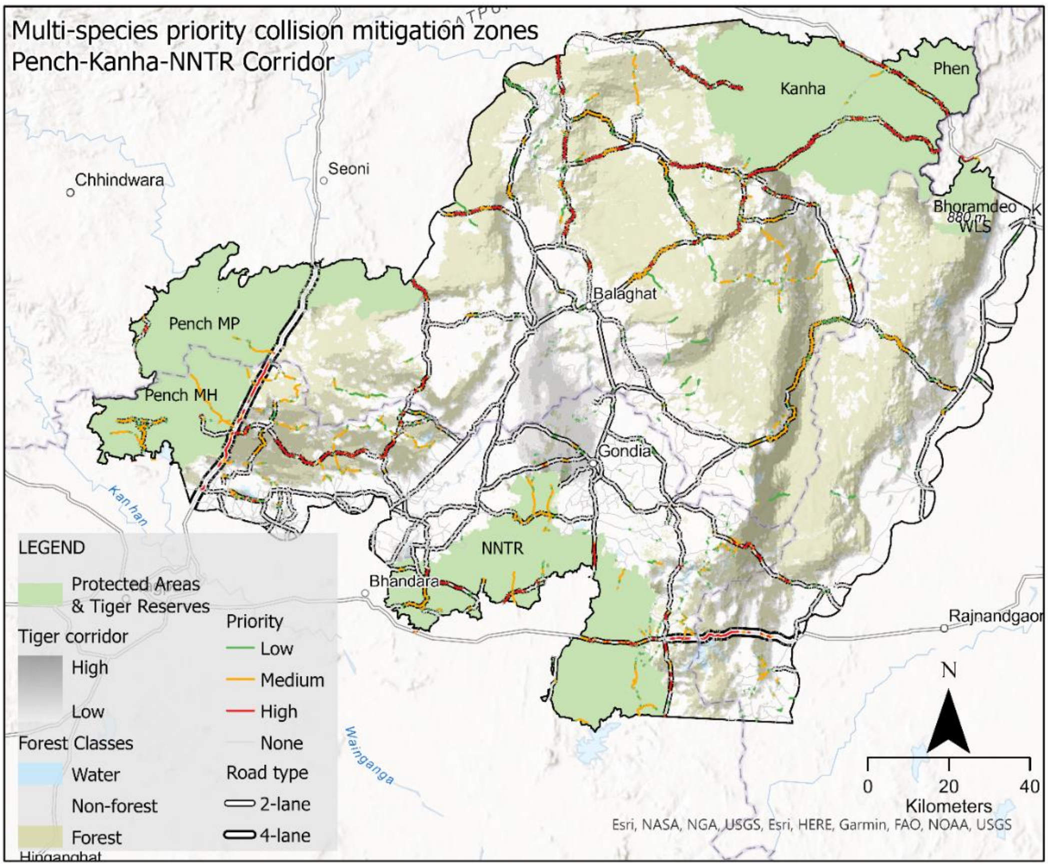


Figure 6.12. Multi-species priority collision mitigation zones for the Pench-Kanha-NNTR Corridor in the central Indian landscape.

Table 6.8. Sums of road lengths under different categories of multi-species priority barrier and collision mitigation zones in the Pench-Kanha-NNTR Corridor in the central Indian landscape.

Area	***Length of roads posing barrier (km)***			***Length of roads posing collision risk (km)***		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
NNTR	19.53	83.85	211.45	32.41	84.66	31.78
Pench-MH	2.25	17.48	80.99	9.06	54.54	6.15
Pench-MP		8.53	20.57	3.04	8.78	3.93
Kanha	4.55	35.58	78.82	57.71	11.88	6.74
Bhoramdeo WLS	0.37	0.29	5.94	4.79	1.47	
Outside PAs	65.96	425.40	1024.51	122.45	246.95	474.09

C. *Pench-Satpura-Melghat-Bor Corridor*

The Pench-Satpura-Melghat-Bor Corridor comprising of Pench (MP and Maharashtra), Satpura, Melghat and Bor TRs and intervening forests is intersected by 7344 km of roads. Within TRs, Bor and Melghat have 54 and 55 km each of roads posing medium barrier risk for animal movement (Table 6.9). In the intervening forests, about 608 km of roads pose high-medium barrier to animal movement (Fig. 6.13). Within TRs, 46.66 km of roads within Melghat pose a medium barrier risk to animal movement. A majority of the roads in the landscape that pose a high-medium barrier are 2-lane roads (479 km) followed by single-lane (155 km) and 4-lane roads (140 km).

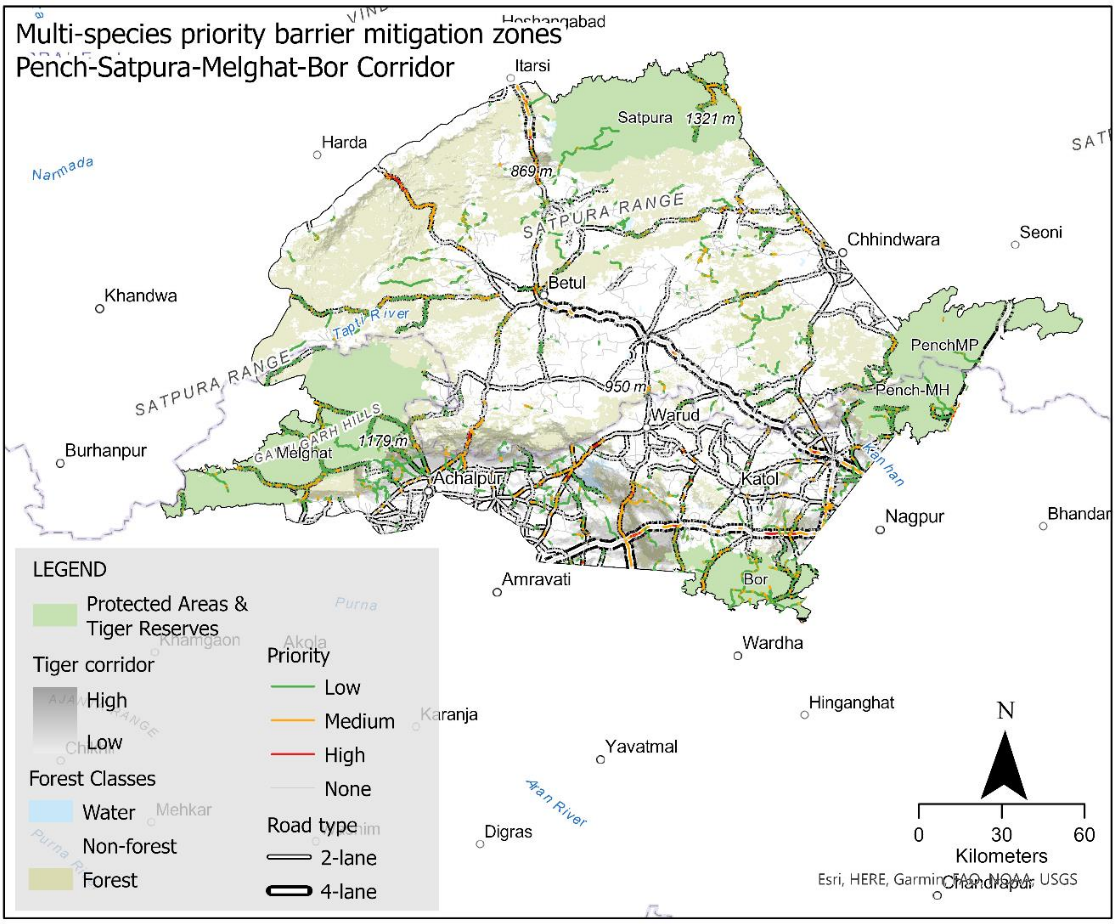


Figure 6.13. Multi-species priority barrier mitigation zones for the Pench-Satpura-Melghat-Bor Corridor in the central Indian landscape.

A total of 839 km of tarred roads pose a high-medium collision risk within the corridor (Fig. 6.14 and Table 6.9). About 482 km of roads within PAs and TRs, and 356 km of roads outside PAs and TRs pose a high-medium collision risk. 2-lane roads pose the greatest collision threat (611 km), followed by single-lane roads (188 km). 4-lane roads measuring 39.5 km pose a high-medium collision risk.

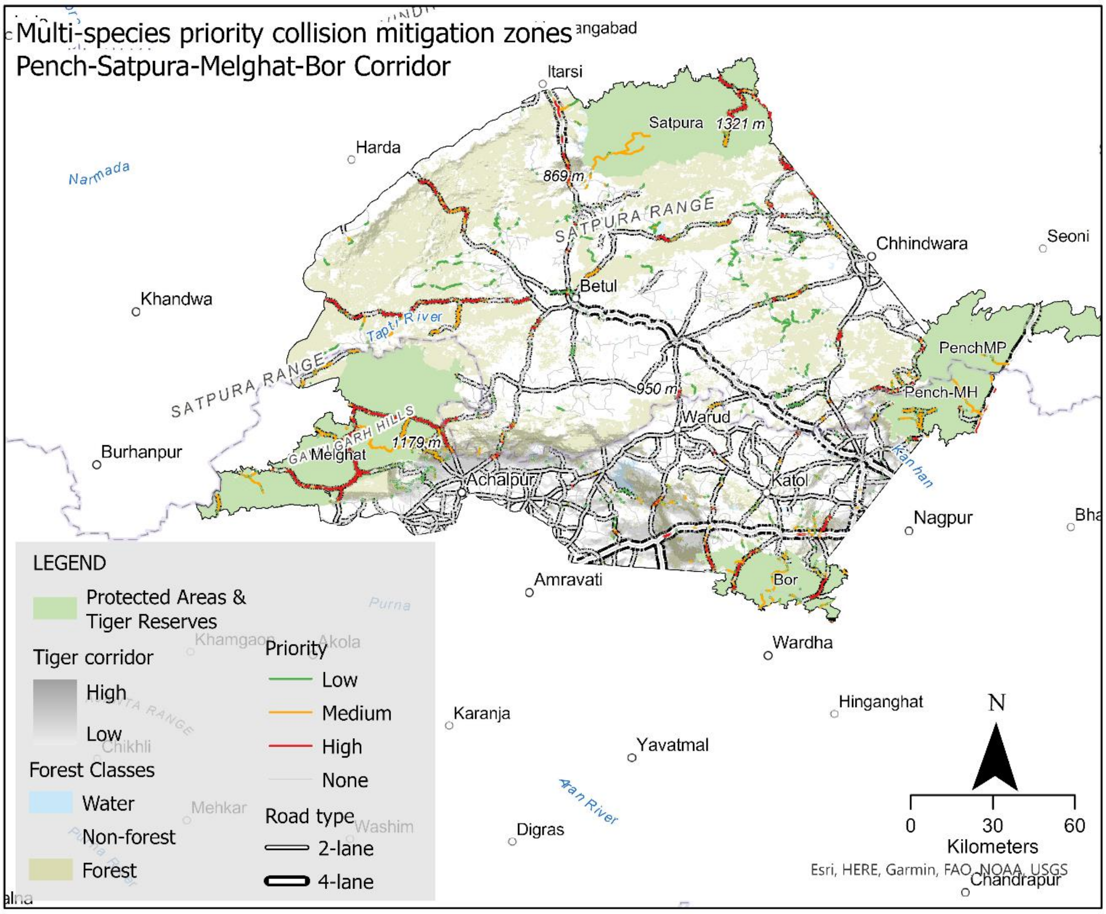


Figure 6.14. Multi-species priority collision mitigation zones for the Pench-Satpura-Melghat-Bor Corridor in the central Indian landscape.

Table 6.9. Sums of road lengths under different categories of multi-species priority barrier and collision mitigation zones in the Pench-Satpura-Melghat-Bor Corridor in the central Indian landscape.

Area	*Length of roads posing barrier (km)*			*Length of roads posing collision risk (km)*		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
Bor	0.82	54.07	134.39	31.26	49.13	22.10
Melghat		55.03	217.44	121.48	102.58	21.57
Pench-MH	2.25	17.48	80.99	9.06	54.54	6.15
Pench-MP		8.53	20.57	3.04	8.78	3.93
Satpura		29.12	88.56	41.29	61.47	6.03
Outside PAs	63.26	544.70	6013.26	129.05	227.59	547.55

D. NNTR-Bor-TATR Corridor

The NNTR-Bor-TATR Corridor connecting Navegaon-Nagzira, Bor, Tadoba-Andhari TRs, Umred Karhandla and Ghodazari WLS, and intervening forests is intersected by 7802 km of tarred roads (Fig. 6.15). Within TRs, 103 km of tarred roads in Navegaon-Nagzira pose a high-medium barrier to animal movement, while the majority of roads inside Tadoba-Andhari (108 km) pose a medium-low barrier to animal movement. Roads outside PAs pose a greater barrier to animal movement within the intervening forests with 1560 km of roads posing a high-medium barrier (Table 6.10). Within the corridor and PAs, fewer lengths of roads pose a high barrier to animal movement (single: 16 km, 2-lane: 95.35 km, 4-lane: 95.86 km), while 2-lane roads (728.38 km) followed by single-lane roads (484.5 km) pose a medium barrier. Most of these high-medium barrier roads lie outside the PAs.

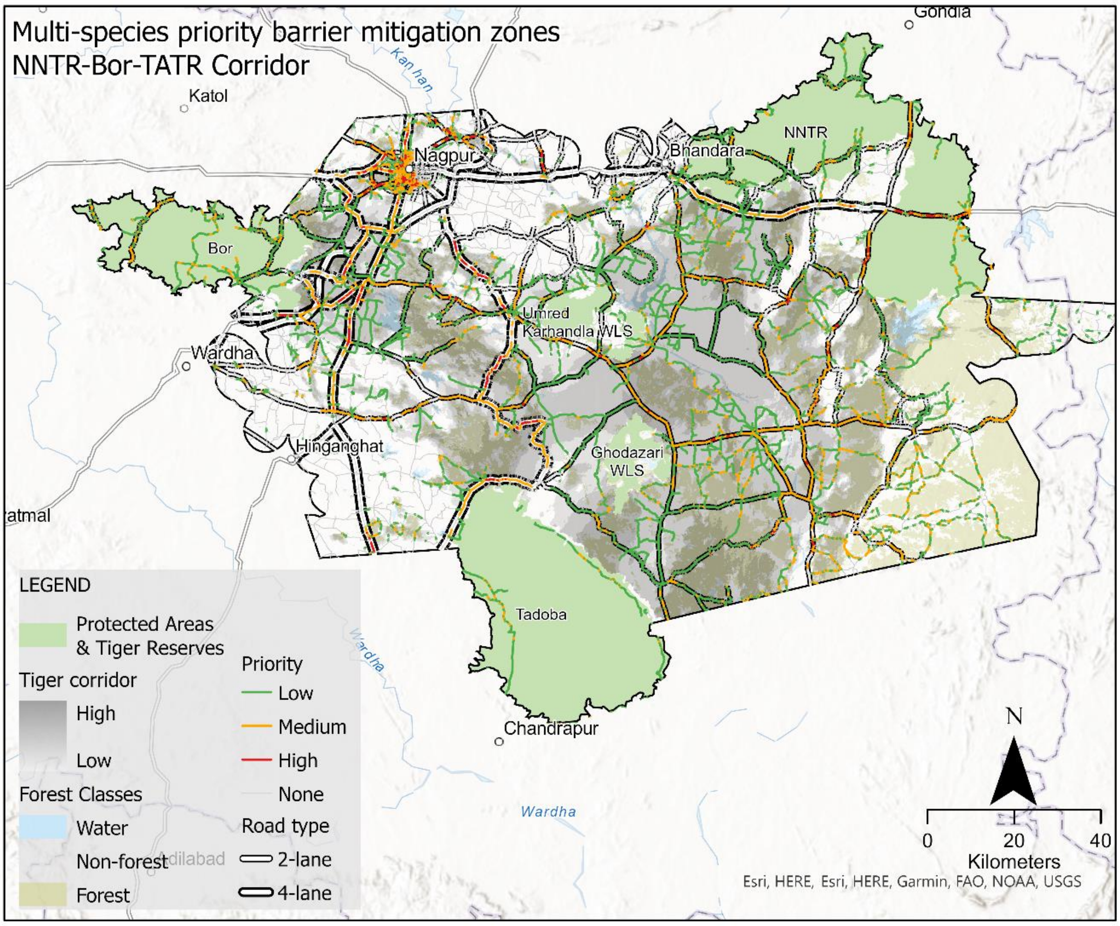


Figure 6.15. Multi-species priority barrier mitigation zones for the NNTR-Bor-TATR Corridor in the central Indian landscape.

A total of 738 km of tarred roads pose a high-medium collision risk within the corridor (Fig. 6.16 and Table 6.10). Most of these roads are outside PAs (500 km), while 237 km of such roads lie within PAs and TRs. 2-lane roads pose the greatest collision threat (421 km), followed by single-lane roads (221 km). 4-lane roads measuring 31 km pose a medium collision risk.

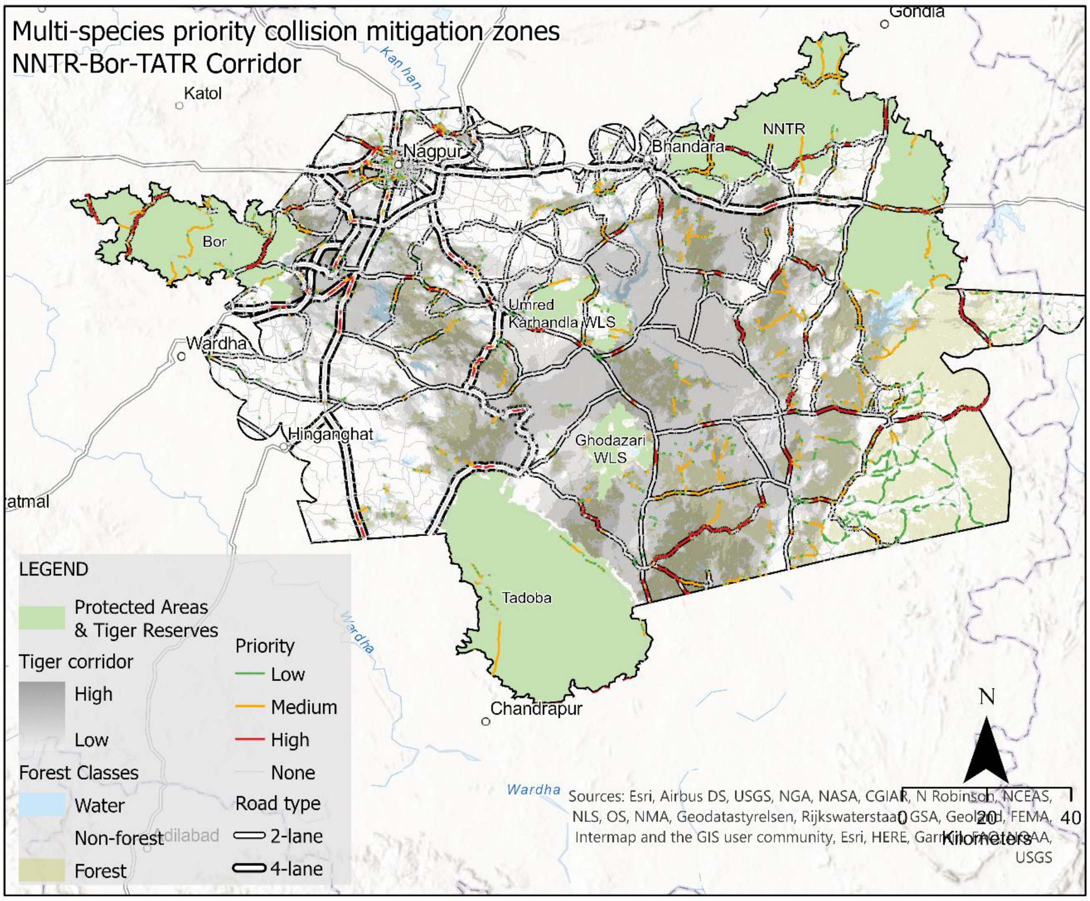


Figure 6.16. Multi-species priority collision mitigation zones for the NNTR-Bor-TATR Corridor in the central Indian landscape.

Table 6.10. Sums of road lengths under different categories of multi-species priority barrier and collision mitigation zones in the NNTR-Bor-TATR Corridor in the central Indian landscape.

Area	***Length of roads posing barrier (km)***			***Length of roads posing collision risk (km)***		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
Bor	0.82	54.07	134.39	31.26	49.13	22.10
NNTR	19.53	83.85	211.45	32.41	84.66	31.78
Tadoba	0.69	13.49	94.52	3.12	19.53	16.48
Umred Karhandla		5.91	21.88		17.65	2.71
Outside PAs	186.22	1373.68	2438.17	201.78	299.05	667.66

E. TATR-Indravati Corridor

The Tadoba-Indravati Corridor connecting the Tadoba-Andhari, Kawal and Indravati Trs, Kanhargaon, Chaprala, Pranhita, Bhamragarh, Bhairamgarh and Lanja-Madugu Sivaram WLS, and intervening forests is intersected by 5999 km of tarred roads. Of these, about 1691 km of roads pose a high-medium barrier to animal movement (Fig. 6.17 and Table 6.11). Indravati is intersected by 62.7 km of roads that pose high-medium barrier risk, which is the highest among all TRs. Kanhargaon WLS is intersected by 26.6 km of tarred roads, of which 4.76 km pose a high-medium barrier risk. Within the entire corridor, high-medium barrier is posed mainly by 2-lane roads (805 km), followed by single-lane roads (477 km) and 4-lane roads (410 km). Most of these roads are present outside PAs.

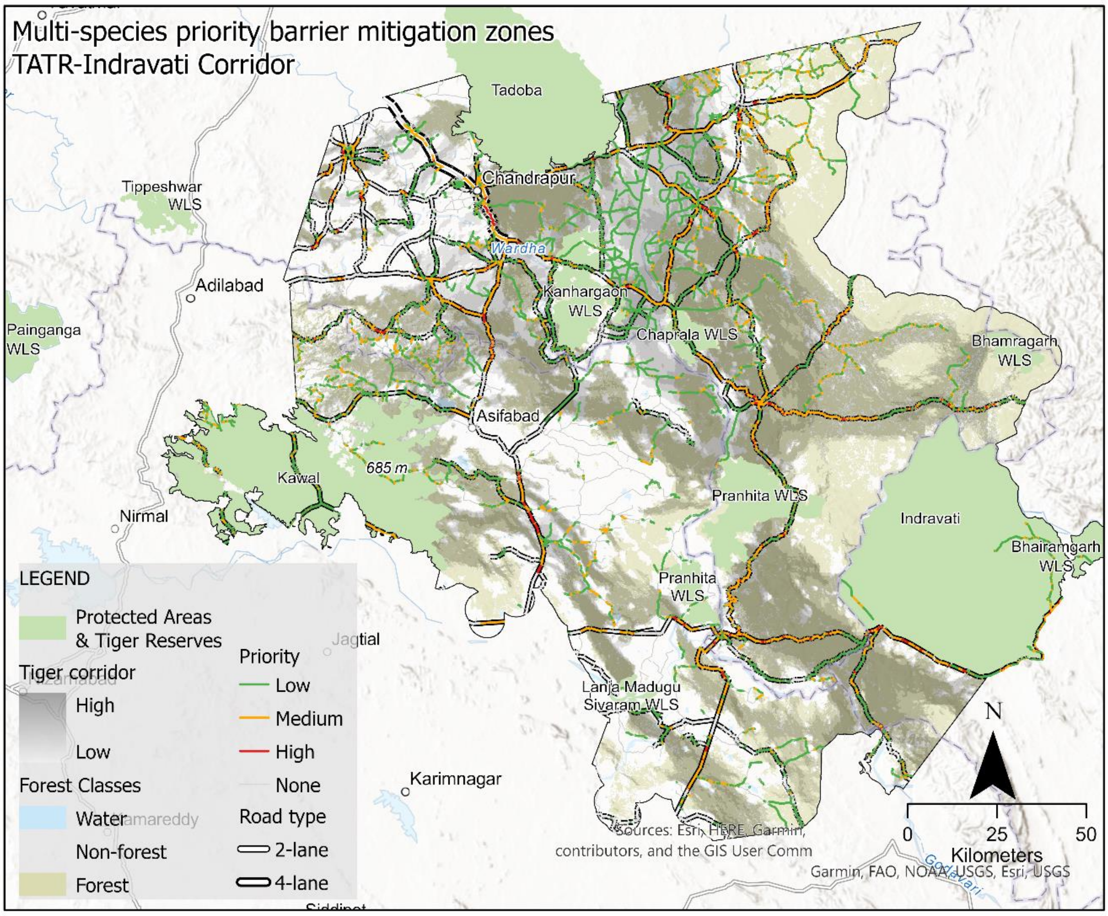


Figure 6.17. Multi-species priority barrier mitigation zones for the TATR-Indravati Corridor in the central Indian landscape.

A total of 1150 km of tarred roads pose a high-medium collision risk within the corridor (Fig. 6.18 and Table 6.11). The majority of these roads are outside PAs (914 km), while 235 km of such roads lie within PAs and TRs. 2-lane roads pose the greatest collision threat (840 km), followed by single-lane roads (303 km). 4-lane roads measuring 7 km pose a medium collision risk.

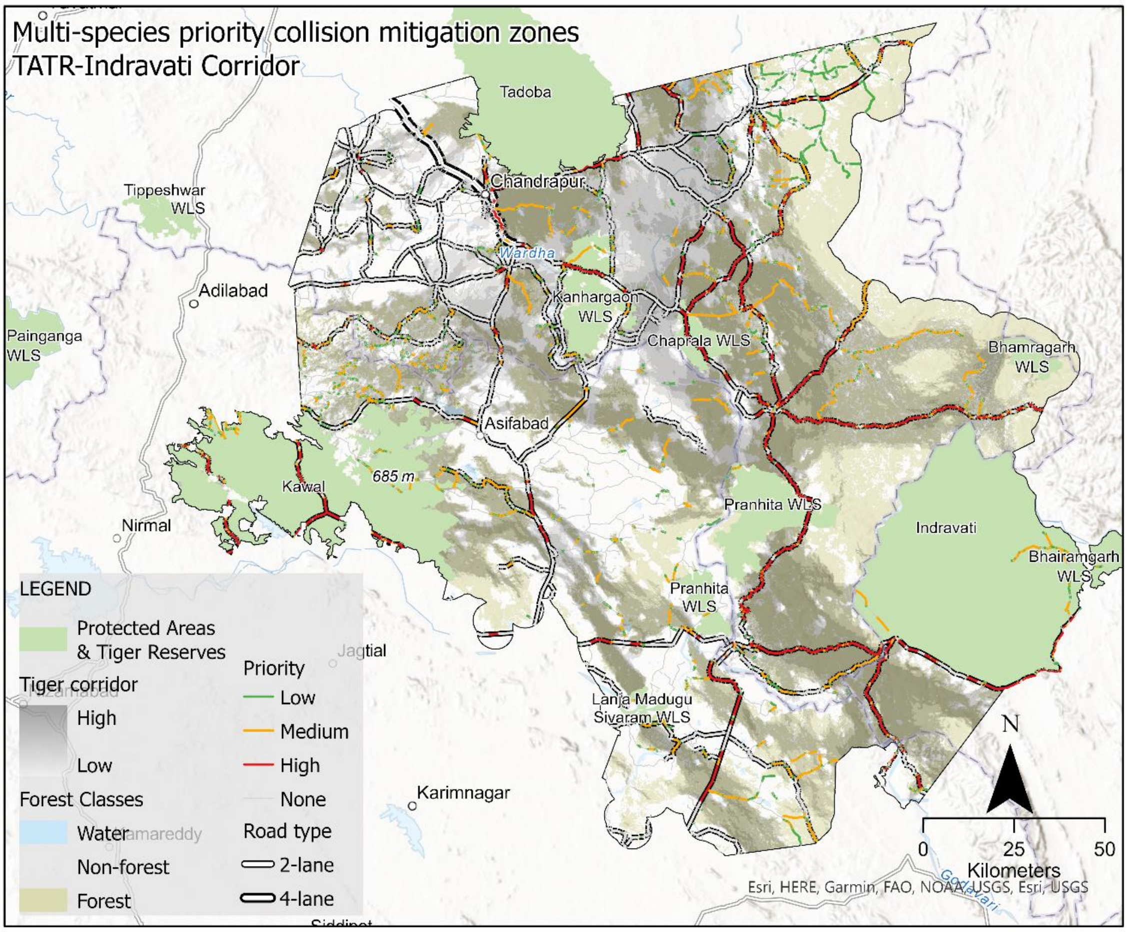


Figure 6.18. Multi-species priority collision mitigation zones for the TATR-Indravati Corridor in the central Indian landscape.

Table 6.11. Sums of road lengths under different categories of multi-species priority barrier and collision mitigation zones in the TATR-Indravati Corridor in the central Indian landscape.

Area	***Length of roads posing barrier (km)***			***Length of roads posing collision risk (km)***		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
Bhairamgarh WLS	0.40	0.81	8.15	0.14	0.52	2.97
Chaprala WLS		3.80	15.61	17.21	1.50	
Kanhargaon WLS	0.28	4.49	21.82	11.03	11.73	3.07
Lanja Madugu Sivaram WLS		0.24	6.91		4.85	2.07
Pranhita WLS	1.10	2.84	14.02	5.27	3.06	6.64
Indravati	11.61	51.12	79.34	40.48	19.91	37.68
Kawal		41.12	104.53	56.64	40.45	17.90
Tadoba	0.69	13.49	94.52	3.12	19.53	16.48
Outside PAs	186.22	2438.17	1373.68	396.76	517.95	763.15

F. Kawal-Tipeshwar-Dhyanganga Corridor

The Kawal-Tipeshwar-Dhyanganga Corridor connects the Kawal TR with Tipeshwar, Painganga, Karanjasohol, Katepurna and Dhyanganga WLS and intervening forests, and is intersected by 7188 km of tarred roads. Of these, about 1070 km pose a high-medium barrier risk to animal movement (Fig. 6.19 and Table 6.12). Within PAs, Painganga WLS is intersected by 14 km of tarred roads that pose a medium barrier risk. About 870 km of 2-lane roads pose high-medium barrier to animal movement in the corridor, followed by single-lane roads (200 km) that pose a medium risk. Most of these roads are outside PAs.

A total of 560 km of tarred roads pose a high-medium collision risk within the corridor (Fig. 6.20 and Table 6.12). The majority of these roads are outside PAs (373.7 km), while 186 km of such roads lie within PAs and TRs. 2-lane roads pose the greatest collision threat (438.5 km), followed by single-lane roads (121.4 km).

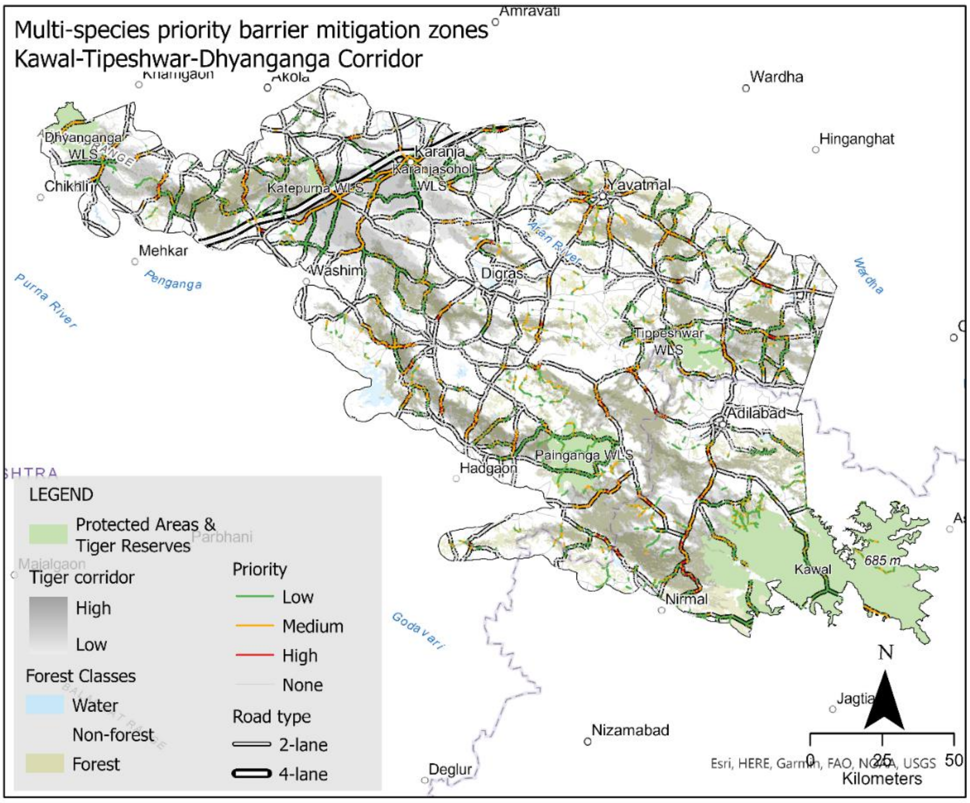


Figure 6.19. Multi-species priority barrier mitigation zones for the Kawal-Tipeshwar-Dhyanganga Corridor in the central Indian landscape.

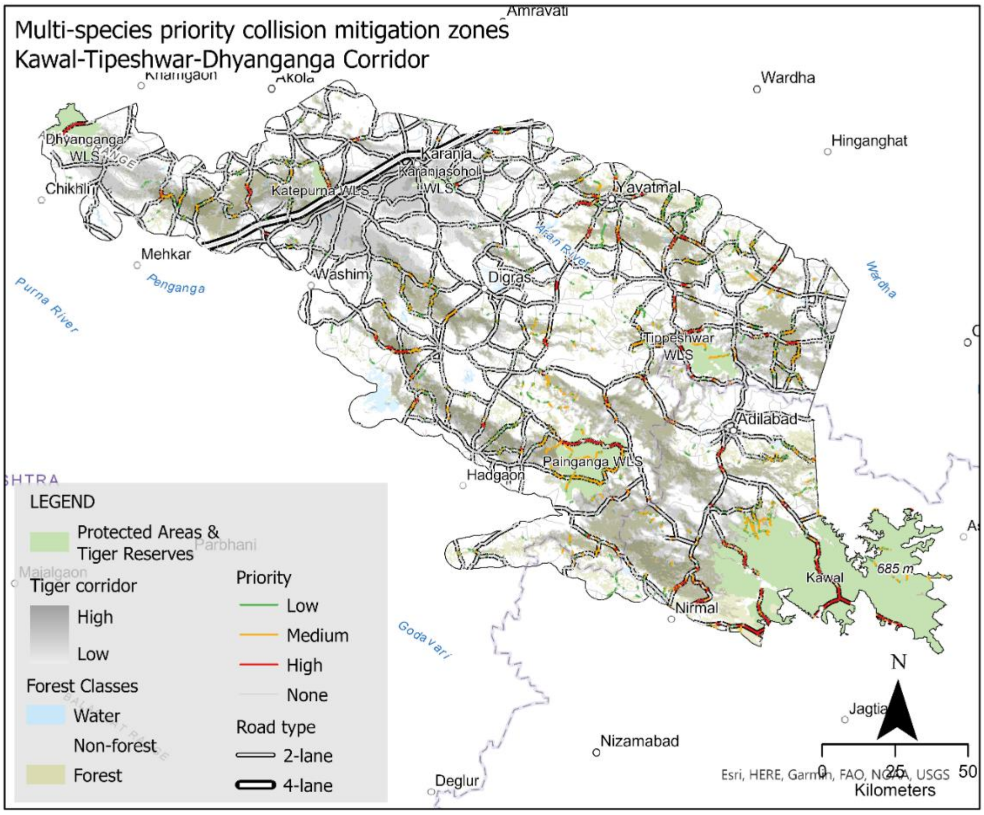


Figure 6.20. Multi-species priority collision mitigation zones for the Kawal-Tipeshwar-Dhyanganga Corridor in the central Indian landscape.

Table 6.12. Sums of road lengths under different categories of multi-species priority barrier and collision mitigation zones in the Kawal-Tipeshwar-Dhyanganga Corridor in the central Indian landscape.

Area	***Length of roads posing barrier (km)***			***Length of roads posing collision risk (km)***		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
Dhyanganga WLS	0.11	11.38	4.10	12.16	2.40	0.87
Karanjasohol WLS		0.34	1.44			
Katepurna WLS	1.07	2.17	0.57	1.53	1.64	0.07
Painganga WLS		14.36	82.65	14.55	45.56	10.84
Tippeshwar WLS		1.18	16.56	1.57	9.66	6.09
Kawal		41.12	104.53	56.64	40.45	17.90
Outside PAs	112.61	886.37	1296.96	111.74	262.04	503.88

6.4. Discussion

Real-time animal movement and mortality data is not always available to inform locations and target species for measures to mitigate barrier and collision because of road networks. In such a scenario, multiple approaches utilising mostly ecological data viz., animal mortality, presence, movement patterns have been used to delineate important mitigation sites. However, such approaches fail to include important road parameters such as traffic volume, road type and traffic speeds, and are limited to single roads or small road networks. I attempted to combine previous research on the influence of the interaction between species and traffic characteristics on animal mortality and barrier (Saxena et al., 2020) with a simple intuitive rule-based framework for spatially assessing landscape-wide barrier and collision likelihood in an ‘exposure-hazard’ framework (Visintin et al., 2016). The present analysis has calculated landscape-wide probable barrier and collision zones that can be used to decide priority of mitigation measures. The framework can be extended to include multiple other species found in the landscape.

Considering the small size of PAs and TRs in the country and landscape, animal movement, particularly of tiger, is essential to maintain long-term viability of these animal populations. Consequently, the rapid development and up-gradation of roads in the forests and corridors connecting these PAs can potentially lead to mortality of healthy, young dispersing tiger individuals and potentially decimate local populations surrounded by a matrix of roads.

Roads inside PAs can be vulnerable to comparatively higher animal mortalities because of high local animal abundance (Grilo et al., 2011). At the same time, PAs can act to buffer the adverse impacts of roads because of the possible absence of associated human activity and presence of good quality habitat (Burson et al., 2000; Sangiwa et al., 2019). Within the PAs and TRs in the central Indian landscape, I found relatively less lengths of roads causing barriers to movement, but greater lengths of tarred roads vulnerable to animal mortality because of high animal presence probabilities, particularly in PAs and TRs like Melghat and Painganga that have large lengths of such roads (224 and 60 km respectively). However, road construction within PAs is highly regulated. With the exception of wide roads (e.g. high speed trunk roads in NNTR) where structural mitigation measures would be required, the mitigation of barrier and collision in these roads can be achieved through regulation of traffic volumes and temporal closures (Gubbi et al., 2012; van Langevelde and Jaarsma, 2009).

Besides causing barriers to animal movement, road-induced mammal mortality outside PAs (Garriga et al., 2012) can have greater impacts on populations, by removing fit dispersing individuals of a population (Bujoczek et al., 2011) and by accelerating isolation of already fragmented animal populations (Cullen et al., 2016). For example, the road networks within the TATR-Indravati corridor followed by the NNTR-Bor-TATR corridor are highly prone to both barrier and collision effects for wildlife, with road lengths up to 2600 km posing high-medium risk. The region, apart from holding important source tiger populations like

Tadoba-Andhari TR in highly a highly fragmented human-dominated landscape, is also facing enormous developmental pressures. This holds true for all six corridors in the study area.

I found that while 2-lane roads made up for 44.8% of roads in the landscape second to single-lane roads (49.5%), they accounted for 61% and 72.7% of roads vulnerable to high-medium levels of barrier and collision risk respectively. The country is undergoing rapid road up-gradation of 2-lane roads to wider roads to accommodate increasing traffic volumes. While construction of new roads is not ecologically advisable (Forman, 2005; Ibisch et al., 2016; Jaeger et al., 2006), road up-gradation allows for opportunities to integrate mitigation measures such as crossing structures into the up-gradation plan (Habib et al., 2016). Thus, it is pertinent to take into account the category or lane status of roads in present circumstances.

The overarching principles to consider while prioritising road networks at the landscape scale for mitigation are (1) to minimise roads in and around large natural patches such as PAs and TRs, and (2) to maximise effective habitat connectivity between large natural patches, particularly wide corridors (Forman, 2005). Studies in the landscape have found large forest patches, high prey abundance and low human footprints as determinants of tiger occupancy (Jhala et al., 2020; Yumnam et al., 2014), all of which stand threatened in scenarios of rapid and extensive road development in the landscape. Moreover even in the presence of large intact and stepping stone habitats (Jaeger et al., 2006; Thatte et al., 2018), it is important to reduce possibility of animal mortality to help maintain local populations (Ceia-Hasse et al., 2018). Priority action for mitigating barrier effect should thus be at road sites intersecting wide corridors away from PAs, and then narrower corridors (even though the movement would be infrequent). Priority action for mitigating collisions should also be near PAs, TRs and forests with high local abundance of wildlife.

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Chapter 7

Conclusion & Synthesis

7.1. Introduction

Globally, roads are the most ubiquitous forms of human disturbance in natural areas. The construction of roads and the subsequent onset of vehicular traffic pose multiple deleterious effects on nature (Jackson, 2000; Laurance et al., 2009), with vast scientific literature attesting to the same. The impacts of roads on mammals like tigers and associated species are particularly severe because of attributes such as low population densities, low dispersal rates and large movement ranges, habitat specialisation, low reproductive rates and large body sizes (Bright, 1993; Rytwinski and Fahrig, 2011). In a landscape with high human densities and consequent developmental pressures like the central Indian landscape, roads and associated activities have the potential to endanger apex carnivores (Quintana et al., 2022). These impacts add up and affect the connectivity of natural landscapes, compromising their ability to support viable wildlife populations.

Road ecology has emerged as a discipline to provide ecologically sound solutions to the multifaceted impacts of roads on wildlife and nature. Information such as types and pathways of impacts, factors that make species vulnerable to these impacts, wildlife responses to different road-related components and threats, and the spatial and temporal variation of these responses provide sound an ecological basis for formulating measures to mitigate the impacts of roads. However, road ecology research in most of the developing world, especially south and south-east Asia, has not been keeping up with the rapid pace of infrastructure growth in these regions, leaving a major research lacuna.

With this background and rationale, I intended to produce a baseline of the ecological impacts of roads in the central Indian landscape through my study. I studied impacts and species' responses to impacts, predicted the extent of the road effect zone for select ungulates in the landscape, and attempted to delineate priority road segments for mitigation of barrier and collision risk in the landscape. The outputs of the study can help understand impacts of roads on Indian mammals better. This would further help managers, conservation professionals and user agencies plan and implement mitigation strategies to ensure that biodiversity conservation in this vital tiger conservation landscape does not come into conflict with goals of economic and infrastructure development.

7.2. Species relative abundance, activity and diversity near roads

Through an intensive camera trap-based sampling of the mammalian community near different segments of the National Highway 44, I found similar species richness near roadside habitat as compared to undisturbed habitat inside the park, and present levels of road-related disturbance are not causing environmental filtering of animal traits. As expected, the disturbance on the highway was found to cause avoidance of the roadside habitat by specialist disturbance-averse species. A significant finding was the comparatively low use of roadside habitat by carnivores, which has direct implications for indirect habitat loss and loss of connectivity, although avoidance also indicates lesser vulnerability to roadkill. Among ungulates and small mammals, intensity of use of roadside habitat could be interpreted by their habitat preferences and tolerance to disturbance. Consequently, the approach also helped understand the response of wildlife to crossing structures on the highway (Saxena and Habib, 2022a). Moreover I observed alterations in temporal activity patterns near the highway which is characteristic of wildlife response to human disturbance (Gaynor et al., 2018). Overall, the study found that species spatio-temporal responses to roads varied with species behaviour and has implications for species receptiveness of mitigation measures and vulnerability to road-related impacts. The importance of protected areas in buffering indirect impacts of roads on wildlife also emerged as an important finding, consequently the impacts of roads on wildlife would be more adverse in forests outside the purview of protection. Finally, the study also revealed the impact of construction of mitigation measures on the large mammalian community in the adjacent habitat through (a) restoration of near-natural spatio-temporal habitat use patterns by species earlier found avoiding the habitat, (b) reduction in use of roadside habitat by species earlier found exploiting roadside habitat, and (c) restoration of near-natural prey-predator activity overlaps.

7.3. Chital behaviour near National Highway 44

While camera trapping revealed the highest use of roadside habitat by chital, I further attempted to understand the behavioural mechanisms that enabled chital to use roadside habitat in the presence of human and vehicular disturbance. Based on findings of the previous chapter, I postulated that reduced use of roadside habitat by predators would result in a predator release situation, enabling chital to seek shelter from predation near the highway. Contrary to expectations, chital were more vigilant on the roadsides, while they spent the same proportion of time foraging as they would in the absence of human disturbance. High frequencies of feeding and vigilance bouts among chital at the roadsides indicated that they are in a state of constant vigilance in response to passing vehicles. Chital also did not exhibit behaviours such as resting, vocalising (rutting calls), and nursing at the roadsides, which could have implications for social interactions and communication for group-living species. The study also revealed differential perceptions of natural and human-caused threats through varied anti-predator behaviour employed by chital towards natural predators (inside the park), moving vehicles (high vigilance), and stationary vehicles and humans on foot (flight). There were no significant differences in average group sizes between sites (park and roadside), but larger groups near roadsides showcased reduced vigilance behaviours. Most significantly, the study revealed that the direct cost borne by chital of remaining vigilant against potential human threat is loss of feeding opportunities, i.e., chital at the roadsides have to continually choose between feeding more and being more vigilant. Thus, chital on the roadsides may be tolerant of apparently non-lethal human disturbance (vehicular traffic), but with sensitisation of direct human approach (humans on foot) which may be the reason behind heightened vigilance responses i.e., flight. The study highlights the ability of chital to adapt to areas used by humans, albeit with fitness and social costs that could have long-term consequences.

7.4. Ungulate habitat use near roads and road effect zones in the central Indian landscape

Central India is among the landscapes with the highest potential for long-term tiger conservation. In addition to presenting impediments to the movement and mortality of large carnivores, roads also decrease persistence of prey species that has direct consequences for large carnivore conservation. I assessed the factors affecting habitat use of four major prey species of the tiger and co-predators in the landscape across different road and forest protection types in the landscape. Like the results of the camera trapping exercise along NH 44, I found that protection of roadside habitat determines habitat use by wild ungulates. This implies that more roadkill of ungulates is expected on roads passing through or near protected areas. Conversely, the impacts of road-related disturbance would be higher on roads away from protected areas as these areas would have greater avoidance by certain species like gaur and sambar. Additionally, habitats near roads outside protected areas would also have increased presence of humans that would further impede use of such habitat by ungulates. Again, similar to the results of the camera trapping exercise, presence of wildlife crossing structures seemed to decrease the use of habitat near roads by species like wild pig and chital that were previously found to exploit roadside habitats. This change can be attributed to the relative increase of predator activity near roads post construction of crossing structures (Saxena and Habib, 2022a). Road effect zone estimates for the four ungulate species reflected the differences in responses to road and environmental characteristics and were wider near roads outside protected areas and narrow in the vicinity of protected areas. Finally, I found that road development scenarios involving construction of crossing structures especially in the vicinity of protected areas would benefit most ungulates, thereby reducing their road effect zones.

7.5. Priority barrier and collision mitigation zones

The absence of real-time animal movement and mortality data makes it difficult for field managers and user agencies to design and locate mitigation measures on roads passing through ecologically sensitive habitats. To overcome this, I used a simple rule-based metric to delineate priority road segments in the landscape for mitigation of barrier and collision risk in an easily reproducible 'exposure-hazard' framework. Integrating species presence probabilities (predicted and assumed), road, traffic and environmental characteristics with the traversability model (Saxena et al., 2020), I estimated 3725 km of roads vulnerable to medium-high collision likelihood, and 3245 km of roads vulnerable to medium-high barrier likelihood within protected areas, corridors and forests of the central Indian landscape. An important finding from the study was that a majority of the roads in these categories are 2-lane roads- with 90% of 2-lane roads posing medium-high barrier likelihood, and 93.4% of roads posing medium-high collision likelihood. This finding makes it imperative to use up-gradation plans (2-lane to 4-lane) in the landscape as an opportunity to include structural mitigation measures for enhancing connectivity and reducing animal mortality in central Indian roads.

7.6. Management recommendations

Both camera trap and habitat use data revealed varying responses to road-related disturbance among the mammal community. Consequently, the resulting impacts such as vulnerability to roadkill, barrier to movement, and changes in spatio-temporal habitat use and behaviour vary. These findings can help interpret trends in varying roadkill rates on roads, varying levels of impediment to animal movement in the landscape, and the differential use of crossing structures among mammals.

While the study revealed that protected areas can help buffer the impact of roads, it also implied that roadkill rates may be higher on roads passing through or in the vicinity of protected areas. Consequently, mitigation of such roads vulnerable to roadkill through construction of crossing structures and installation of fencing must be prioritised because of high local abundances of wildlife.

Crossing structures are important permanent mitigation measures that not only help reduce roadkill rates and help enhance movement between adjacent habitat patches, but also attenuate ‘predator release’ type scenarios by restoring near-natural spatio-temporal use by both predators and prey, given crossing structures are large enough to not act as ‘prey-traps’ (Saxena and Habib, 2022b). Thereby such measures can help avoid long-term consequences such as trophic cascades and changes in community structure and dynamics. Consequently, a decrease in the vulnerability of such species after construction of mitigation measures is expected, which can be ascertained through monitoring of roadkill on such road sections.

Decreasing animal presence probabilities away from protected areas would translate to greater impacts because of roads in corridor areas away from such core habitats. Consequently, construction of mitigation measures on corridor areas would ensure successful movement of mammals.

Future road development strategies in the landscape should be aimed at conserving intact habitats by avoiding road building in large natural patches and corridors (Forman, 2005). Mitigation measures should be prioritised on roads in protected areas, tiger reserves and corridors.

Most importantly most 2-lane roads in the landscape were found to be vulnerable to both medium-high barrier and collisions likelihoods, all road up-gradation projects in the landscape should include mitigation measures in the form of crossing structures. Contrary to the assertions of Laurance et al. (2015), road up-gradation is an opportunity for integrating mitigation measures in roads that were previously harmful (Habib et al., 2016). Allowing for road up-gradation to accommodate increased traffic volumes in most cases has a lower impact than building new roads (Rhodes et al., 2014). Thus, present levels of habitat and corridor fragmentation in the landscape because of roads and other anthropogenic activities necessitate that road up-gradations occur with mitigation measures.

In addition to adopting measures to mitigate impacts such as roadkill and barrier, mitigation measures and strategies should also aim to reduce secondary impacts such as increased human access to natural areas, environmental degradation by pollutants associated with road construction and operation, and proliferation of secondary human infrastructure/development along roads.

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Appendix 3. *Relative abundance, activity and diversity of mammals near National Highway 44, Pench Tiger Reserves, Maharashtra and Madhya Pradesh.*

Table A3.1. All candidate generalised linear mixed effects models for eight mammals explaining roadside habitat use near National Highway 44, near Pench Tiger Reserve, Maharashtra and Madhya Pradesh.

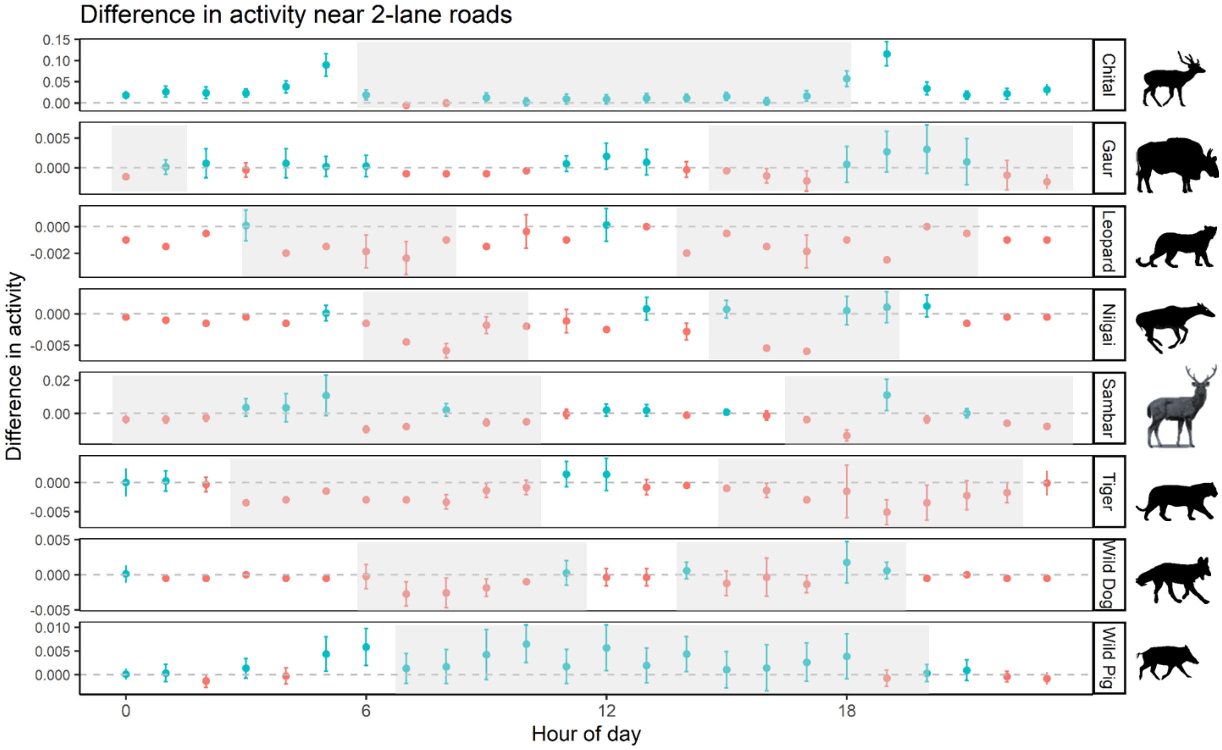
Models	*Variables*	*df*	*logLik*	*AICc*	*ΔAICc*	*weight*
CHITAL						
chital6	**Distance to settlement + Distance to road + Road type + Protection + Road type * Distance to road**	**12**	**-409.84**	**844.69**	**0**	**0.7**
chital5	Distance to settlement + Distance to road + Road type + Protection + Road type * Distance to road + Protection * Distance to road	14	-409.19	847.75	3.06	0.15
chital2	Roughness + Distance to settlement + Distance to road + Distance to PA + Human + Road type + Protection + Road type * Distance to road	15	-408.6	848.77	4.08	0.09
chital3	Roughness + Distance to settlement + Distance to road + Distance to PA + Road type + Protection + Road type * Distance to road + Protection * Distance to road	16	-408.31	850.42	5.73	0.04
chital1	Roughness + Distance to settlement + Distance to road + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	17	-408.22	852.47	7.78	0.01
chital	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + (Human) + Road type + Protection + Road type * Distance to road + Protection * Distance to road	18	-408.2	854.67	9.98	0

GAUR						
gaur4	**Distance to settlement + Distance to road + Road type + Protection + Road type * Distance to road**	**12**	**-433.56**	**892.13**	**0**	**0.42**
gaur3	**Distance to settlement + Distance to road + Distance to PA + Road type + Protection + Road type * Distance to road**	**13**	**-432.58**	**892.35**	**0.22**	**0.38**
gaur2	Roughness + Distance to settlement + Distance to road + Distance to PA + Road type + Protection + Road type * Distance to road	14	-432.57	894.52	2.39	0.13
gaur1	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Road type + Protection + Road type * Distance to road	15	-432.33	896.24	4.11	0.05
gaur	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road	16	-432.33	898.46	6.33	0.02
SAMBAR						
sambar5	**Distance to settlement + Distance to road + Distance to water + Road type + Protection**	**11**	**-421.29**	**865.44**	**0**	**0.46**
sambar4	**Distance to settlement + Distance to road + (Distance to water) + Distance to PA + Road type + Protection**	**12**	**-420.61**	**866.25**	**0.81**	**0.31**
sambar3	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Road type + Protection	13	-420.16	867.51	2.07	0.16
sambar2	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection	14	-420.1	869.57	4.13	0.06
sambar1	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type	16	-419.55	872.9	7.46	0.01

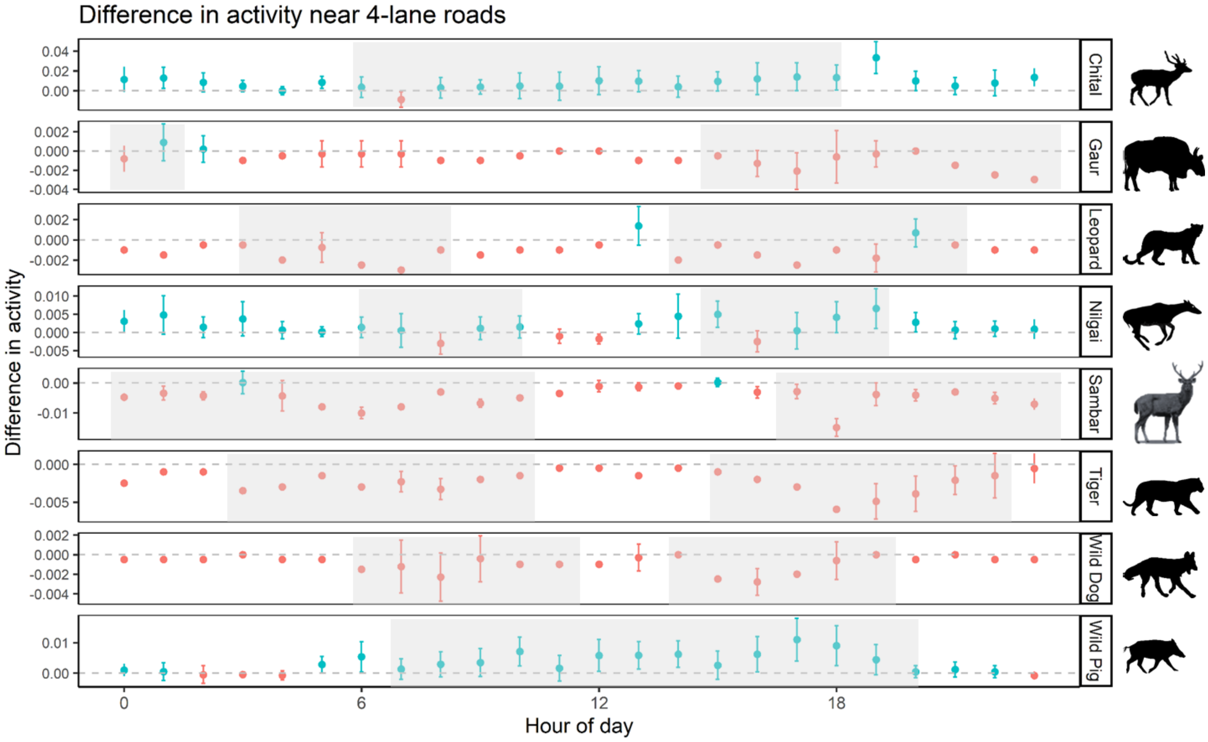
	+ Protection + Protection * Distance to road					
sambar	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	18	-419.23	876.73	11.29	0
WILD PIG						
wildpig9	**Road type**	**6**	**-436.85**	**885.98**	**0**	**0.38**
wildpig7	**Distance to PA + Road type + Protection**	**9**	**-434.19**	**886.96**	**0.98**	**0.24**
wildpig8	**Road type + Protection**	**8**	**-435.31**	**887.08**	**1.1**	**0.22**
wildpig6	Roughness + Distance to PA + Road type + Protection	10	-434.01	888.74	2.76	0.1
wildpig5	Roughness + Distance to water + Distance to PA + Road type + Protection	11	-433.86	890.58	4.6	0.04
wildpig4	Roughness + Distance to road + Distance to water + Distance to PA + Road type + Protection	12	-433.85	892.73	6.75	0.01
wildpig3	Roughness + Distance to road + Distance to water + Distance to PA + Road type + Protection + Protection * Distance to road	14	-432.44	894.25	8.27	0.01
wildpig2	Roughness + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Protection * Distance to road	15	-432.36	896.3	10.33	0
wildpig1	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Protection * Distance to road	16	-432.29	898.37	12.39	0
wildpig	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	18	-431.39	901.04	15.07	0
NILGAI						

nilgai1	**Distance to settlement + Distance to road + Distance to water + Distance to PA + Road type + Protection + Road type * Distance to road + Protection * Distance to road**	**16**	**-411.11**	**856.02**	**0**	**0.85**
nilgai	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	18	-410.6	859.48	3.46	0.15
LEOPARD						
leopard4	**Distance to settlement + Distance to water + Road type + Protection**	**9**	**-446.48**	**911.54**	**0**	**0.46**
leopard3	**Distance to settlement + Distance to road + Distance to water + Road type + Protection**	**10**	**-445.89**	**912.49**	**0.95**	**0.28**
leopard2	**Distance to settlement + Distance to road + Distance to water + Human + Road type + Protection**	**11**	**-445.33**	**913.52**	**1.98**	**0.17**
leopard1	Roughness + Distance to settlement + Distance to road + Distance to water + Human + Road type + Protection	12	-445.2	915.42	3.88	0.07
leopard	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection	13	-445.14	917.47	5.93	0.02
TIGER						
tiger3	**Roughness + Distance to settlement + Distance to water + Distance to PA + Human + Road type + Protection**	**11**	**-444.03**	**910.92**	**0**	**0.65**
tiger2	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection	12	-443.99	913	2.08	0.23
tiger1	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road	13	-443.56	914.31	3.39	0.12

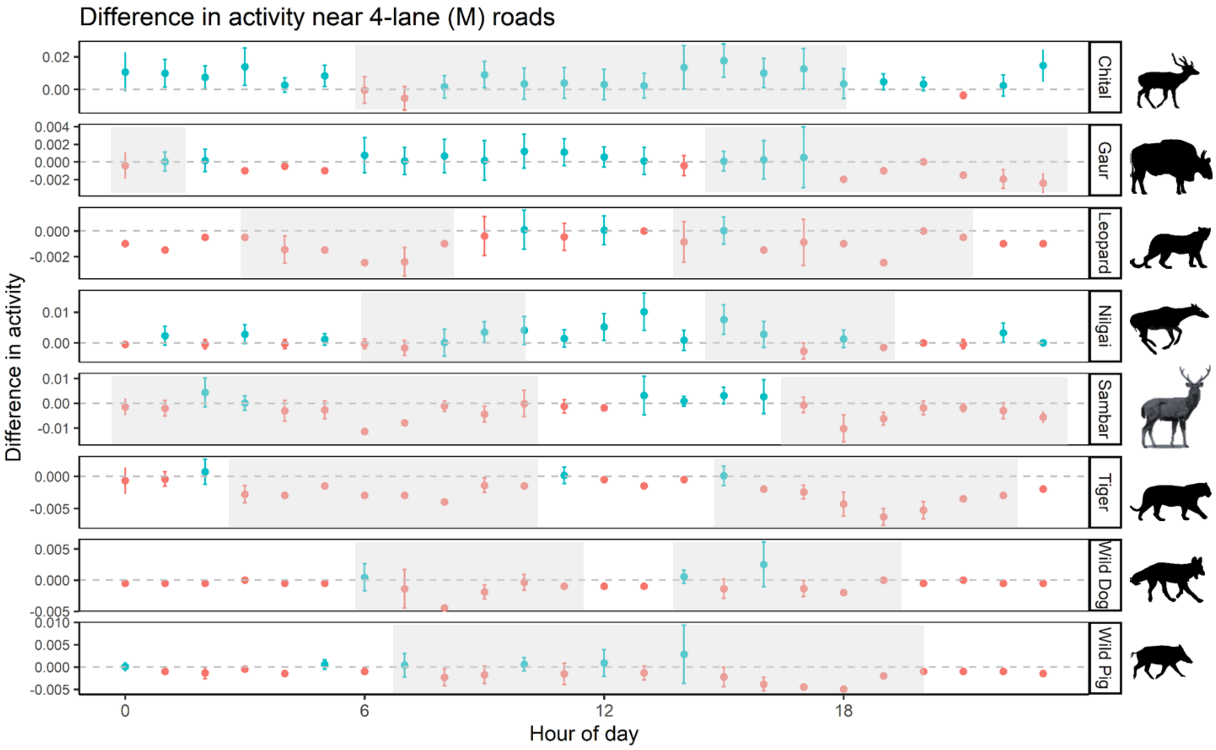
tiger	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	17	-443.38	922.8	11.88	0
WILD DOG						
wilddog4	**Distance to road + Distance to water + Human + Road type + Protection + Road type * Distance to road**	**13**	**-444.37**	**915.94**	**0**	**0.35**
wilddog3	**Roughness + Distance to road + Distance to water + Human + Road type + Protection + Road type * Distance to road**	**14**	**-443.29**	**915.96**	**0.02**	**0.34**
wilddog2	**Roughness + Distance to road + Distance to water + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road**	**16**	**-441.57**	**916.93**	**0.99**	**0.21**
wilddog1	Roughness + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	17	-441.46	918.94	3	0.08
wilddog	Roughness + Distance to settlement + Distance to road + Distance to water + Distance to PA + Human + Road type + Protection + Road type * Distance to road + Protection * Distance to road	18	-441.45	921.18	5.24	0.03


Difference in activity near 2-lane roads
Difference in activity
Hour of day
0
6
12
18
0.15
0.10
0.05
0.00
0.005
0.000
-0.002
-0.005
0.02
0.010
Chital
Gaur
Leopard
Nilgai
Sambar
Tiger
Wild Dog
Wild Pig

(a)


Difference in activity near 4-lane roads
Difference in activity
Hour of day
0
6
12
18
0.04
0.02
0.00
0.002
0.000
-0.002
-0.004
0.010
0.005
-0.005
-0.01
0.01
Chital
Gaur
Leopard
Nilgai
Sambar
Tiger
Wild Dog
Wild Pig

(b)



(c)

Figure A3.1. (a – c). Difference in hourly activity patterns of eight large mammals near National Highway 44, near different road types. Solid dots represent mean difference in activity and bars represent upper and lower limits of confidence intervals. Grey shaded areas represent peak activity hours in control habitat. Horizontal dashed grey line represents zero.

Appendix 5. *Ungulate use of habitat near roads in the central Indian landscape and species-specific road-effect zones under different road and traffic scenarios.*

Table A5.1. Estimates of the road effect zone widths for four ungulates under three road development scenarios in the central Indian landscape.

Species	**Scenario**	**Road effect zone estimate**	**SE**
Chital	Present	1201.27	9.20
	Scenario3	1163.24	9.28
	Scenario4	1142.98	9.57
Gaur	Present	1345.41	6.96
	Scenario3	1049.27	91.20
	Scenario4	1097.53	7.44
Sambar	Present	1692.34	14.90
	Scenario3	1701.71	15.22
	Scenario4	1731.58	16.04
Wild Pig	Present	2406.20	1019.81
	Scenario3	2319.49	46.12

Table A5.2. Estimates of the road effect zones widths for four ungulates under three road development scenarios with different roadside forest protection types in the central Indian landscape.

Species	**Scenario**	**Protection**	**Road effect zone estimate**	**SE**
Chital	Present	Buffer	1253.00	22.15
	Present	Core	1243.41	46.89
	Present	Other	1188.47	10.31
	Scenario3	Buffer	1214.33	22.44
	Scenario3	Core	1179.41	53.72
	Scenario3	other	1152.55	10.33

	Scenario4	Buffer	1178.57	23.44
	Scenario4	Core	1290.10	59.86
	Scenario4	other	1129.65	10.59
Gaur	Present	Buffer	1573.81	21.06
	Present	Core	1658.12	13.94
	Present	Other	1227.39	5.68
	Scenario3	Buffer	411.18	97.28
	Scenario3	Core	667.84	780.47
	Scenario3	Other	1556.96	72.55
	Scenario4	Buffer	1657.18	35.81
	Scenario4	Core	1835.50	21.62
	Scenario4	Other	1037.63	5.47
Sambar	Present	Buffer	1629.17	32.29
	Present	Core	1549.35	29.51
	Present	Other	1796.24	20.01
	Scenario3	Buffer	1643.41	32.72
	Scenario3	Core	1540.39	29.33
	Scenario3	Other	1823.80	20.64
	Scenario4	Buffer	1704.22	33.80
	Scenario4	Core	1555.43	27.58
	Scenario4	Other	1888.35	23.31
Wild Pig	Present	Other	2406.20	1019.81
	Scenario3	Buffer	2695.52	633.20
	Scenario3	Core	2302.42	51.95
	Scenario3	Other	2383.85	101.94

Table A5.3. Estimates of the road effect zone widths for four ungulates under 3 road development scenarios near different road types in the central Indian landscape.

Species	Scenario	Road type	Road effect zone estimate	SE
Chital	Present	1	1106.38	10.80
	Present	2	1338.67	16.08
	Present	4	1322.72	87.65
	Present	41	1000.32	121.53
	Scenario3	1	1106.38	10.80
	Scenario3	4	1258.54	16.80
	Scenario3	41	1000.32	121.53
	Scenario4	1	1106.38	10.80
	Scenario4	41	1215.15	18.73
Gaur	Present	2	1346.77	6.97
	Present	4	1513.10	1907.39
	Present	41	1205.58	83.82
	Scenario3	4	989.28	121.38
	Scenario3	41	1205.58	83.82
	Scenario4	41	1097.53	7.44
Sambar	Present	1	1788.89	20.08
	Present	2	1586.93	22.32
	Present	4	2251.26	159.50
	Present	41	1518.02	114.50
	Scenario3	1	1788.89	20.08
	Scenario3	4	1603.04	23.40
	Scenario3	41	1518.02	114.50
	Scenario4	1	1788.89	20.08
	Scenario4	41	1639.82	26.35
Wild Pig	Present	2	2406.20	1019.81
	Scenario3	4	2319.49	46.12

Appendix 6. *Identification and prioritization of crossing zones to mitigate barrier and collision likelihood in the central Indian landscape*

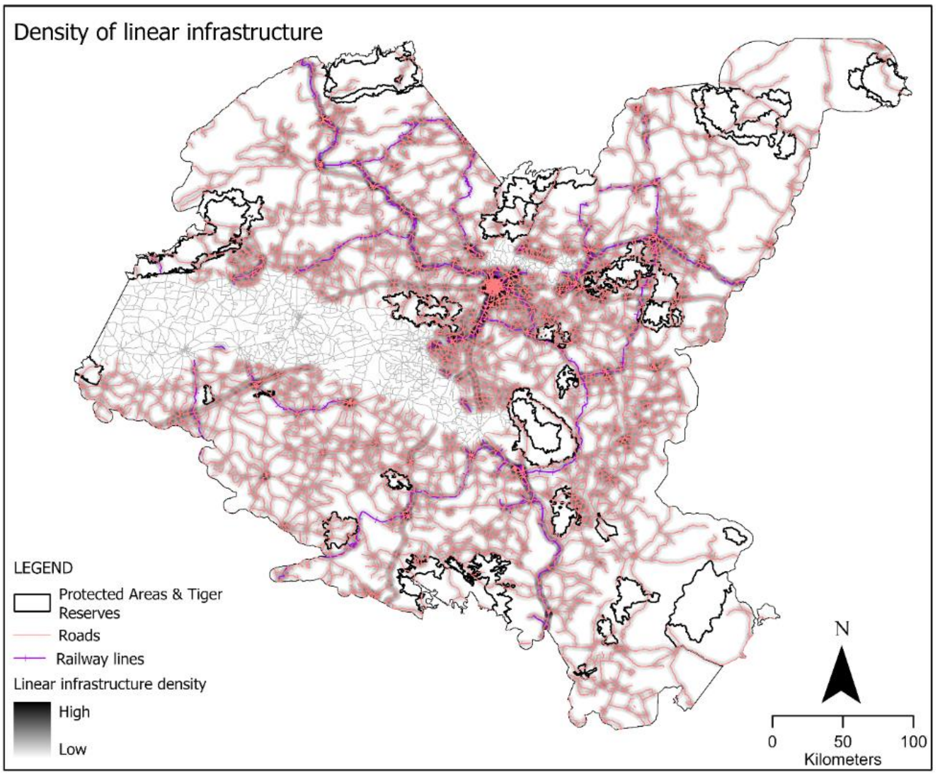


Figure A6.1. Density of linear infrastructure including roads and railway lines in the central Indian landscape.

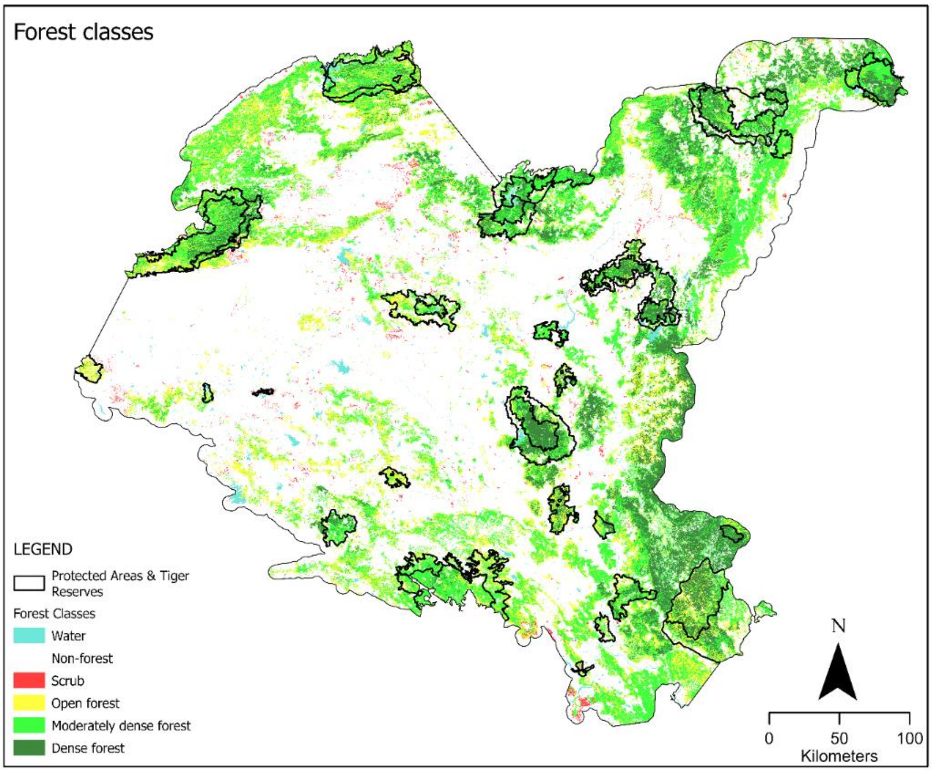


Figure A6.2. Forest types in the intensive study area in the central Indian landscape.

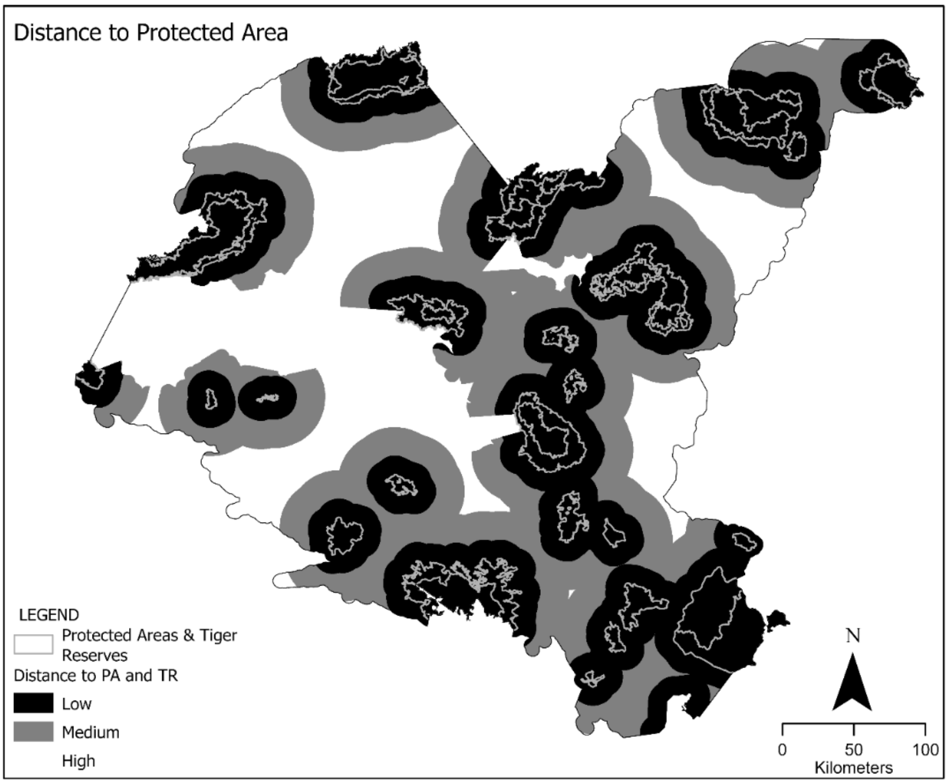


Figure A6.3. Distance to nearest protected area/tiger reserve categorized as low, medium and high in the intensive study area in the central Indian landscape.

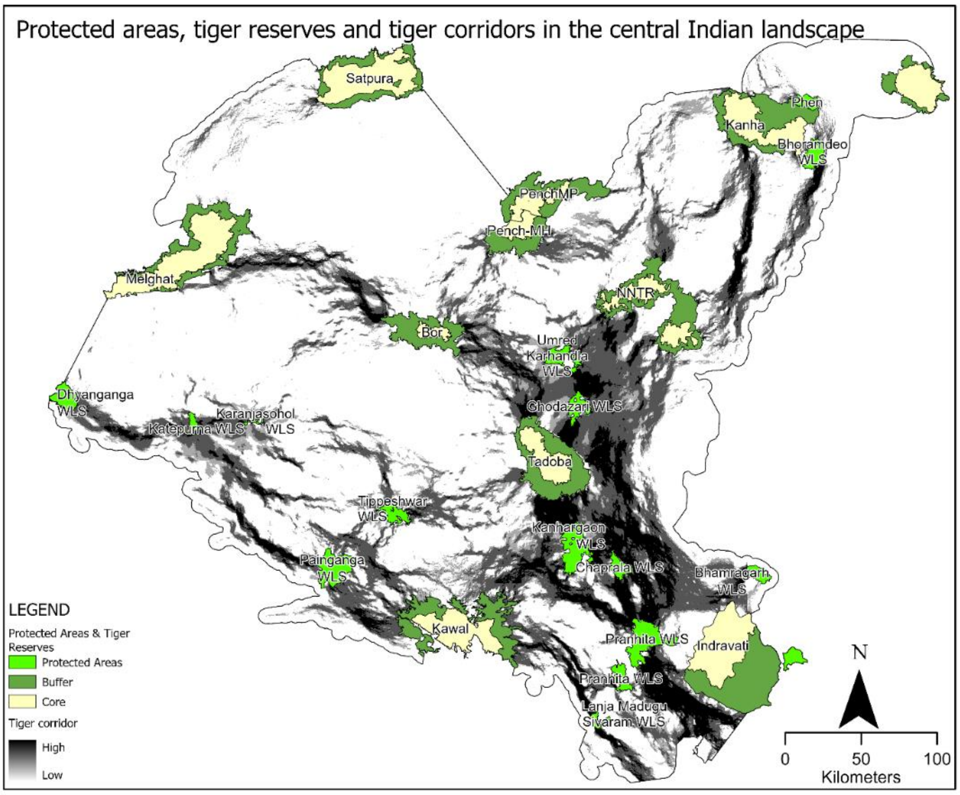


Figure A6.4. Telemetry based tiger movement corridor as predicted by (Habib et al., 2021) and protected areas and tiger reserves in the central Indian landscape used for assigning tiger and leopard presence scores.

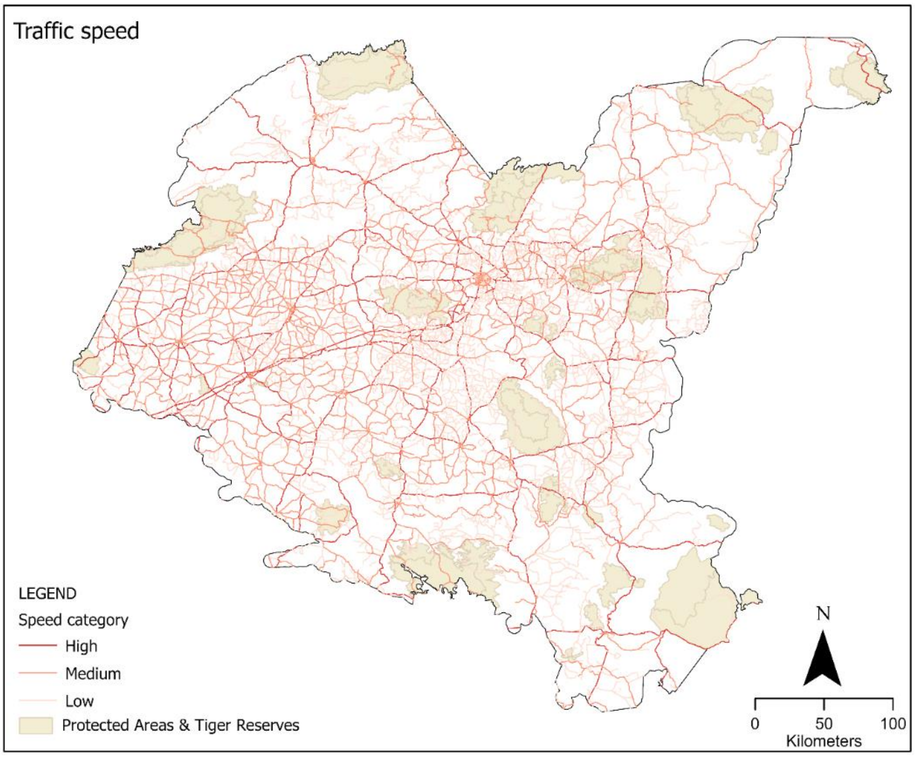


Figure A6.5. High, medium and low speed roads in the intensive study area in the central Indian landscape.

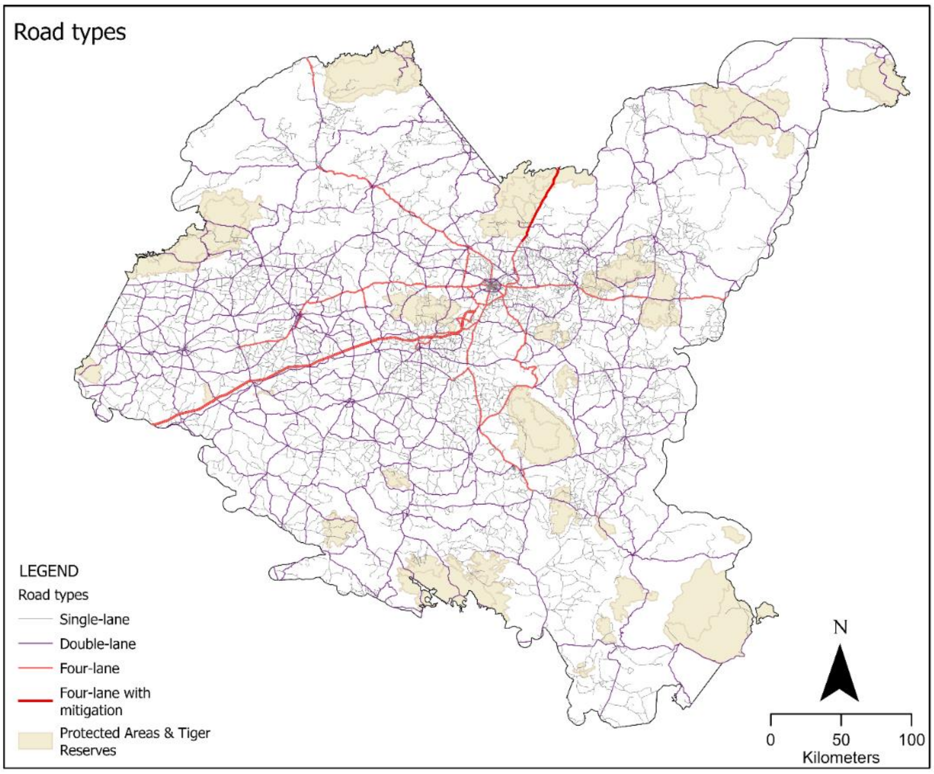


Figure A6.6. Different road types based on the number of lanes in the intensive study area in the central Indian landscape.

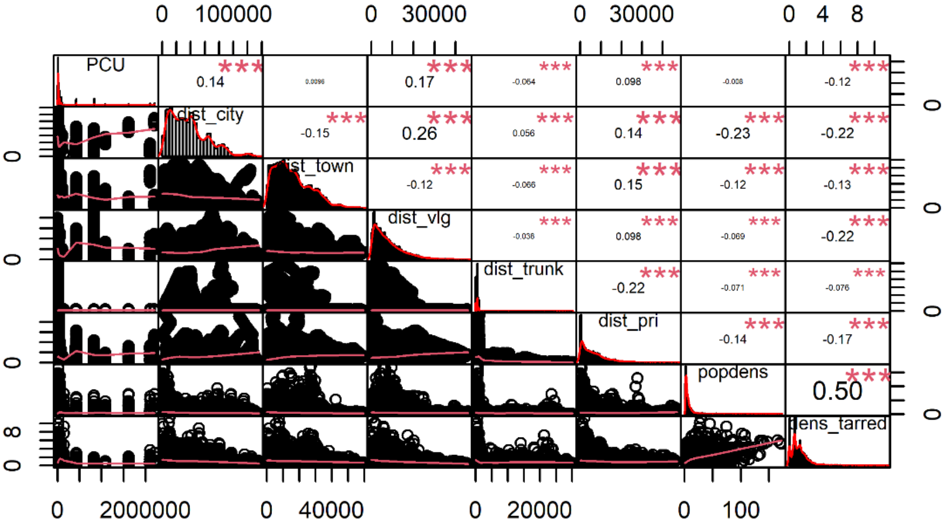


Figure A6.7. Correlation matrix of continuous independent variables used for predicting traffic volume in the intensive study area in the central Indian landscape.

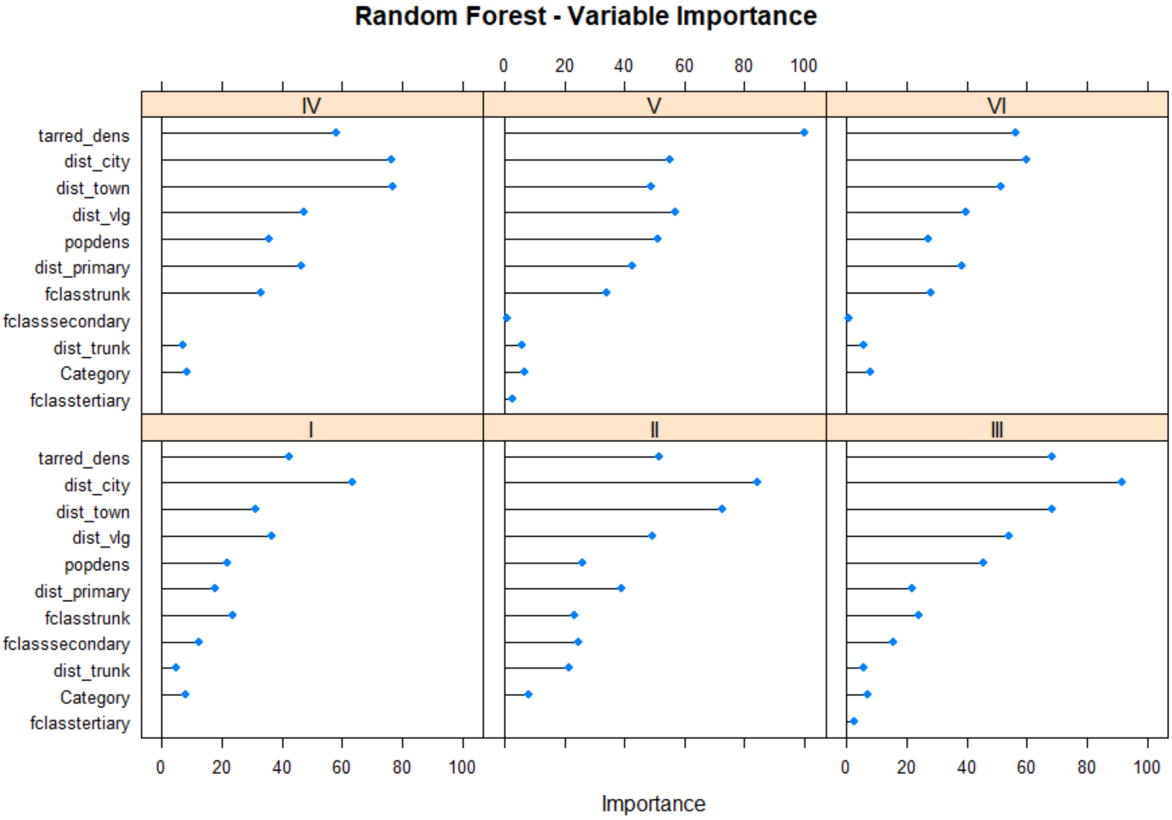
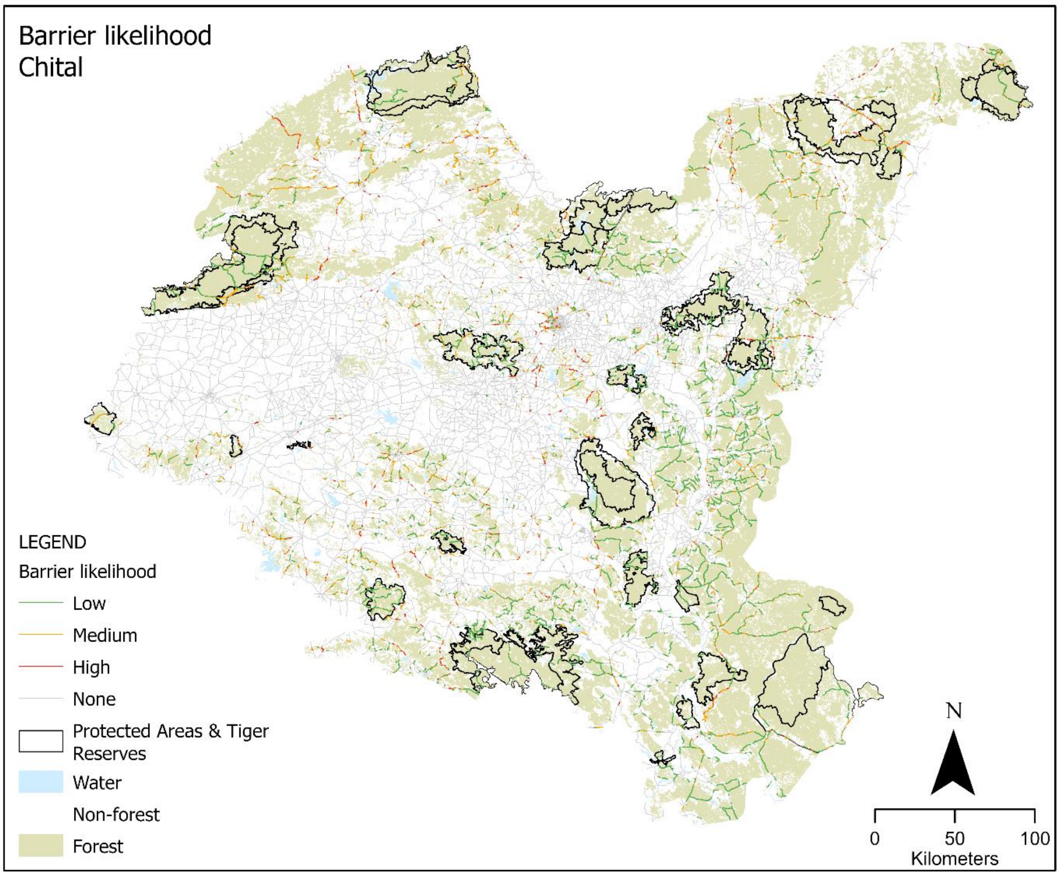
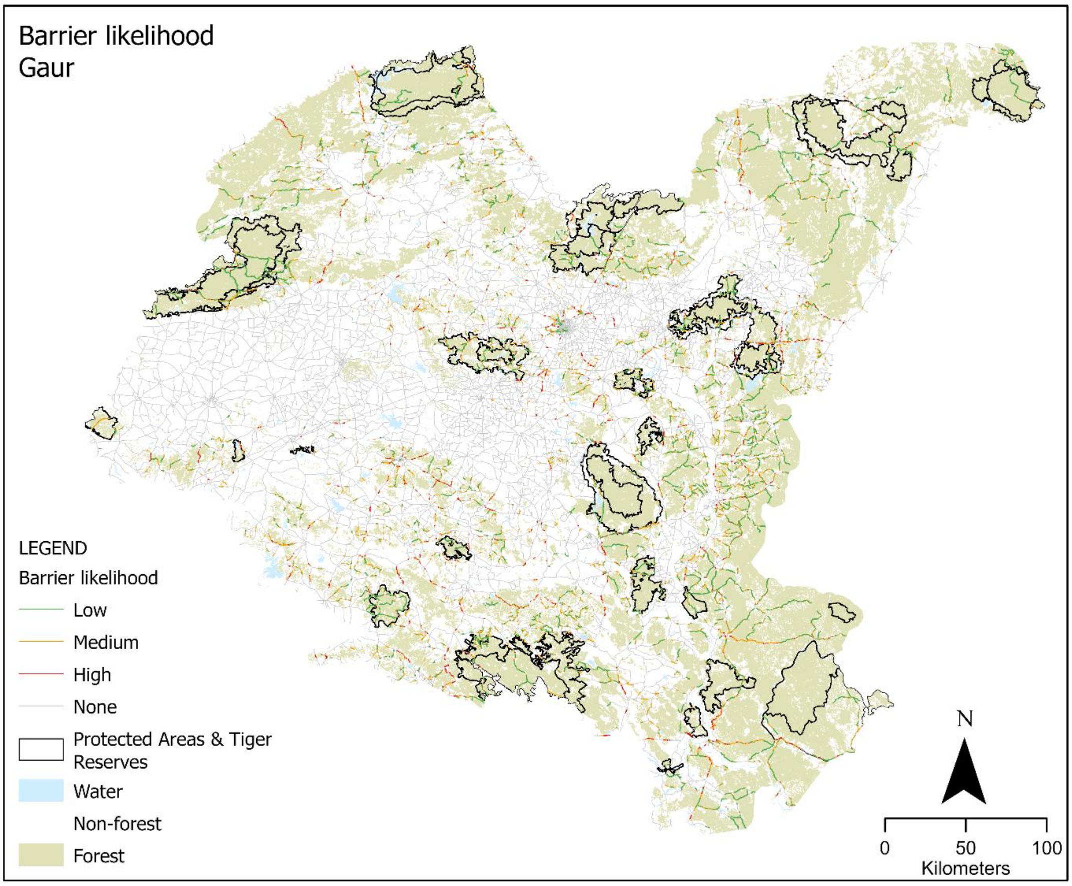
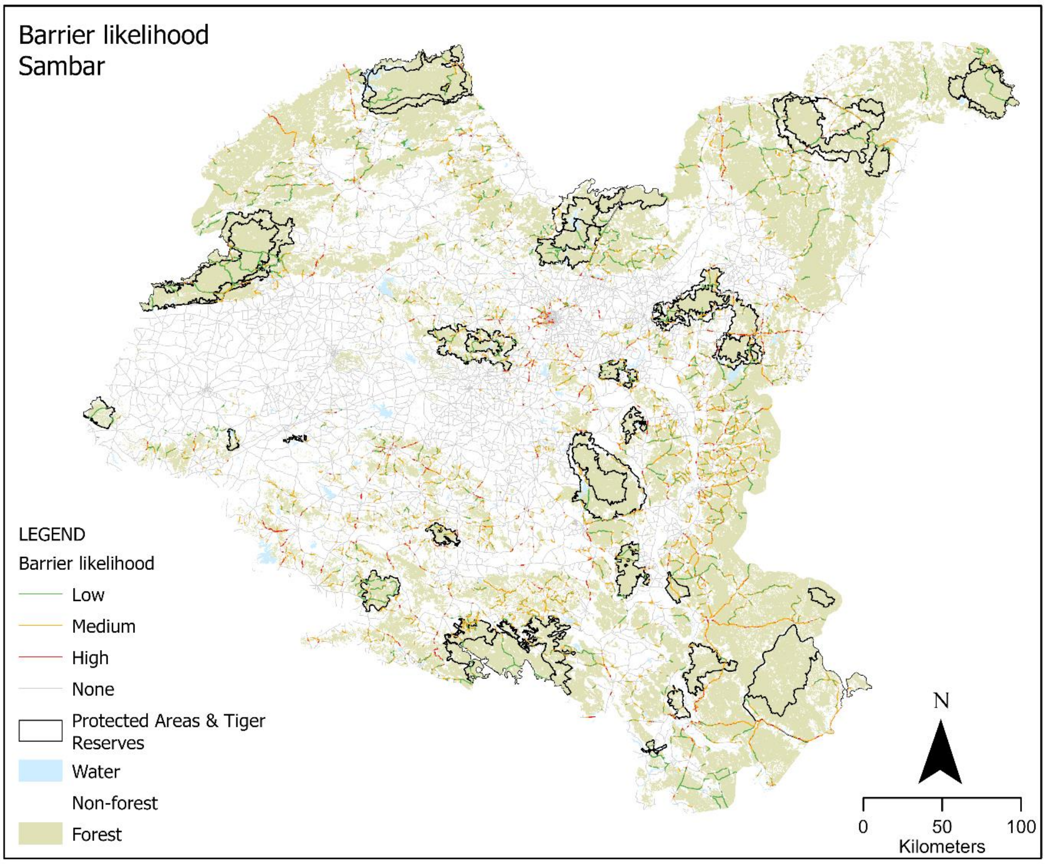
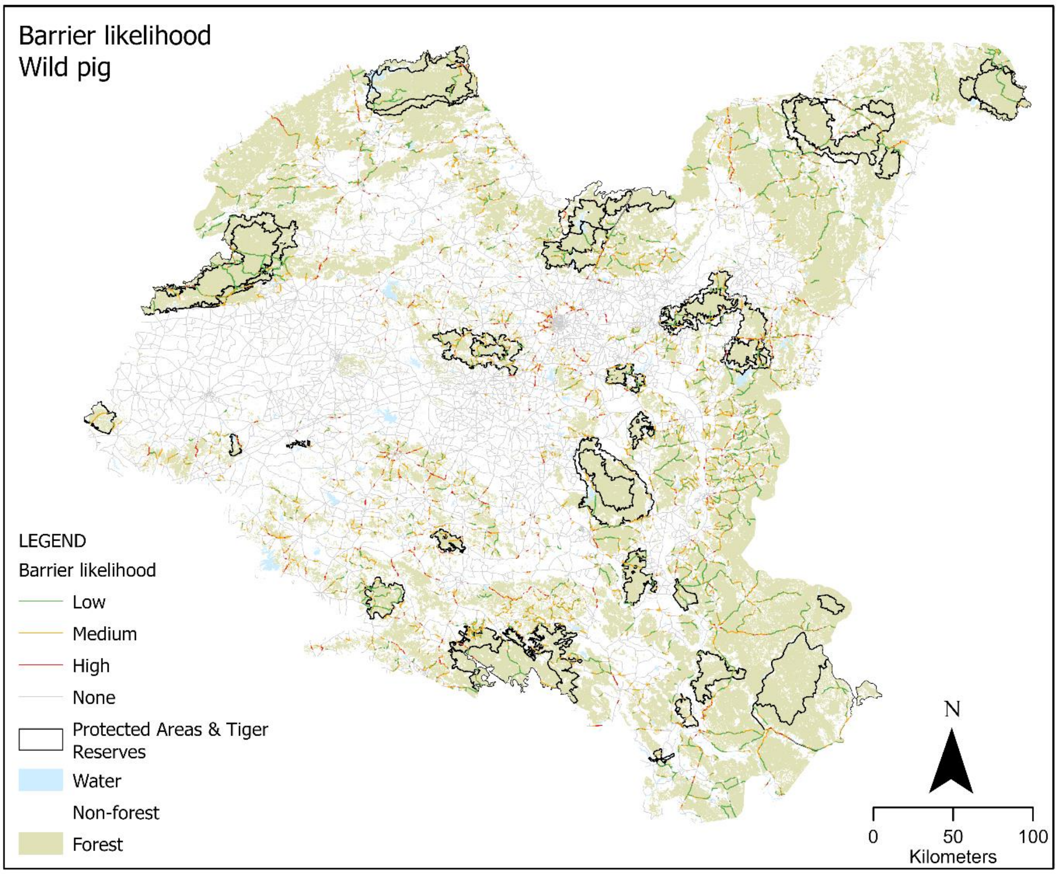


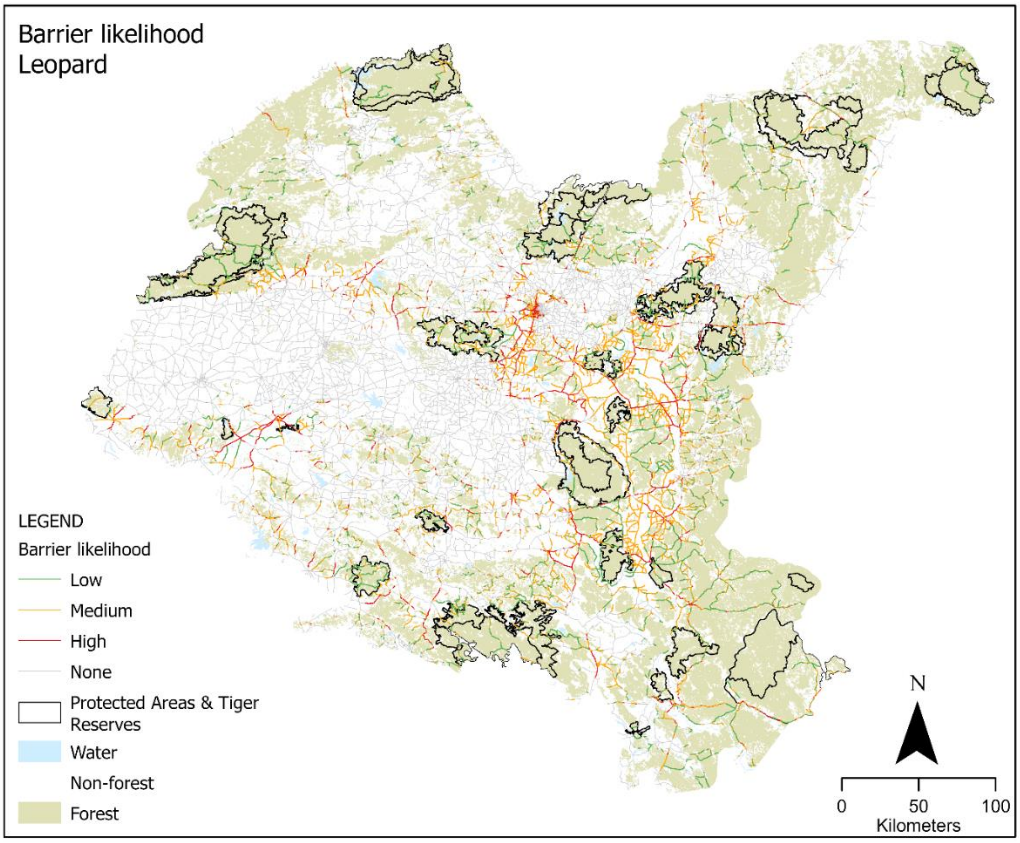
Figure A6.8. Variable importance of independent variables for different PCU categories as predicted by random forest models.


Barrier likelihood
Chital
LEGEND
Barrier likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
N
0
50
100
Kilometers


Barrier likelihood
Gaur
LEGEND
Barrier likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
N
0
50
100
Kilometers


Barrier likelihood
Sambar
LEGEND
Barrier likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
N
0
50
100
Kilometers


Barrier likelihood
Wild pig
LEGEND
Barrier likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
N
0
50
100
Kilometers



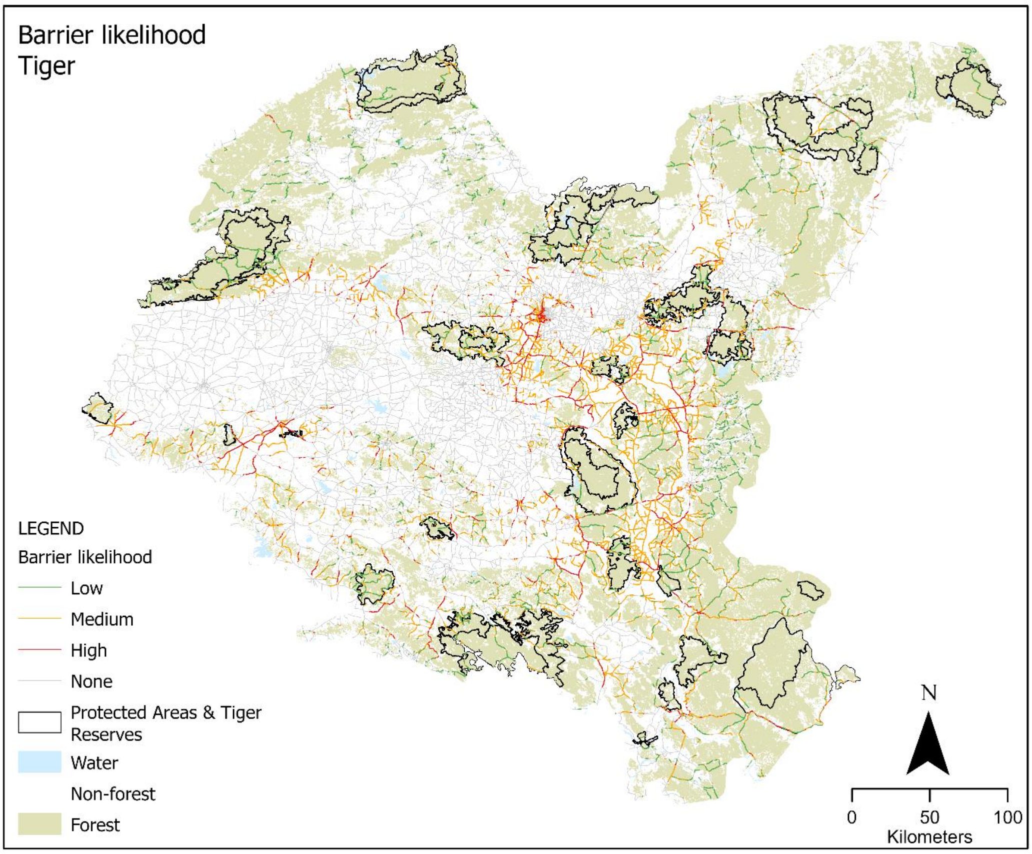
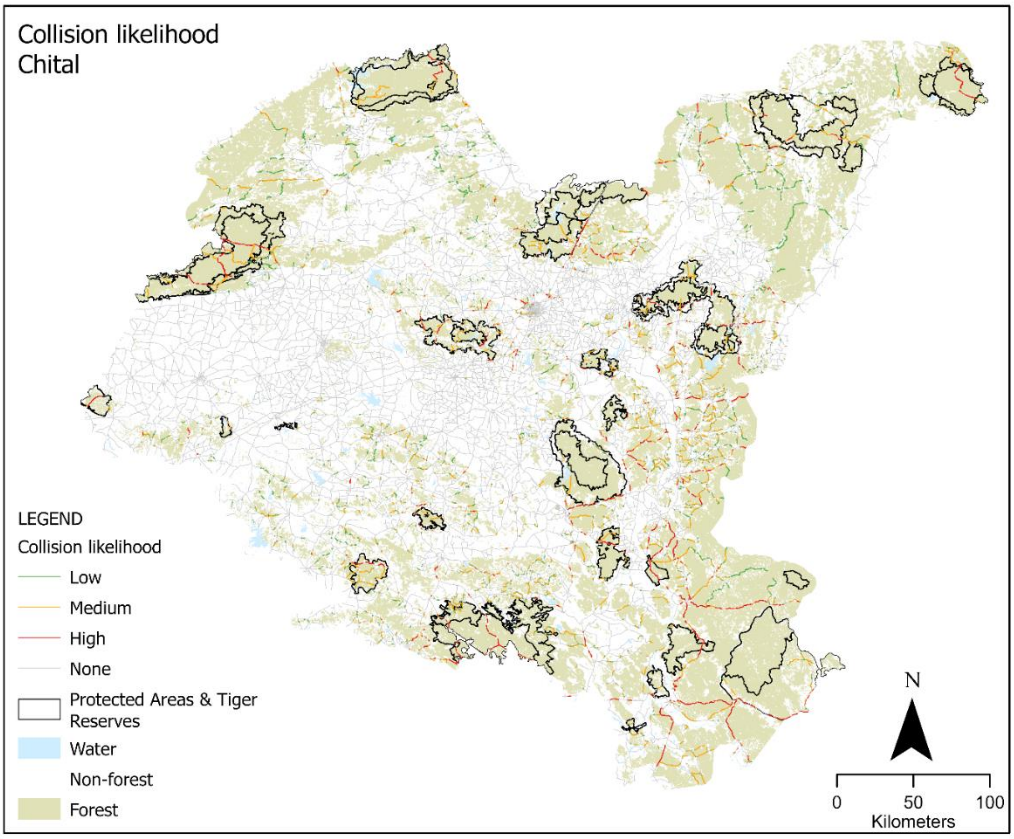
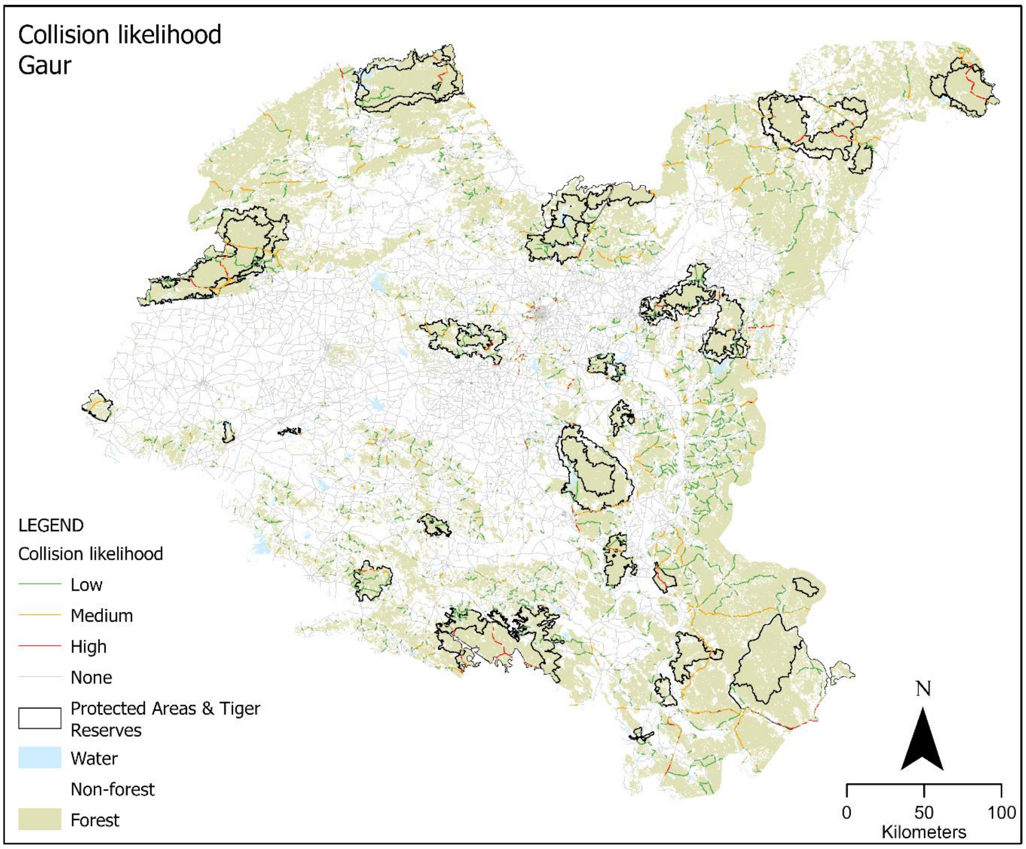


Figure A6.9. (a-f). Species-specific maps of barrier likelihood for (a) chital, (b) gaur, (c) sambar, (d) wild pig, (e) leopard, and (f) tiger in the central Indian landscape.


Collision likelihood
Chital
LEGEND
Collision likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
N
0
50
100
Kilometers


Collision likelihood
Gaur
LEGEND
Collision likelihood
Low
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None
Protected Areas & Tiger Reserves
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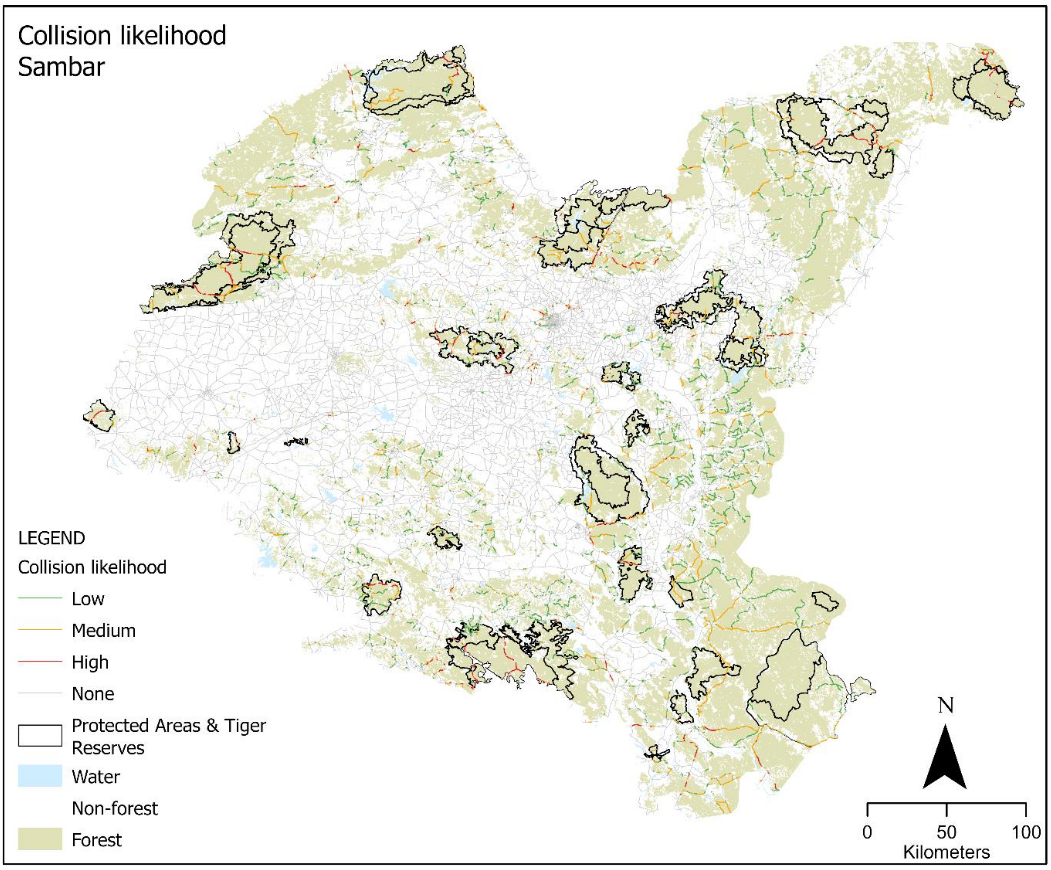
Collision likelihood
Sambar
LEGEND
Collision likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
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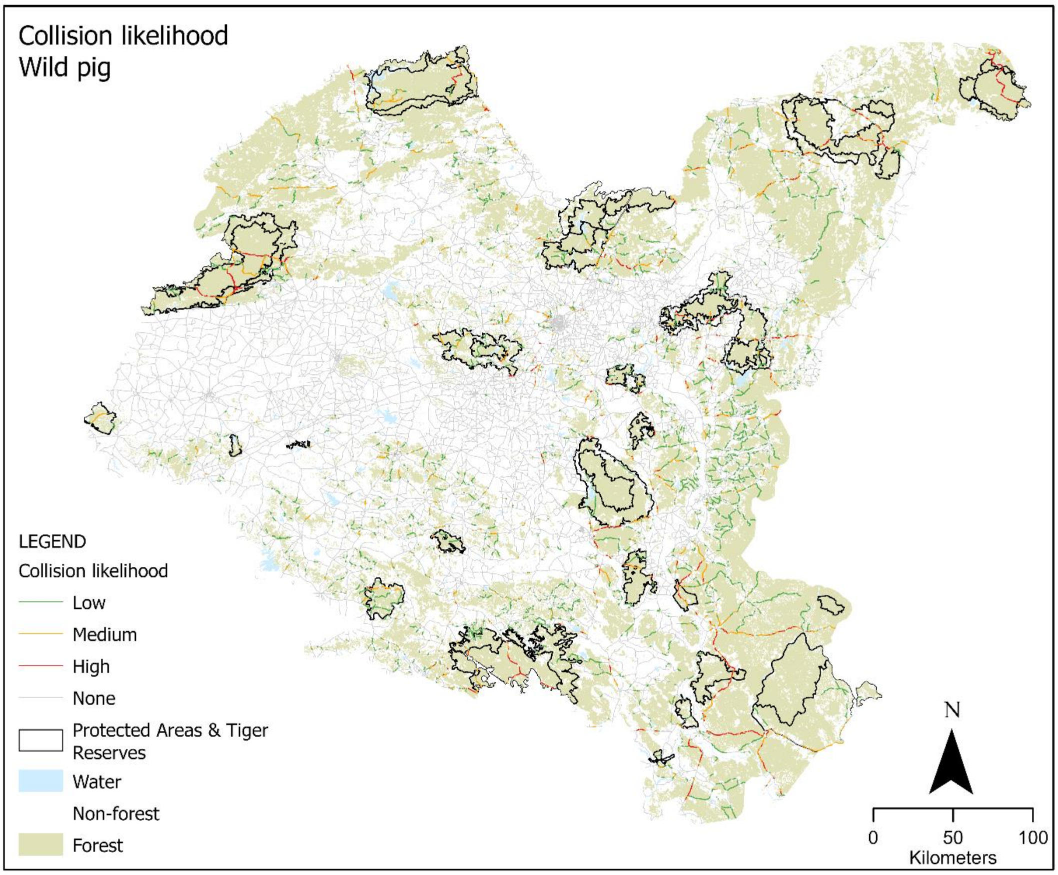
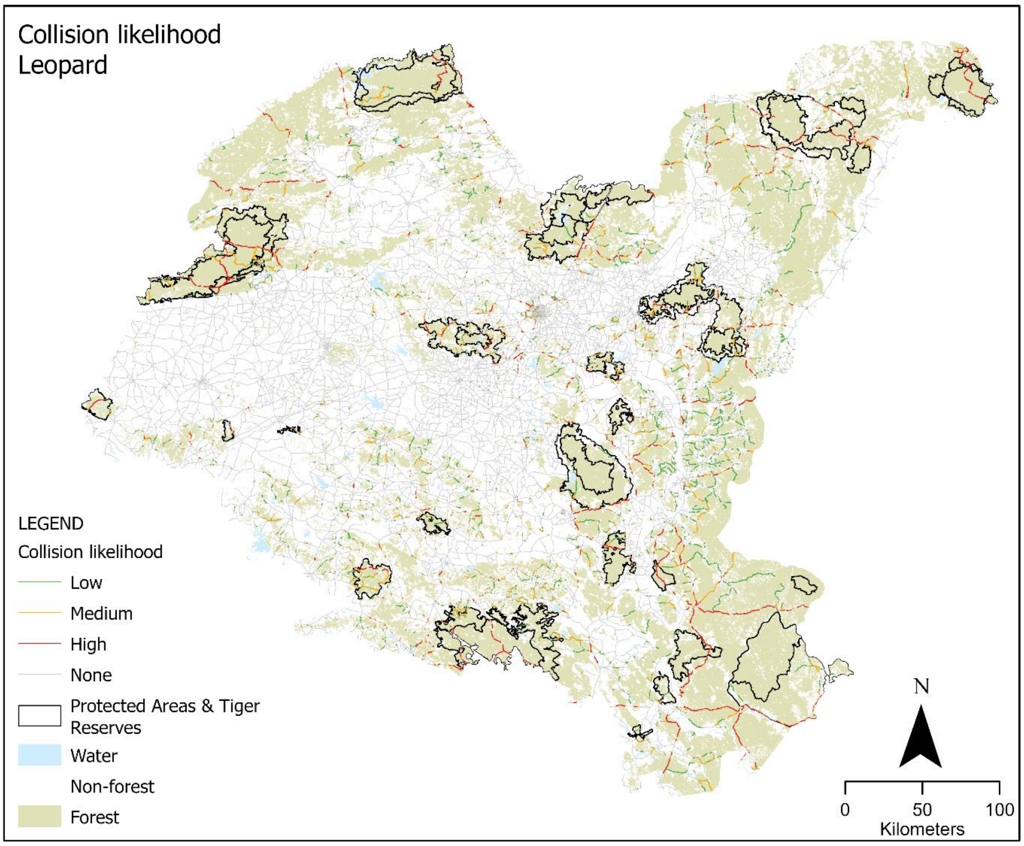
Kilometers


Collision likelihood
Wild pig
LEGEND
Collision likelihood
Low
Medium
High
None
Protected Areas & Tiger Reserves
Water
Non-forest
Forest
N
0
50
100
Kilometers



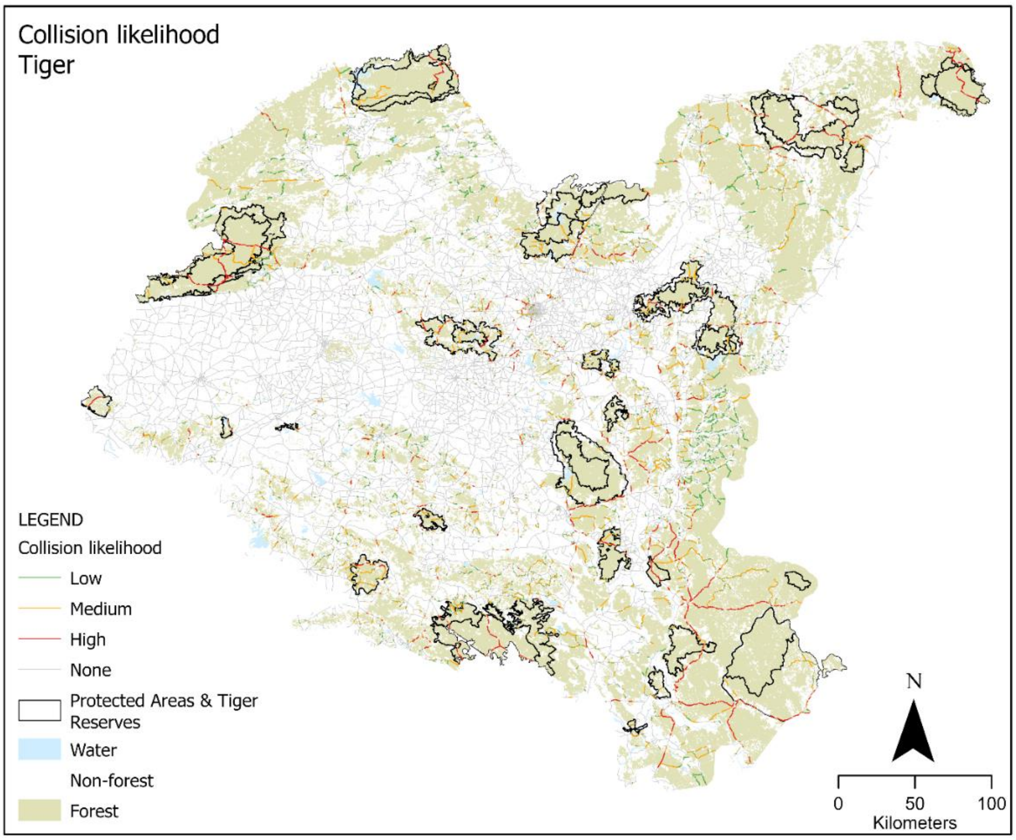


Figure A6.10. (a-f). Species-specific maps of collision likelihood for (a) chital, (b) gaur, (c) sambar, (d) wild pig, (e) leopard, and (f) tiger in the central Indian landscape.

Table A6.1. Confusion matrix of accuracy of best random forest model for traffic model prediction on the test dataset.

	Reference					
Prediction	I	II	III	IV	V	VI
I	88	16	18	5	0	11
II	2	144	10	10	0	5
III	15	28	430	32	26	26
IV	13	18	56	309	39	16
V	0	3	14	49	251	30
VI	5	6	6	2	2	106

Table A6.2. Lengths of tarred roads in tiger reserves, protected areas and wildlife corridors in the central Indian landscape under different barrier and collision likelihood.

Area	**Length of roads posing barrier (km)**			**Length of roads posing collision risk (km)**		
	High	**Medium**	**Low**	**High**	**Medium**	**Low**
Tiger reserves						
Navegaon-Nagzira	19.53	83.85	211.45	32.41	84.66	31.78
Pench-MH	2.25	17.48	80.99	9.06	54.54	6.15
Pench-MP		8.53	20.57	3.04	8.78	3.93
Kanha	4.55	35.58	78.82	57.71	11.88	6.74
Bor	0.82	54.07	134.39	31.26	49.13	22.10
Melghat		55.03	217.44	121.48	102.58	21.57
Satpura		29.12	88.56	41.29	61.47	6.03
Tadoba	0.69	13.49	94.52	3.12	19.53	16.48
Indravati	11.61	51.12	79.34	40.48	19.91	37.68
Kawal		41.12	104.53	56.64	40.45	17.90
Wildlife Sanctuaries						
Bhoramdeo	0.37	0.29	5.94	4.79	1.47	
Umred Karhandla		5.91	21.88		17.65	2.71
Bhairamgarh	0.40	0.81	8.15	0.14	0.52	2.97
Chaprala		3.80	15.61	17.21	1.50	
Kanhargaon	0.28	4.49	21.82	11.03	11.73	3.07
Lanja Madugu Sivaram		0.24	6.91		4.85	2.07
Pranhita	1.10	2.84	14.02	5.27	3.06	6.64
Dhyanganga	0.11	11.38	4.10	12.16	2.40	0.87
Karanjasohol		0.34	1.44			
Katepurna	1.07	2.17	0.57	1.53	1.64	0.07
Painganga		14.36	82.65	14.55	45.56	10.84
Tippeshwar		1.18	16.56	1.57	9.66	6.09
Corridors						
Kanha-Achanakmar	3.97	32.86	154.20	63.76	46.41	37.63
Pench-Kanha-NNTR	65.96	425.40	1024.51	122.45	246.95	474.09

Pench-Satpura-Melghat-Bor	63.26	544.70	6013.26	129.05	227.59	547.55
NNTR-Bor-TATR	186.22	1373.68	2438.17	201.78	299.05	667.66
TATR-Indravati	186.22	2438.17	1373.68	396.76	517.95	763.15
Kawal-Tipeshwar-Dhyanganga	112.61	886.37	1296.96	111.74	262.04	503.88

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Corridors at Crossroads: Linear Development-Induced Ecological Triage As a Conservation Opportunity

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The transportation infrastructure of a nation forms the backbone of its economic growth and social development, and, as a developing country, India is no exception. However, with imperatives to improve connectivity for economic and social growth, ecological costs are often at stake. Roads, old and new, cut through protected forests and connecting habitats, resulting in a plethora of ecological effects. These may include the severing of natural corridors thereby compromising the role of landscapes as conservation units especially for landscape-dependent wild animal species. Consequent loss of biodiversity and ecosystems and decline in innumerable ecosystem services emanating from these natural reserves are other serious impacts. As India aspires for better, modern roads, the ecological concerns regarding many road upgradation projects have recently been the cause of disputes between the transportation sector and the conservation community. Delayed consideration of ecological concerns into linear development project planning leads to inadequate appropriation of funds needed for mitigating impacts of such developments. It is in these circumstances that the question of prioritizing areas and strategies for mitigation given limited mitigation funds arises. We examine the different facets to the debate of triage vis-à-vis conservation, development and mitigation planning in the transportation sector in a developing country context. We suggest that it is important and possible to secure investment toward conservation in areas outside the purview of legal protection through project mitigation costs and other mechanisms. We also make suggestions to avoid the "laissez-faire" approach to linear development projects that is prevalent in India.

Keywords: roads, corridors, conservation, triage, sustainable development, mitigation

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INTRODUCTION

Much of India's economic growth in the past two decades has been driven by infrastructure development, prominent among them being development in the transportation sector. This can be attributed to reorientation of government spending toward public infrastructure (Ministry of Finance, 2016), including road-based transportation infrastructure. India today has the second largest road network in the world (ca. 5.2 million km), after the United States of America[1]. For a developing country like India, the importance of an efficient transportation system cannot be

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[1] National Highways Authority of India (http://www.nhai.org)

understated: roads facilitate social well-being and economic development (Elisseeff, 1998). The manufacturing centers, commercial and cultural centers, that are the nuclei of development, are already connected via a well-built network of over 24,000 km of roads[1]. Many rural areas in India are now being connected to better civic amenities and economic opportunities via roads networks. With an annual economic growth pegged at 7–7.5 percent for the fiscal year 2016–17 (Ministry of Finance, 2016), the scale of infrastructure development is also set to increase.

Concurrent with India's high-paced development is the country's unique global position in terms of its biodiversity. Being one of the 17 megadiverse countries of the world (with 7–8% of the world's species, of which 12.6% of mammals, 4.5% of birds, 45.8% of reptiles, 55.8% of amphibians and 33% of Indian plants[2] are endemic), four of the world's biodiversity hotspots (Myers et al., 2000) are also located in India- Western Ghats and Sri Lanka (Western Ghats), Himalaya (Indian Himalaya), Indo-Burma (parts of North east India) and Sundaland (Nicobar Islands) (Pande and Arora, 2014). The vast biological wealth is comparable to the diversity of geographical features (plateaus, mountains, plains) and habitats and ecosystems (forests, grasslands, wetlands, deserts).

India is also home to 57% of the world's tiger population (Jhala et al., 2015; WWF, 2016). The tiger, being a keystone species, regulates prey populations thus reducing trophic cascades. In India, the protection and management of forested ecosystems has thus been envisaged through its conservation as a flagship species (Leader-Williams and Dublin, 2000) through a network of tiger reserves in landscapes across the country. The populations in these tiger reserves act as meta-populations, across which genetic exchange is vital for long-term persistence of the national animal. Securing the habitats and movement pathways of the tiger by extension equates to conserving all other species that share these forests (Roberge and Angelstam, 2004) and the invaluable ecosystem services provisioned by these forests. Habitat connectivity for tigers in Indian landscapes has been evaluated and mapped through GIS-based landscape permeability models (Qureshi et al., 2014; Mondal et al., 2016), and genetic analysis in combination with landscape permeability models (Joshi et al., 2013; Yumnam et al., 2014), generating structural corridors. These corridor maps are used to identify corridors that may be threatened by road construction/expansion. Securing these corridors is vital for maintaining landscape-level gene flow (Yumnam et al., 2014) and is an essential, and critical component of conservation of such species (Bennet, 1990). Similar corridors have been identified for connecting and conserving elephant populations (Menon et al., 2005).

However, a great part of these corridors lies outside the protected area (PA) network and under different land ownership tenures. It is in such areas that the challenge of building roads and nature conservation become most daunting. Many high-traffic highways crisscross the few remaining forested landscapes of the country and cause an array of short- and long-term ecological impacts. Intrusion of roads in natural areas and activities associated with road building and operation adversely impact native biodiversity through multiple pathways (Jalkotzy et al., 1997; Kumara et al., 2000; Forman et al., 2003; Donaldson and Bennett, 2004). Road-related disturbances create a filter to animal movement across their habitats on either side of the roads and, in the long-run, can cause populations of animals to disappear from habitats that have become isolated and fragmented by roads (Riley et al., 2006). In India, roads have affected daily and seasonal movement pathways of elephants, hoolock gibbons, one-horned rhinoceros and other mammals (Choudhury, 1987; Joshi and Singh, 2007; Gubbi et al., 2012; Krishna et al., 2013; Wildlife Institute of India, 2014). In the Central Indian Landscape alone, an important tiger conservation landscape (TCL), tiger corridors are bisected by at least 4302 km of national and state highways, upgradation of many of which are currently underway.

The objectives of road infrastructure development often conflict with efforts to maintain undisturbed and well-connected swathes of forested areas across landscapes. Development agencies see the merit of promoting upgradation of highway infrastructure in keeping with development aspirations of the country. However conservation groups advocate avoiding further development in sensitive habitats/wildlife corridors, opting for alternative alignments, adopting best possible mitigation measures for maintaining habitat connectivity and reducing animal mortality (where development cannot be avoided), and better and early integration of conservation issues into project inception, planning and design. In reality, however, development priorities take center-stage and several issues confound or hinder any cooperation between conservation and development proponents.

The lack of strategic/landscape-level planning in India (Saxena et al., 2016) to enable consideration of conservation objectives in transportation development policies, plans and programs results in a lack of or delayed participation of conservation proponents in the decision-making process. Such projects are therefore constrained in terms of allocation of resources for exploring options of avoidance, minimization, rehabilitation and offsetting. Considering these constraints, delayed intervention through litigation from conservation proponents after necessary permissions have been obtained by the developers leaves few options for mitigation planning and ensuing mitigation planning has to be prioritized considering limitations in the form of funding and political will to formulate and implement such plans.

This paper explores different facets to the debate on the "triage-like" situation that arises as a result of competing development and conservation objectives in the context of road upgradation projects in India using a prominent recent example. The case exemplifies the present status of delayed mainstreaming of conservation concerns into infrastructure development projects in the country. This delay in assessment of the anticipated threats to a vital wildlife corridor from the soon-to-be upgraded road translated into limited options to mitigate these threats. The ensuing prioritization exercise regarding choice of alignment, locations and specifications of mitigation measures made in light of the conservation

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[2] http://thewesternghats.indiabiodiversity.org/biodiversity_in_india

importance of corridors, severity of threats, cost and possibility of positive conservation outcomes through mitigation, based on ecologically-informed alignment and mitigation alternatives have also been discussed. It concludes that implementation of mitigation measures in road upgradation projects in India can offer better avenues for promoting conservation in areas outside the purview of legal protection than *status quo*. To avoid future stand-offs resulting from the prevalent piece-meal approach to development, we suggest strategic environmental assessments and landscape-scale inter-sectoral planning for the road development sector to better include conservation concerns into development plans. We also suggest science-based prioritization exercises to delineate "no-go" zones by weighing costs and benefits of developing some lands and conserving others, and at the same time identifying areas where development is inevitable but conservation action can be mainstreamed into development projects.

USING TRIAGE TO ENABLE CONJUNCTION OF HUMAN AND WILDLIFE PASSAGE

Ecological triage is an informed prioritization of species to conserve, given their ecological role and chances of averting extinction through investment in conservation actions, after which funds for conserving these species are allocated accordingly (Hobbs and Kristjanson, 2003). However, triage of species must now move toward triage of habitats (Hudson, 2011), since pouring money to save a single species when its habitat is not preserved is moot (Shepard, 2011). Saving tigers and their habitats in India follows the same approach. However, given different threats to corridors outside the purview of protection, and limited funds for mitigation and conservation sourced from developers, it becomes imminent to prioritize areas where these funds would give the most positive conservation outcomes. Given duly established criteria for prioritizing landscapes for conservation are in place, the criteria to be given the highest weighting should be the magnitude of threats to the habitat.

Although development in the road sector in India is imminent and undeniably essential, it is the upgradation of arterial high-traffic highways passing through ecologically rich and sensitive areas that has to be dealt in light of factors justifying the need for expansion, increasing trends in traffic volume and the conservation importance commanded by the areas being traversed by roads. This was best exemplified in the case of upgradation of the National Highway (NH) 7, an arterial highway that connects major cities in Central India to the northern and southern parts of India. Upgradation work on the highway was initiated under Phase III of the National Highways Development Plan (NHDP). After upgradation work was completed in the non-forested sections of the road stretches, upgradation work was halted in a forested stretch that cut across the Pench-Kanha corridor, a critical tiger corridor in Central India for which clearances were required as conservation and forest authorities were not included in the project planning stages. The 2-lane configuration of NH 7 had not incorporated animal passageways as part of its original design, barring the natural drainage structures, which were used by wildlife in the absence of other suitable structures (Rajvanshi et al., 2013). Sandwiched between the upgraded segments (**Figure 1**), the forested 2-laned segment received greater number of vehicles per unit time than the 4-laned segments, thereby posing a threat of creating a barrier for animal movement across the corridor.

An alternative route via Chhindwara, Maharashtra, involving an additional length of 70 km (55% increase in distance) was suggested by a conservation organization. This alignment posed a threat to the connectivity of the Pench-Satpura-Melghat corridor which is vital for connecting six tiger reserves in the landscape. Opting for this alignment would also require re-alignment of 122 km of an existing highway (17% of which was in the hills), diversion of 163 ha of forest land and felling of 81,500 trees (Wildlife Institute of India, 2012).

The imminent threat to the Pench-Kanha corridor because of increase in and funneling of traffic on NH 7 was greater given its high use (daily traffic volume on NH 7 increased from 3048 to 6151 in three years Wildlife Institute of India, 2012; Habib et al., 2015). This meant that abandoning upgradation plans on this stretch would hinder movement in the corridor further. So long as mitigation measures conducive to animal movement were incorporated in the initial alignment, the possibility of recovery of this corridor was thought to be greater. Considering implications for wildlife conservation and future projections of road development and traffic growth, it was thus considered prudent to allow upgradation of the existing alignment (Habib et al., 2015).

PRIORITIZING MITIGATION ACTIONS, STRUCTURES AND TARGETS

Choosing the target species/group for mitigation planning requires prioritization of the goals of mitigation that could be aimed at maintaining viable populations of select species across the landscape, reducing the risk to human lives due to animal-vehicle collisions (van der Grift et al., 2013), or at reducing road-related animal mortality, and vice-versa. This would however depend on local conditions, development objectives and conservation priorities that need to be set out clearly at project inception stages.

In case of NH 7, it was considered best to focus on the entire suite of locally available species (30 mammals-22 of which belong to Schedule I and II of the Wildlife (Protection) Act, 1972) to achieve the desired goals. Moreover, since it is not always feasible to address the concerns of each species in a landscape, measures that would address the concerns of most animals in the landscape were considered. The predominant criteria was, however, to provide connectivity for the flagship species, for which we relied on corridor maps created for tigers in the landscape. Thus, it was proposed to build flyovers across all forested corridors by an appraisal of the initial project plan (Wildlife Institute of India, 2012). The objective was to provide structures large enough to offer natural

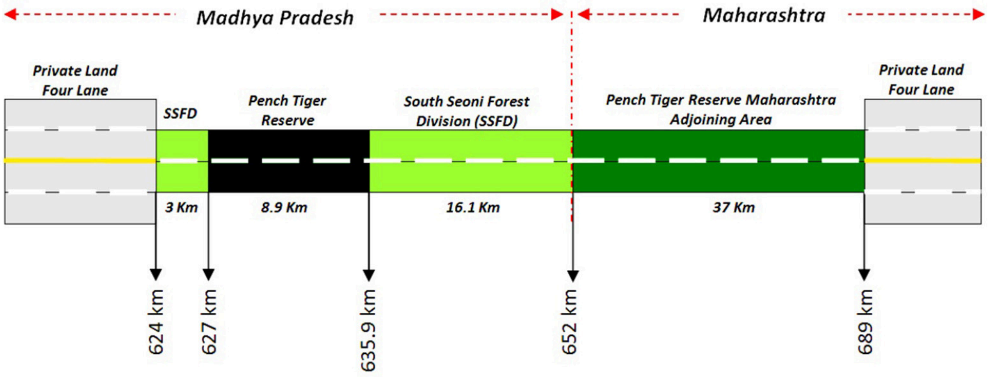

FIGURE 1 | Location of 2-laned segment of NH 7 between upgraded 4-laned segments causing a funneling of traffic.

passage to animals in the soon-to-be upgraded sections of the highway.

We achieved this by demarcating animal crossing zones based on sign surveys and then prioritizing locations of crossing structures based on the intensity of use by animals, and presence of villages and other ancillary development along the road stretch. In places where animal signs were found adjacent to villages and farmlands with weak connectivity to adjacent habitat patches, crossing structures were not suggested considering the possibility of conflict with humans. Some crossing zones were found to overlap natural drainage and in these places it was suggested to enhance existing drainage structures to facilitate use by animals, resulting in a multi-use structure.

USING TRIAGE TO CONNECT PEOPLE AND HABITATS: CONCLUSIONS AND WAY FORWARD

The average size of PAs in India is ca 220 sq. km[3], and is not enough to sustain long-term viable wildlife populations, particularly of landscape-dependent species such as elephant and tiger (Woodroffe and Ginsberg, 1998; Yumnam et al., 2014). These areas thus need to remain connected through a network of forested tracts outside the PA network, which often fall under different land ownership tenures. Existing and new roads in these lands inevitably lead to conflict with the objectives of maintaining connectivity among protected areas. Such roads, when upgraded, also present us with an opportunity to implement mitigation measures that offset the development impacts and those of the existing infrastructure. The internalization of mitigation costs incurred by developers into India's economic development can prove to be minimal in the long-term (Hudson, 2011).

Given the lack of strategic land-use planning in India and late consideration of conservation concerns into project planning, mitigation funds are not always adequate. Therefore science-based prioritization exercises of areas that are threatened by development and have a positive chance of recovery via investments in mitigation need to be outlined. Landscape conservation plans could also be used to guide the application of mitigation planning of development plans by overlapping development plans (present and future) with conservation objectives and align development and mitigation plans accordingly. Such exercises would also help delineate "no-go" zones for linear developments (Kiesecker et al., 2009). Hobbs and Kristjanson (2003) outlined a grid-like prioritization system that has been modified from emergency health-care for the "treatment" of landscapes. This approach helps assign appropriate levels and types of care to the landscapes considering relative level of threat and probability of recovery, factors critical for setting priority (Joseph et al., 2009). Prioritizing which corridors or habitats to save in no way means abandoning areas that are difficult to save or those with development interests; it merely allocates limited mitigation funding strategically to achieve conservation goals through effective mitigation planning (Bottrill et al., 2009).

New mechanisms for funneling development funds for conservation outside the PA system are currently being formulated in India. For example, under a new program, the MoEFCC is working on new guidelines to incentivize proponents to carry out afforestation and purchase and transfer land within recognized corridors as part of the compensatory afforestation program.

Strategic or landscape-level inter-sectoral assessments and land-use planning exercises could also help avoid issues that ensue as a consequence of a piece-meal approach to development, the prevalent practice in India today. This would also ensure that instead of keeping conservationists at the periphery in dealing with large development interests (Klages, 2010), they are engaged early in planning stages to evolve scientifically sound approaches in favor of the protection of ecosystems and ecosystem services within the mitigation hierarchy of such development plans. This strategy would both influence and be influenced by the allocation of

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[3] http://www.wiienvis.nic.in/Database/Protected_Area_854.aspx

funds dedicated to avoiding and ameliorating development impacts to natural landscapes, and the business and political willingness to do so. There is also a need to initiate dialogue on science-based prioritization criteria suited to the conservation and development needs of India among conservation scientists which would then translate into prioritization in planning.

As conservationists, we cannot stop progress but we can shape it (Rosner, 2013). Identifying opportunities for positive conservation action through unavoidable development imperatives can help bridge the gap between our desire to conserve and our ability to conserve.

AUTHOR CONTRIBUTIONS

BH, AS, AR, and VM: Designed the paper, drafted and revised the paper, and approved the final version of the manuscript before submission. All authors contributed equally to this paper.

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Saving wildlife on India's roads needs collaborative and not competitive efforts

Akanksha Saxena, Adrian Lyngdoh, Asha Rajvanshi, Vinod Mathur and Bilal Habib

Roads – uniting humans, dividing nature

Transportation infrastructure is central to the functioning and development of human societies. However, the widespread network of transportation infrastructure worldwide has also altered natural landscapes drastically in the past century. These networks pervade far beyond any other human infrastructure, and pose multiple negative impacts to the natural elements of the landscapes they cut across[1,2]. Road networks worldwide have splintered previously undisturbed swathes of forests into nearly 600,000 patches, only 7% of which are larger than 100 km^2 in size[3], making movement across these patches challenging for wildlife. Road and traffic emissions such as noise, gaseous and liquid pollutants, and solid waste also cause disturbance and may result in avoidance of these forests by wildlife[4].

Roads with traffic affect wildlife by creating barriers to their movement across landscapes, particularly affecting long-ranging species such as tiger, elephant, leopard, dhole and wolf[5,6]. This can lead to fragmentation and eventually isolation of populations[7]. The most conspicuous impact of roads is mortality of animals. Ecologically, road-related mortality because of collision with moving vehicles is detrimental to animal populations as it is non-selective, i.e. it affects healthy as well as weak individuals of a population[8]. It can also lead to local extinction of species[9]. Animal–vehicle collisions also cause injuries and fatalities to humans and economic losses due to vehicular damage[10]. Roadkill is also the most studied impact of roads on wildlife, with literature on the subject available from as early as 1935 (ref. 11). Most road ecology studies in India too are centred on road-related mortality.

Mitigation measures such as overpasses, underpasses and restricted timings on the use of roadkill-prone highway segments are commonly used strategies to curb mortalities of wildlife. Proper implementation of such measures requires reliable long-term roadkill and ecological data. Given the spread of the Indian road network, the task of collecting information on roadkill on roads passing through forest areas throughout the country is an enormous task.

More eyes on the road

Citizen science, which is the collection and analysis of scientific data by the general public, has been successful for recording natural observations[12], bird observations and migrations[13], and many others all around the world. The dawn of information technology has further given an impetus to the involvement of the public in conservation issues through citizen science. This has helped reduce pressure on scientific research groups by increasing the spatial coverage of data collection and has revealed interesting results which would otherwise have been beyond the scope of individual research projects. In short, the right combination of citizen science projects and methods of participation can benefit conservation significantly.

A similar app-based citizen science approach has been initiated by two conservation NGOs in India to record roadkill. The apps aim at increasing the spatial and temporal spans of data collection, engaging the general public and affecting policy change through increased public interest in the issue. Two separate mobile-based roadkill recording apps were launched earlier last year within two days of each other – RoadKill by the Wildlife Conservation Trust, Mumbai and RoadWatch by the Wildlife Trust of India, Noida. Both apps have user-friendly interfaces through which travellers can record roadkill on-the-go from anywhere in the country on their mobile devices by submitting photographs and identifying species or broad species type. The RoadKill app aims to 'democratize data collection' to contribute to better planning and installation of mitigation measures on new and upgraded roads in order to reduce wildlife mortality on roads and improve passenger safety[14]. Data collected under this initiative would be made available through Creative Commons license. The RoadWatch app aims to map hotspots of animal mortality, identify worst-affected species groups and assess effectiveness of existing mitigation measures[15]. Data collected through the app is 'open source', however, data-sharing details are not clear. The RoadWatch website showed 873 roadkill observations (reptiles 343, mammals 203, birds 113, amphibians 126, unidentified 88) at the time of writing this note.

Both the apps are easily available on the internet and their convenient, user-friendly interface makes it easier for the layman to contribute to this important issue. However, the main proposition of developing and promoting such apps is that data on roadkill would prepare conservation agencies better to manage and mitigate the loss of wildlife on the roads. However, such data provide an incomplete picture of the broader understanding of road ecology per se. Additionally, the information generated thus would also be inadequate to inform mitigation measures on new roads.

It is not all about the roadkill

Although it is a great opportunity to channel public interest in conservation, professional conservationists ought to know that roadkill is only a small fraction of the real threat that roads pose to wildlife, and merely represents a symptom of the real problem. It indicates a loss of connectivity among adjacent habitat patches. The road is like a death trap that animals must navigate to make it to the other side. Forests on the roadsides that may seem structurally pristine are made less inhabitable by road and traffic emissions like noise, gaseous pollutants, off-roading of vehicles, littering by motorists, etc. These factors affect the use of roadside habitat by animals that may adapt by changing their patterns of habitat use or by avoiding roadside habitats entirely[16–18]. Therefore, the absence of roadkill from a road may not imply that traffic on that road does not pose any hazard to wildlife. The pieces of the puzzle lie not on the asphalt, but in the forests surrounding these roads.

Roadkill data for any species or taxa would remain incoherent in the absence of data on the population status and habitat use of animals in the adjacent forest patches. Roadkill numbers may vary with traffic volume and age of the road (time in years during which the road has been operational), where local animal populations across older and high-traffic roads would get depressed over time[19]. This would also influence per capita mortality rates across populations on high- and low-traffic segments, i.e. the chance of an individual of a population getting road-killed[20]. This rate is difficult to assess without reliable estimates of regional populations. Therefore, roadkill hotspots that include data for multiple species may not accurately depict the impact that roadkill has on population structures of different species.

Moreover, shifts in roadkill hotspots have been observed from high-traffic segments to low-traffic segments[21]. Habituation, avoidance and reactions of animals would influence road-crossing behaviour and affect roadkill rates[22]. Therefore, the absence of roadkill of a particular taxon on certain roads does not imply that the taxon is absent from the area, or that the road is not affecting these animals. Such absence may also indicate the activity of scavengers that can remove up to 60–97% of roadkill[23].

The degree to which different taxa get affected by wildlife–vehicle collisions also varies with factors like species characteristics, behaviour and diet. For example, reptiles and amphibians are the most commonly encountered roadkill taxa[24]. This is because they are slow-moving, dependent on roads for their thermoregulatory requirements[25], and are thereby compelled to encounter roads more often. Large mammals have greater cognitive abilities and are able to avoid crossing roads or avoid collision[22]. Roadkill data would therefore be insufficient and misdirected in informing mitigation strategies for maintaining connectivity of landscapes for mammals.

Merely documenting roadkill helps little in understanding the underlying animal movement patterns – what causes the animals to choose certain crossing zones over others? Which animals are most likely to use these crossing zones and, consequently, what placement of crossing structures would benefit most of the species? Navigating through anthropogenic landscapes and across linear features is not as predictable as moving within forests, and depends on myriad factors – sex and age class of the animal, season, vegetation type and traffic volume among others. Radio-tagging animals and camera trapping helps us understand, among other things, the choices they make when confronted with human infrastructure, as has been documented in several studies in the West[17,26]. The science of road ecology is therefore much more than mere reporting of roadkill. Hence, information gathered through field studies is indispensable. Like any other scientific approach, citizen science has its limitations and the application of data collected through these apps to road ecology should be done with caution, as such data overlook many important factors highlighted earlier in the text and are incomplete to inform mitigation strategies. Nevertheless, the initiative of citizen science apps to collect data on roadkill is a welcome step. Such efforts generate awareness and are important tools to sensitise public and policymakers. Utilizing social information networks makes scientific studies more participatory, leading to greater buy-in of the public regarding issues of conservation importance.

Mind the (g)app

The fact that two functionally similar apps were launched by different organizations simultaneously makes the matter moot. Motivated citizens are consequently made to choose between the apps, because of which both the apps will end up collecting non-overlapping subsets of data, which would also get divided and skewed in terms of areas visited. When conservation is a common goal, stakeholders cannot afford diluted, deflected and competing efforts. Instead, a pan-India effort like this requires collaborative work to present the public with a single, simple and effective data-collection platform.

We suggest a unified, well-managed platform directed at collecting roadkill data in order to make a more substantial contribution. Additional features in this unified app that would enable users to report observations of animals using roadside habitats, attempting to cross roads, in addition to those being involved in collisions – would also optimize the scope of these apps (see http://www.roadwatchbc.ca/). This information would help identify commonly used animal-crossing zones. Additionally, involving citizen scientists who commit to driving a specified route would remove spatial bias in data collection. Established protocols for recording roadkill are also missing in the current app formats. For example, removal of animal carcasses must be ensured to avoid chances of their double counting and reducing the occurrence of scavenger–vehicle collisions. Investment in capacity building of citizen scientists would increase the prospects of improved data quality and more meaningful involvement of citizens in furthering the contribution to road science. Thus, a holistic understanding of road ecology and mitigation of the ill-effects of roads on wildlife calls for a unified effort from all stakeholders, instead of divided and competing initiatives.

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Integrating large mammal behaviour and traffic flow to determine traversability of roads with heterogeneous traffic on a Central Indian Highway

Akanksha Saxena, Nilanjan Chatterjee, Asha Rajvanshi & Bilal Habib

Roads impact wildlife in multiple ways, most conspicuous amongst which are animal-vehicle collisions (AVCs). Mitigation measures to reduce AVCs at the local scale are often centred on species-specific crossing zones and collision hotspots. However, at the road network scale, consideration of interactions among road, species and traffic characteristics influencing AVC occurrence is required to design effective mitigation strategies. We modelled traversability—the probability of an animal successfully crossing a road- across an Indian highway for six large mammal species under different scenarios of road and traffic characteristics. Among the study species, group-living and slow-moving animals had higher AVC probabilities that increased significantly with increasing traffic volume and proportions of heavy vehicles in the traffic flow. The risk of AVC was higher for species that were active near roadside habitat during peak traffic hours. Our approach could help identify roads that pose potential mortality risks to animals using empirical data on animal and traffic characteristics. Results suggest that regulating traffic volume and heterogeneity on existing road stretches could potentially reduce animal mortality and barrier effect. Mitigation on roads expected to carry heavy traffic loads passing through ecologically-sensitive areas should be prioritised to ensure traversability for animal communities.

The transportation infrastructure of a nation is vital for its social and economic growth, especially for a developing economy. However, the construction and operation of roads come at great costs to wildlife and forests dissected by linear infrastructure[1,2]. The most conspicuous impact of roads is wildlife-vehicle collisions, which is a major cause of decline in animal populations in human-dominated landscapes[3]. Road-related mortality affects animal populations more adversely than natural mortality since it is non-selective, and affects healthy and unhealthy individuals of a population equally[4,5].

Roads also cause some species to respond by avoidance of habitat near high traffic roads at peak traffic hours[6,7]. This avoidance of roadside habitat could result in the road becoming a barrier to animal movement[8]. In addition to the risk of local species extinction[9], mortality and barrier effects together alter wildlife movement[10,11] leading to isolation of populations[12,13]. With the global road network growth projected at more than 60%[14], and rampant increase in worldwide vehicle ownership[15], these impacts are set to accelerate in magnitude.

Variations in roadkill rates among species have been attributed to various environmental and species-specific features such as age group or life history stage[16–19], sex and diet[20,21], and animal activity patterns[6,22]. Therefore these traits are critical for identifying species most vulnerable to mortality and barrier effects for effective mitigation. Environmental and landscape features such as food resource distribution and habitat type[20,21], and road-related features like traffic volume, vehicle speed, road width and road type[21,23–27] also affect roadkill rates. Large traffic volumes may reduce the frequency of attempted crossings[7,22], leading to low roadkill numbers, and could also cause the road to become a physical barrier to animal movement[28–31].

Mitigation of roadkill and barrier effects of rapidly expanding road networks requires identification of road sections that may cause animal mortalities and barriers to animal movement, and species most likely to be involved in AVCs[8]. Studies that take into account road, traffic and landscape characteristics along with species presence, activity and movement characteristics[8,25,32] have been able to predict mortality and barrier hotspots

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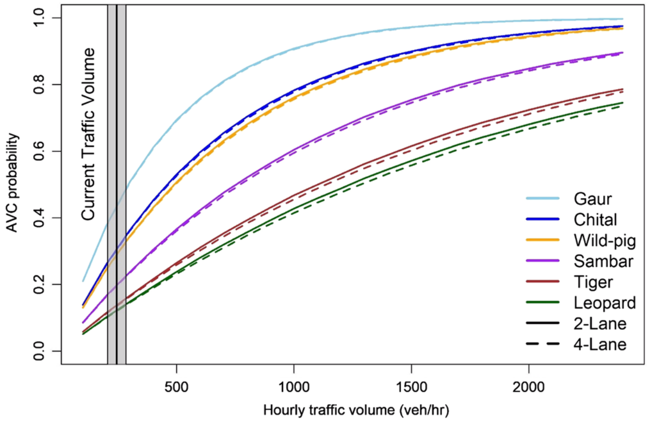

Figure 1. Animal Vehicle Collision probabilities with increasing hourly traffic volume (projected) at present traffic heterogeneity conditions on 2-lane (solid lines) and 4-lane (dashed lines) sections of the National Highway 44, passing through the Pench Tiger Reserve, India. Figure created using R[45] version 3.6 (https://www.rstudio.com/).

across road networks. However, the interaction among risk factors contributing to roadkill and barrier effects to inform mitigation strategies is largely missing from such models. Moreover, mitigation for rapidly expanding road networks should also be informed by road and traffic characteristics such as road types, and projections of traffic growth[33] and traffic composition or 'heterogeneity' that is the proportion of different vehicle types in a traffic flow[8].

We present a framework to identify species and roads vulnerable to AVC as a function of road, traffic and species characteristics, using data from traffic simulations under different traffic heterogeneity and volume scenarios, and morphometry and behavioural data of six widespread large mammals of Central India. The study was conducted on a 60 km stretch of the National Highway 44 (NH 44) passing through the Pench Tiger Reserve (PTR) in Madhya Pradesh and Maharashtra states.

We sought to answer four questions: (1) which species traits increase AVC probability (defined as the probability of an animal colliding with a vehicle while crossing a road, and is to be interpreted as the opposite of traversability)? (2) Which road and traffic characteristics make roads less traversable (i.e. increase AVC probability) for animal movement? (3) At what traffic volumes and compositions do roads become barriers for animal movement? (4) Does animal activity near roads increase AVC risk (defined as the hourly AVC probability as a function of animal activity)?

We hypothesised that slow-moving and group-living animals would have greater AVC probabilities under fast-moving highly heterogeneous traffic conditions. Additionally, we hypothesised that animals with high activity overlaps with traffic would have greater AVC risk.

Results

Influence of species traits on AVC probability.

Among the six study species, group-living species (gaur, chital, wild pig, sambar) had the highest AVC probabilities under hourly traffic volumes ranging between 100 and 2400 vehicles/h with present traffic heterogeneity (61% car, 13% bus/truck, and 26% MAVs) on NH44 (Fig. 1). Under present traffic heterogeneity and average hourly traffic volume (245 ± 20 vehicles/h) on NH44, lowest average daily AVC probabilities were found for tiger (0.13 ± 0.05) and leopard (0.11 ± 0.04) (Fig. 1). Chital (0.29 ± 0.10) and wild pig (0.29 ± 0.20) had similar average daily AVC probabilities, while sambar (0.42 ± 0.13) had a lower AVC probability among ungulates. Across both lane types, gaur had the highest average daily AVC probability.

We found that an increase in group size increased the probability of hit (species length PIC 0.003; 95% CI 0.001–0.005) while increasing animal velocity decreased the probability of hit (PIC −0.005; 95% CI −0.011 to −0.002). Animal width did not influence AVC probability significantly (PIC 0.04; 95% CI −0.043–0.1) (Fig. 2).

Influence of road and traffic characteristics on AVC probability.

The average daily traffic volume on NH 44 during the study period was 5883 ± 168 vehicles, while the average hourly traffic volume was 245 ± 20 vehicles/h, comprising of 61% car, 13% bus/truck, and 26% MAVs. Simulations for present traffic heterogeneity on NH 44 at different hourly traffic volumes showed that heavy vehicles (MAVs) had the lowest, and lighter vehicles viz., cars had the highest free flow speeds within a traffic flow (Fig. 3).

For simulated heterogeneity scenarios at different hourly traffic volumes, the average harmonic traffic flow speeds of homogeneous traffic scenarios were higher than that of heterogeneous scenarios with greater proportions of heavy vehicles. Results of the traffic flow speed simulation under different heterogeneity scenarios have been provided in Supplementary Figure S1.

Across all simulated traffic heterogeneity scenarios, the AVC probability (P_h) for all species increased with increase in traffic volume and showed similar variation among species as under present traffic heterogeneity.

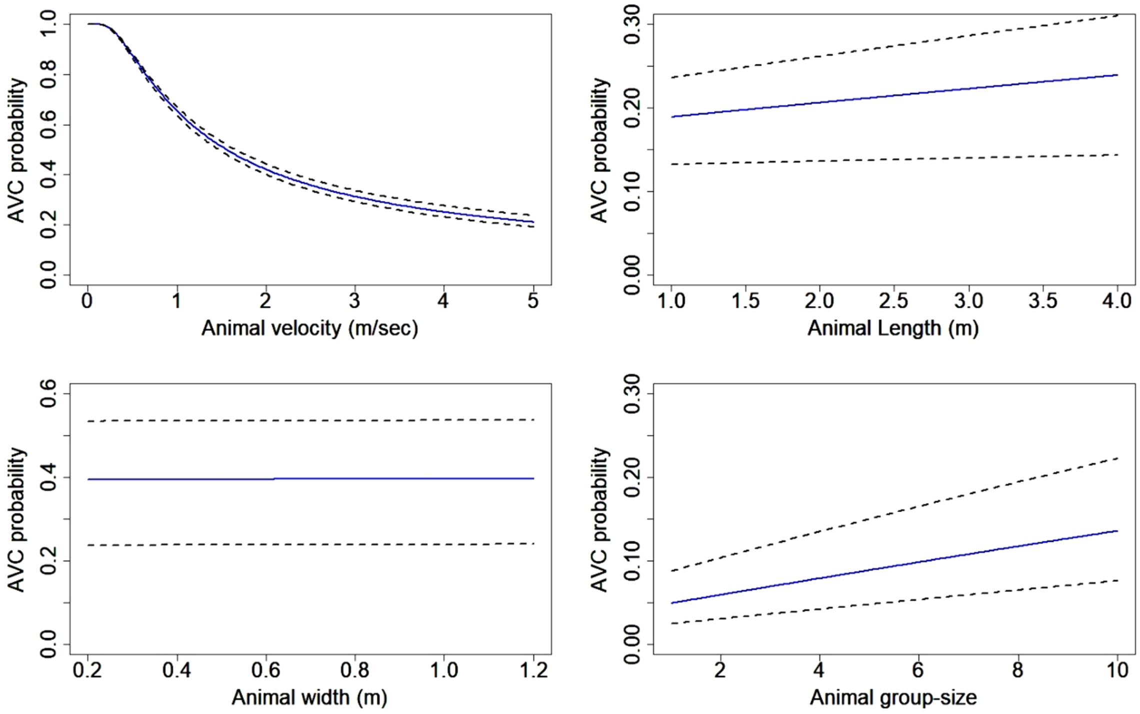

Figure 2. Relative effects of species traits on Animal Vehicle Collision (AVC) probability. To calculate the change in AVC probability with unit change in the target variables, the mean values of other variables were plugged into Eq. (1). Dotted lines indicate 95% confidence intervals around coefficient estimates. Figure created using R[45] version 3.6 (https://www.rstudio.com/).

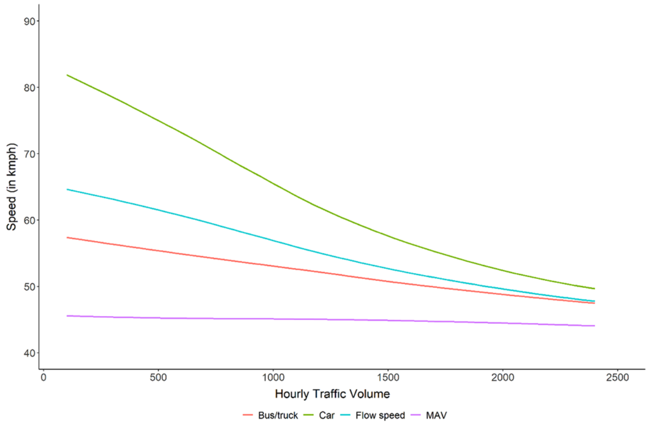

Figure 3. Simulated average harmonic traffic flow speed of present heterogeneity H_0 (blue curve) on NH 44 at different traffic volumes, and free flow speeds of different traffic components viz., car (green), Bus/truck (red) and MAV (purple) in the same simulation. Figure created using R[45] version 3.6 (https://www.rstudio.com/).

All animals had high P_h for traffic mostly comprising of heavy vehicles (scenarios H_3, H_5, H_6) while low P_h was observed for scenarios where traffic mostly composed of light vehicles (H_0, H_1) (Fig. 4).

The threshold traffic volume at which AVC probability was equal to probability of successful crossing ($P_h = 0.5$) varied for different species. Under present traffic heterogeneity, this threshold traffic for group living animals like chital, gaur and wild pig was 300–400 vehicles/h. This threshold traffic volume was higher for sambar (700 vehicles/h), and highest for tiger and leopard (1100–1300 vehicles/h). Across all simulated scenarios, traffic volumes of 200–300 vehicles/h decreased the chances of a successful crossing by half for gaur. For chital, this traffic volume lies above 400–500 vehicles/h in traffic composed of light vehicles (H_0, H_1, H_4, H_7). This threshold volume is higher for sambar (1100 vehicles/h) in traffic composed mostly of heavy vehicles (H_3, H_5, H_6). Hourly traffic volumes above 1000 vehicles/h posed a barrier to < 50% successful traverses for tiger and leopard at most traffic heterogeneity scenarios. The threshold traffic volume for solitary species was lowest (800 vehicles/h) at

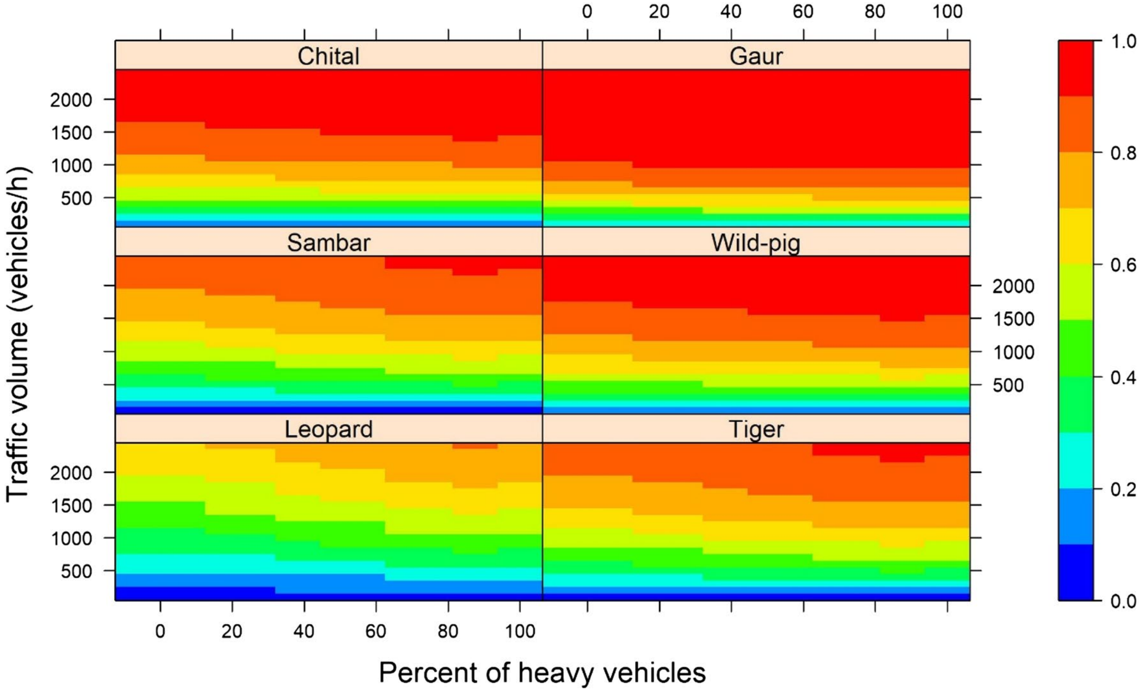

Figure 4. Gradient of Animal Vehicle Collision (AVC) probability for six study species across increasing traffic volumes under different percentages of heavy vehicles (representative of different heterogeneity scenarios). Colour bar to the right of plots depicts AVC probability (P_h). Figure created using package 'lattice'[58] in R[45] version 3.6 (https://www.rstudio.com/).

scenario H_3 which comprised of only MAVs. Beyond this threshold traffic volume, higher fatalities are expected to occur.

For all study species, we found that the time on the road during which an animal is vulnerable to AVC (expressed as AVC exposure in seconds) was almost double (197.94% ± 1.72) on 4-lane segment as compared to 2-lane segment at the same traffic volumes (at present traffic heterogeneity) (Fig. 5). For chital, gaur and wild pig, AVC exposure at hourly volumes beyond 1300 vehicles/h almost reached asymptote i.e., the animal was at risk of collision for the entire traversing duration.

Change in traffic volume and traffic flow speeds had the strongest influence on P_h (Fig. 6). From the sensitivity analysis we found that AVC probability was positively influenced by length of the vehicle (PIC 0.032; 95% CI 0.02–0.039), and negatively influenced by velocity of vehicles (PIC − 0.093; 95% CI − 0.11 to − 0.07). We found no significant contribution of width of the vehicle (PIC − 0.015; 95% CI − 0.016–0.047). Traffic flow speeds decreased with increasing traffic volume and this change in speeds tended to increase P_h across all traffic heterogeneity scenarios on both lane types (Supplementary Fig. S1).

Influence of animal activity on AVC risk. We photo-captured a total of 6043 photographs across 23 mammals, and 3624 images of our study species. The total sampling effort was 3024 camera-days at 216 camera trapping locations. Tiger and leopard were not considered for this analysis owing to low number of captures (n = 12 and n = 1 respectively) and larger home ranges as compared to the trapping area.

We used species-specific hourly AVC probabilities and corresponding hourly detection probabilities calculated from captures of chital (n = 802), gaur (n = 34), sambar (n = 21) and wild pig (n = 79) to calculate hourly AVC risks for the four study species. We found differential effects of traffic and animal activity on AVC risk (Fig. 7). At peak traffic hours, AVC risk for wild pig was higher than for chital on both 2-lane and 4-lane roads. For sambar and gaur, there was no risk of AVC during peak traffic hour because their activities near the road did not coincide with traffic activity at peak traffic hour. The peak activity of chital during evening hours coincided with a traffic activity peak, and thus the AVC risk for chital was expected to be highest during this time, on both 2-lane and 4-lane road. Moreover, the activities of sambar and gaur showed lesser overlap with traffic activity while chital and wild pig had comparatively higher overlap (Supplementary Table S4).

Discussion

We demonstrated the applicability of the traversability model to determine species-specific AVC probabilities and AVC risk across different traffic heterogeneity and traffic volume scenarios. We found that slow moving animals and animals with large group sizes were at higher risk of AVC as a consequence of greater time required to traverse roads. Further, AVC probability is expected to be greater on wider roads, particularly high traffic roads with predominantly heavy vehicles.

Among the six study species, lowest AVC probabilities were observed for tiger and leopard, primarily because these are solitary fast moving species. Body size had negligible effect on AVC probability[23], but increase in group

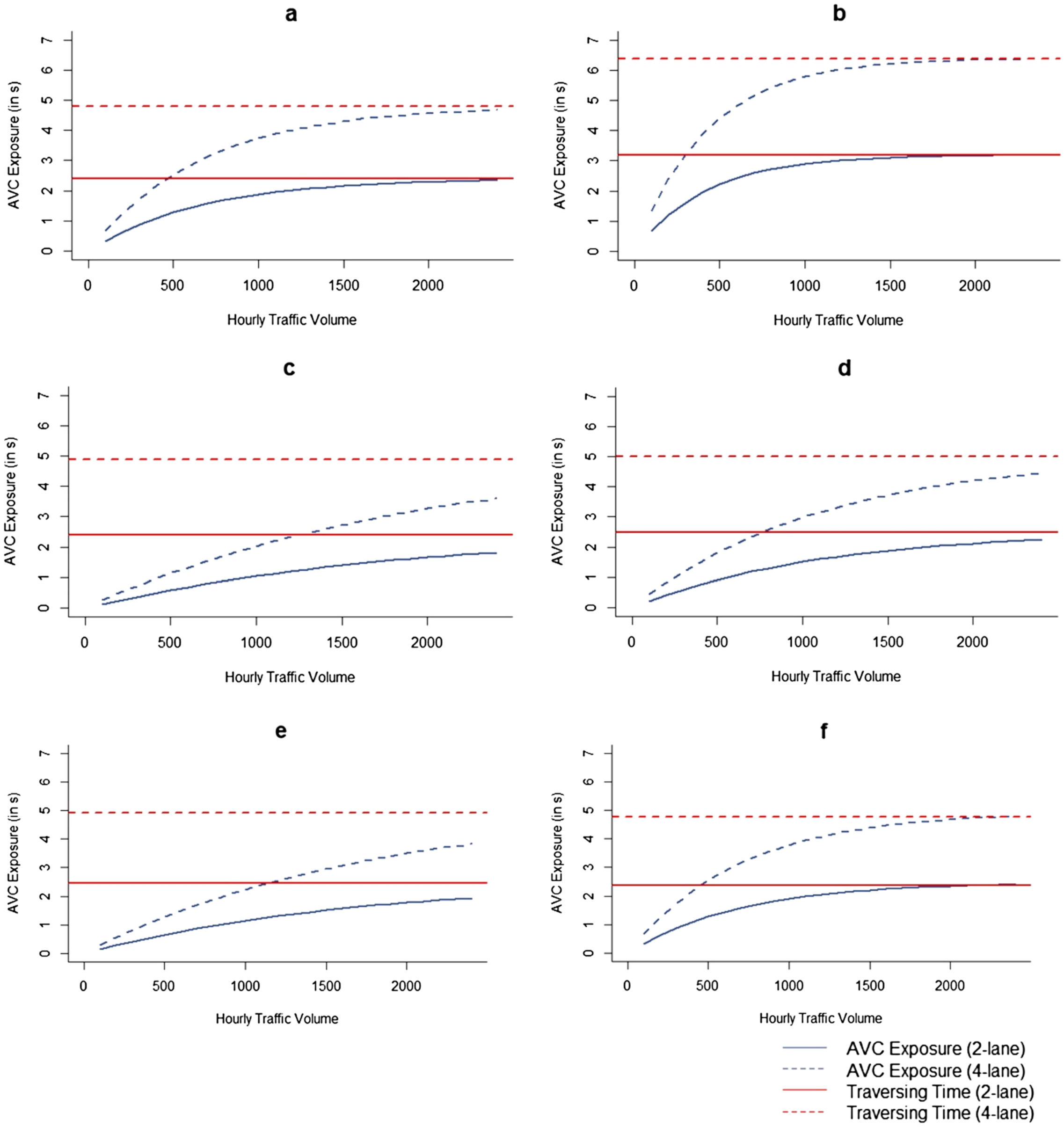

Figure 5. AVC exposure (blue curves; in seconds) of (**a**) chital, (**b**) gaur, (**c**) leopard, (**d**) sambar, (**e**) tiger, and (**f**) wild pig, a function of the duration of time an animal needs to traverse different widths of roads (red lines) and the Animal Vehicle Collision (AVC) probability under the hourly traffic volume at that time. Figure created using R[45] version 3.6 (https://www.rstudio.com/).

size increased the probability resulting in higher AVC probabilities for group living species. Among social species, lower group size of sambar translated to lower AVC probability than chital and wild pig, despite having similar maximum running speeds. Group size of gaur was similar to that of wild pig; yet gaur had the highest AVC probabilities across all heterogeneity scenarios as a result of its low running speed.

Mammals with low reproductive rates and high mobility, like carnivores show more negative responses to roads and traffic[34], and carnivore movement is affected more than herbivores[35,36] at high traffic volumes. Even though both carnivores in our study had the lowest AVC probabilities among all study species, they may not attempt crossing wider roads at high traffic volumes which could ultimately present a barrier to their movement[19].

The AVC probability across different heterogeneity scenarios showed variability, largely as a consequence of the speeds of traffic flow. Results show that the highest AVC probabilities occurred for traffic compositions with higher proportions of heavy vehicles. Since heavy vehicles impede the cumulative traffic flow speed, the probability of occurrence of a vehicle at any point on the road increases, consequently translating to higher probabilities of hit mostly for slow-moving and group living animals. On the contrary, in a traffic flow with high flow speed, there is greater inter-vehicular distance available which translates to higher probability of an animal to cross the road without encountering a vehicle. This finding has implications for speed-regulating mitigation measures like

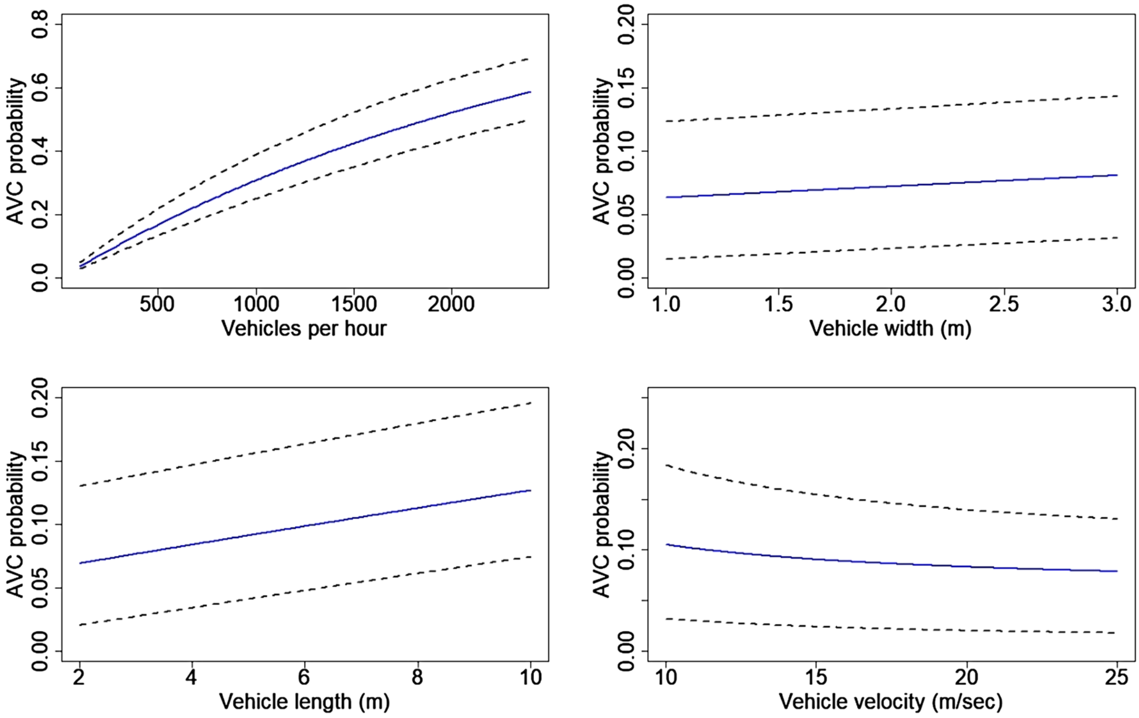

Figure 6. Relative effects of traffic characteristics on Animal Vehicle Collision (AVC) probability. To calculate the change in AVC probability with unit change in the target variables, the mean values of other variables were plugged into Eq. (1). Dotted lines indicate 95% confidence intervals around coefficient estimates. Figure created using R[45] version 3.6 (https://www.rstudio.com/).

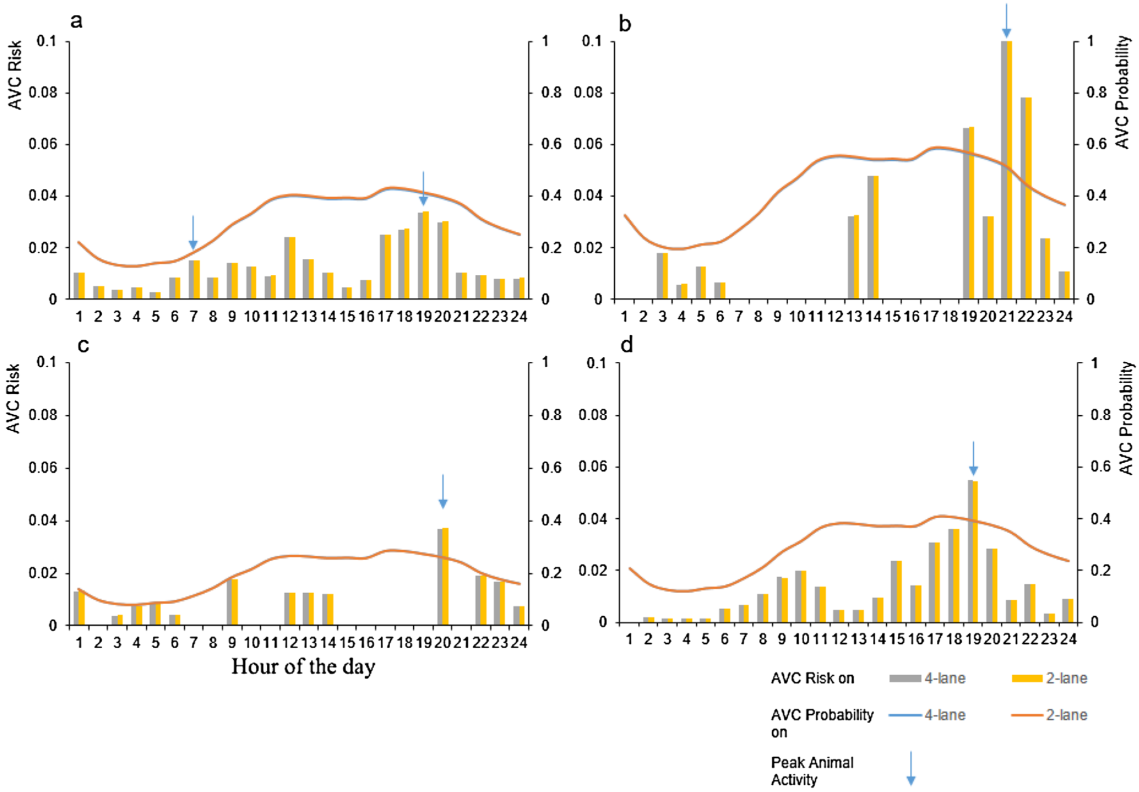

Figure 7. Animal Vehicle Collision (AVC) risk (yellow and grey bars) and AVC probability (red and blue curves) across 24 h for (**a**) chital, (**b**) gaur, (**c**) sambar and (**d**) wild pig. The AVC risk plotted on the secondary axis was computed as the product of AVC probability and hourly detection probability (used as a proxy for animal activity). Figure created using R[45] version 3.6 (https://www.rstudio.com/).

speed breakers and rumble strips that can potentially decrease inter-vehicular distances at medium–high traffic volumes, leading to creation of a barrier-like situation for animal movement.

At higher traffic volumes the barrier effect sets in due to continuous flow of traffic, where road crossing by animals may not occur. Thus higher traffic volumes would result in a barrier-like situation because of avoidance of animals at high traffic segments[6,7] reducing the number of attempted crossings by wildlife. This avoidance would reflect as low roadkill counts on high traffic roads[22].

Even though AVC probabilities on wide road segments were similar to probabilities on narrow roads, the exposure of an individual/animal group to AVC while traversing a 4-lane segment was found to be almost double than the exposure on 2-lane segment. This risk of exposure was highest for species with large group sizes. Greater exposure on 4-lane roads at moderate traffic levels could cause more roadkill than on 2-lane roads, while on 2-lane roads the same traffic levels could become a barrier to animal movement.

The traversability model[37] did not consider animal activity near roads. For an animal-vehicle collision to take place, an animal and a vehicle must co-occur on the road. We accounted for this by using animal activities near the road as a proxy for the probability of an animal encountering a road. Creation of edge habitats by linear intrusions like roads facilitate the use of such habitats by some ungulate species. Consequently for edge-tolerant species like chital and wild pig[38] that were found to use road-forest edges, hourly roadkill risk is a function of hourly traffic volume since their activities near the road coincide with peak hours of traffic activity (Chital and Traffic Overlap Coefficient Dhat1 = 0.82; Wild pig and Traffic Overlap Coefficient Dhat1 = 0.82). Hence use of roadside habitat by chital and wild pig, makes them more vulnerable to mortality effects. For gaur and sambar that are generally crepuscular and nocturnal species with low road-forest edge use, the roadkill risk is a direct consequence of its activity in the early morning or late evening hours (Supplementary Table S4).

At present, traffic on NH 44 may not present a barrier to movement of chital and wild pig as we frequently encounter chital and wild pig roadkill at present traffic volumes. Gaur and sambar, on the other hand, are more vulnerable to barrier effect through avoidance behaviour of roadside habitat that reflects a lower tolerance to traffic disturbance[39,40].

As in the aforementioned studies[8,23,37], the aim of the study is not to determine the actual number of mortalities, but to help determine high-risk roads, traffic compositions and species groups most vulnerable to collision and barrier effects. Our model defines a way to identify components of a road network most vulnerable to roadkill, and could be used to identify road network components requiring prioritised mitigation action. In the absence of data on animal movement near roads, the present approach using species traits and behaviour could help prioritise mitigation for species most vulnerable to collision with vehicles.

Our framework can help inform mitigation of AVC and barrier effects in two ways: by identifying existing and proposed roads in a network that are or may become barriers to animal movement because of present and projected traffic volume, and by informing measures on existing roads with no structural mitigation measures based on traffic and animal activity. This is important for developing economies with rapidly increasing traffic loads on existing unmitigated road networks.

For existing road networks, our approach could help identify roads that are vulnerable to high roadkill rates as a function of their traffic volume and traffic composition. Measures may include speed restrictions for traffic predominantly consisting of small vehicles, temporal limitations on heavy vehicles and construction of animal passages on high traffic multiple use roads. Other actions such as alternate road network alignments considering projected traffic growth, combined with additional information on animal corridors, species occurrence and animal activity, can inform future road developments at the landscape scale.

Planning mitigation measures in a rapidly expanding road network with multiple use roads and highly heterogeneous traffic has to be futuristic and strategic i.e., it should consider large-scale and long-term conservation needs. Under such conditions, traffic volume is a critical parameter that would inform landscape-level prioritization with respect to present and projected traffic loads. Accommodating increased traffic on existing roads versus building new roads is an ongoing debate—while it has been stated that accommodating increased traffic growth on existing roads would be less damaging[33], threshold traffic volumes may reduce animal road crossing rates, and create barrier to animal movement[39]. Thus, including traffic growth projections while planning mitigation for new roads (planning mitigation structure types, rerouting) would make mitigation viable for the long-term.

Methods

Study area. We conducted our study on a 60 km segment of the NH 44 (previously NH 7) that straddles the Maharashtra-Madhya Pradesh interstate boundary (Fig. 8) in central India. The highway forms the North–South transportation corridor, connecting major Indian economic and urban centres. The study was conducted on a 16 km 4-lane segment passing through Pench Tiger Reserve, Maharashtra, and a 29 km 2-lane segment passing through Pench Tiger Reserve, Madhya Pradesh. The tiger reserves are part of the Central Indian Landscape, which is a priority tiger conservation unit[41]. The forest in the area is mostly of the moist and dry deciduous type[42]. Tiger *Panthera tigris*, leopard *Panthera pardus*, sloth bear *Melursus ursinus* and wild dog *Cuon alpinus* are the major carnivores, and gaur *Bos gaurus*, chital or spotted deer *Axis axis*, sambar *Rucervus unicolor*, wild pig *Sus scrofa*, nilgai or blue bull *Boselaphus tragocamelus*, chausingha or four-horned antelope *Tetracerus quadricornis* are the major ungulate prey species found in the landscape. Tiger and leopard—the two apex predators, and gaur, spotted deer, sambar, and wild pig, common prey species of tiger and leopard were selected as the study species.

Influence of species traits on AVC probability. We modelled the probabilities of successful crossing or hit for different animal species based on the traversability model[37]. The model is based on the calculation of headway distributions in a traffic flow, i.e., the frequency of the distance between successive vehicles at a

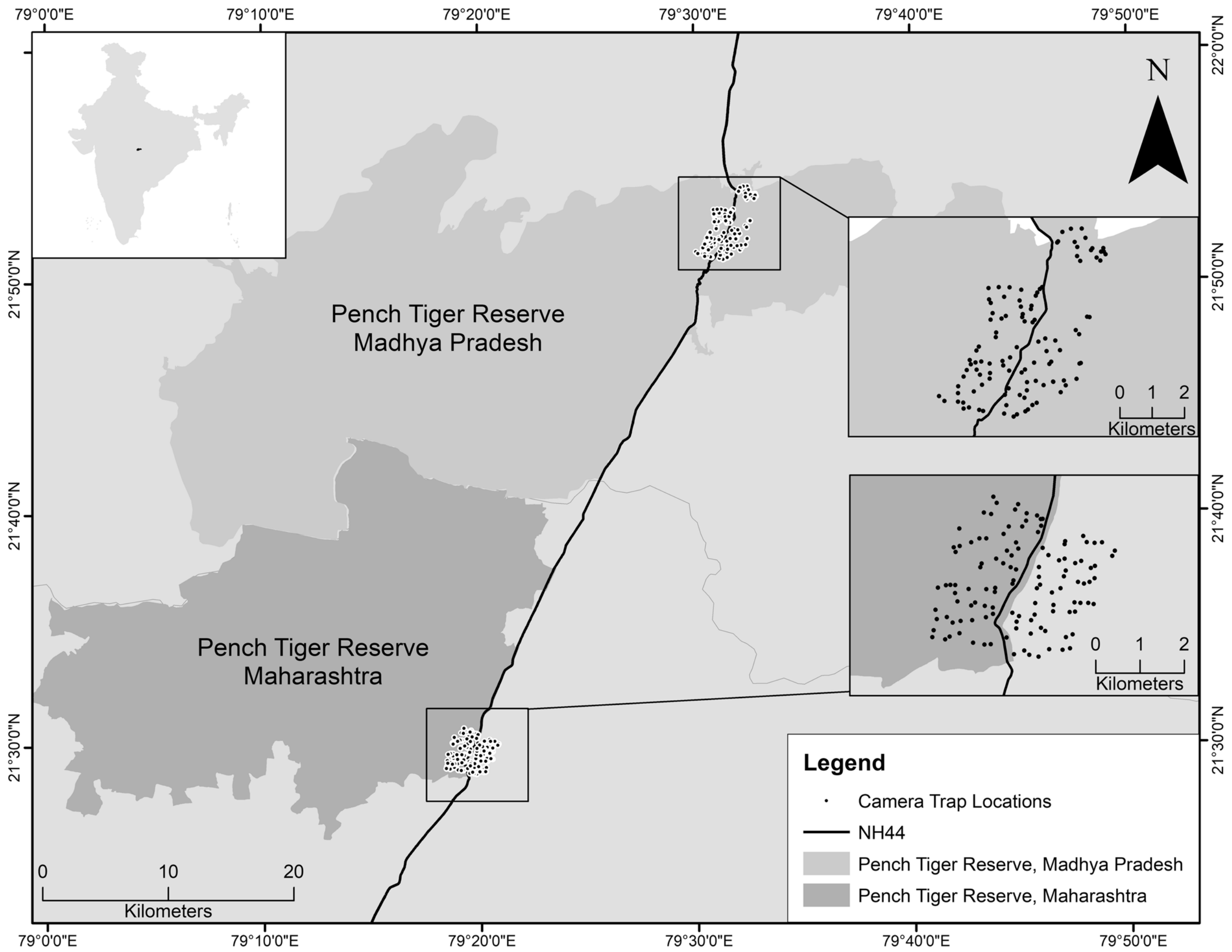

Figure 8. National Highway 44 passes through the Pench Tiger Reserves, Madhya Pradesh and Maharashtra. [Inset] Camera trapping locations on two forest stretches along NH 44. Map generated using ArcGIS 10.8[59] (www.esri.com).

given cross-section, which is assumed to follow Poisson distribution[43]. The probability of successful crossing (P_a) depends on the time 'T' (in seconds) during which the animal and vehicle are co-incident on a road, and depends on traffic, road and species characteristics. Therefore,

$$P_a = e^{-\lambda\left(\frac{W_c+L_a}{V_a}+\frac{L_c+W_a}{V_c}\right)} \tag{1}$$

where W_c, L_c and V_c are the width and length (in m), and speed of vehicles (in m/s), W_a, L_a and V_a are the width and length (in m), and speed of animals (in m/s), and 'λ' is the traffic volume (in vehicles/s).

W_c, L_c and V_c (vehicle characteristics) were calculated for different traffic heterogeneity scenarios, and W_a, L_a and V_a (animal characteristics) were calculated for different study species.

The probability of hit or AVC probability (P_h) was then calculated as

$$P_h = 1 - P_a. \tag{2}$$

The model assumes that traversing of roads by animals is 'blind' for animals in that they do not respond to the presence of vehicles (i.e. do not stop or turn around), and for drivers in that they do not respond to the presence of animals on the road by braking. Therefore, we define P_h as the probability of hit of an animal that is attempting to cross the road, as we cannot account for the number of crossing attempts that translate into actual presence of animal on the road for an AVC to occur.

Sensitivity of P_h to change in model parameters viz., traffic (vehicle length, vehicle width, vehicle speed and hourly volume) and animal characteristics (body length, width, speed and average group size) was calculated using package "pse"[44] in R version 3.6[45]. Change in AVC probability with unit change in each model parameter was calculated at 95% confidence intervals while keeping other variables at mean values. We used uniform probability distribution for all the variables except length of animals, length of vehicles and velocity of vehicles for which we used normal probability distribution. We used 1000 bootstraps of the Latin hypercube sampling (LHS) to understand the effect of the variables and to estimate the uncertainty for evaluation of the confidence interval

Animal species	Average weight (kg)	Body length (max) (m)	Body width (m)	Mean group size	Maximum running speed (m/s)	Traversing speed (m/s)
Chital *Axis axis*	65	1.55	0.6	8.15	17.49	2.91
Gaur *Bos gaurus*	825	3.3	1	4.75	13.14	2.19
Leopard *Panthera pardus*	49.25	2.43	0.4	1	17.17	2.86
Sambar *Rusa unicolor*	202.5	2.1	0.8	2.85	16.82	2.80
Tiger *Panthera tigris*	173.75	3.1	0.6	1	17.08	2.84
Wild pig *Sus scrofa*	90	2	0.5	5.87	17.6	2.93

Table 1. Species characteristics including morphometric data and behaviour used for calculation of animal vehicle collision probabilities.

and partial inclination coefficients (PIC). Confidence interval non-overlapping zero signifies a considerable effect of the variable and the sign of the PIC denotes the direction of the effect of the variable.

Road and traffic characteristics. We obtained traffic volume data for NH 44 from the regional Project Implementation Unit of the National Highway Authority of India for a period of 2 weeks during the study, and extracted the daily and hourly traffic patterns and heterogeneity viz., car/van, LCV (light commercial vehicle), bus/truck, MAV (multi-axle vehicle) and OSV (off-shore vehicle).

Traffic flow speeds were simulated at different hourly traffic volumes (100–2400 vehicles per hour) for present traffic heterogeneity using the traffic-simulation software VISSIM 11.00 Student Edition[46]. We simulated traffic flow on a road section or 'link' of 1 km on the VISSIM interface, and specified the width, number of lanes and direction of traffic flow. We set the road type as 'Freeway (free lane selection)', and number of lanes at 2 for 4-lane road, and 1 for 2-lane road. For 4-lane road with a median, we generated average speed of vehicles on one side (2-lanes). We followed the same approach for 2-lane road, assuming that overtaking on undivided road did not take place. We set lane widths at 3.5 m[47], and vehicle composition or heterogeneity as containing three major types of vehicles—car (categories car and LCVs were merged), bus/truck, and MAV (categories MAV and OSV were merged). The headways of the heterogeneous traffic flow were assumed to follow negative exponential distribution[48], and the free flow speeds of different vehicle types was assumed to follow normal distribution[49]. All model parameters viz., driving behaviour characteristics, vehicle length and width and desired free-flow speed for each vehicle type (following Bains, Ponnu and Arkatkar[50]), and relative flow (proportion of vehicle type in traffic flow or heterogeneity) have been detailed in Supplementary Table S1.

We placed vehicle input points at the beginning of the link, and data collection points midway along the road, and specified the hourly traffic volume at each vehicle input point. The average harmonic speed of traffic flow at each traffic volume and free flow speeds of different traffic components were selected as data collection measurement attributes (outputs of the simulation). Each simulation was run for 600 s (10 min) with 20 replicates. Simulation resolution of 10 time steps/second was set to maximize speed data collection at data collection points.

Species characteristics. We obtained data on species morphometry viz., length, width[51], and average group size[51–55] for the six study species (chital, gaur, leopard, sambar, tiger and wild pig) (Table 1). To account for collective risk for group living species, the average group size was factored into the average length of animal[23] in Eq. (1).

We calculated the maximum animal speeds from the equation for terrestrial animals (running) given by Hirt, Jetz, Rall and Brose[56], based on average animal body weights 'M'.

$$V_{max} = 25.5M^{0.26}(1 - e^{-22M^{-0.6}}) \tag{3}$$

During the study period, we recorded the walking speeds (in m/s) of the study animals in their natural habitats inside PTR, Maharashtra, to calculate the average moving speed. For each species, we averaged 14–20 observations of various walking speeds which was found to be close to 1/6th of the top running speed (Supplementary Table S2).

Influence of road and traffic characteristics on AVC probability. With respect to different traffic compositions in a traffic flow (in terms of types of vehicles) specified in Supplementary Table S1, traffic flow speeds for different heterogeneity scenarios namely H_1–H_9 were simulated using VISSIM for hourly traffic volumes ranging from 100 to 2400 vehicles per hour (as defined in Section A of Methods under 'Road and traffic characteristics').

We calculated AVC probability (P_h) under different scenarios of traffic heterogeneity on 2-lane and 4-lane sections of the road using Eq. (1). The exposure risk in seconds i.e., the time on the road for which an animal would be vulnerable to collision as a function of road width and P_h was also calculated.

Influence of animal activity on AVC risk. The behaviour of animals, in terms of activity patterns in the vicinity of roads, was incorporated into the model in the form of AVC risk, which is the AVC probability under a specific hourly traffic volume for a species, multiplied by the activity (hourly detection probability) of the animal near the road.

To quantify animal activity, we deployed motion-activated ScoutGuard Long Range Incandescent Flash Trail Cameras (https://www.scoutguard.com.au/) in two forest segments (8 × 5 sq. km each) along NH 44 in PTR, Maharashtra and PTR, Madhya Pradesh (Fig. 8). The selected forest segments were intersected by the highway—a 5 km long 2-lane section through PTR, Madhya Pradesh, and a 5 km long 4-lane section through PTR, Maharashtra, Both forest segments were divided into 400 × 400 m grids on both sides of the road, and were similar in terms of vegetation and habitat type, hourly traffic volume, traffic load, and animal densities. Single-sided camera traps were deployed along forest trails and dirt roads in both sections in two phases during July–August 2017, at increasing distances from the highway. The hourly capture rates of animals calculated from camera traps within 0–400 m from the road (n = 47) were used to calculate the roadkill risk under present traffic heterogeneity conditions, assuming that animals captured at this distance were most likely to encounter roads. Roadkill risk was calculated by multiplying hourly capture rates, an indicator of time spent close to road (activity), with the probability of being hit by a vehicle (AVC probability or P_h). Overlap of animal and traffic activity was calculated using functions 'overlapEst' and 'bootEst' in package 'overlap'[57] in R version 3.6[45].

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Author contributions

B.H. conceived the idea, B.H. and A.S. designed methodology; A.S. collected the data; A.S. and N.C. analysed the data; A.S. and B.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

The authors declare no competing interests.

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Crossing structure use in a tiger landscape, and implications for multi-species mitigation

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A B S T R A C T

Crossing structures (CS) for wildlife are important mitigation strategies to offset impacts of roads on wildlife. However, information on CS use for the Indian subcontinent or the global tiger landscapes is scarce. We monitored wildlife use of nine CS on a national highway in a critical tiger conservation landscape in India. 21 wild mammals were found to use the CS within a span of 2 years. Tigers, wild dogs, most small mammals and ungulates were found to use CS that were near protected area, while ungulates and small mammals preferred CS with proximal vegetation cover. High species richness was observed under large CS. Similar capture rates for large carnivores between CS and adjacent habitat were observed. We found varied responses by structure generalists and specialists, a consequence of animal behavior and tolerance to human disturbance. We posit that animal behavior holds the key to designing and managing effective wildlife CS.

1. Introduction

Habitat fragmentation because of linear infrastructure including roads and railway lines has emerged as one of the greatest threats to landscape scale connectivity and conservation of wildlife (Ibisch et al., 2016). Roads can cause wild animal populations to diminish through different mechanisms (Van Der Ree et al., 2015), including isolation through avoidance (D'Amico et al., 2016), reduction in crossing frequencies (Leblond et al., 2013), and selective mortality of fit individuals of a population (Ceia-Hasse et al., 2018; Lodé, 2000). The impacts are more severe for threatened wildlife populations (Ferreras et al., 1992). As new roads are built across the world to accommodate increasing economic demands and vehicular traffic, impacts of roads are set to increase in magnitude. To mitigate the impacts of roads, several measures like wildlife crossing structures (CS) (Smith et al., 2015) and animal-proof fencing along the road corridor (Clevenger et al., 2001; Rytwinski et al., 2016; Van Ree et al., 2015) have been implemented around the world. Such measures are increasingly being adopted in developing countries as well (Okita-Ouma et al., 2021; Poudel et al., 2020).

Even though implementation of mitigation measures to reduce mortality and enhance connectivity of wildlife populations is win–win solution for both humans and wildlife (Ascensão et al., 2021), the efficacy of installed CS must be continuously monitored (a) to justify the cost of construction of mitigation measures and garner acceptance of such measures by user agencies; (b) to inform future design of CS suited to native species, communities and landscapes; and (c) to inform management of existing mitigation measures (Gagnon et al., 2011; Mysłajek et al., 2020). This is even more critical for developing countries like India, where developmental needs often supersede conservation imperatives.

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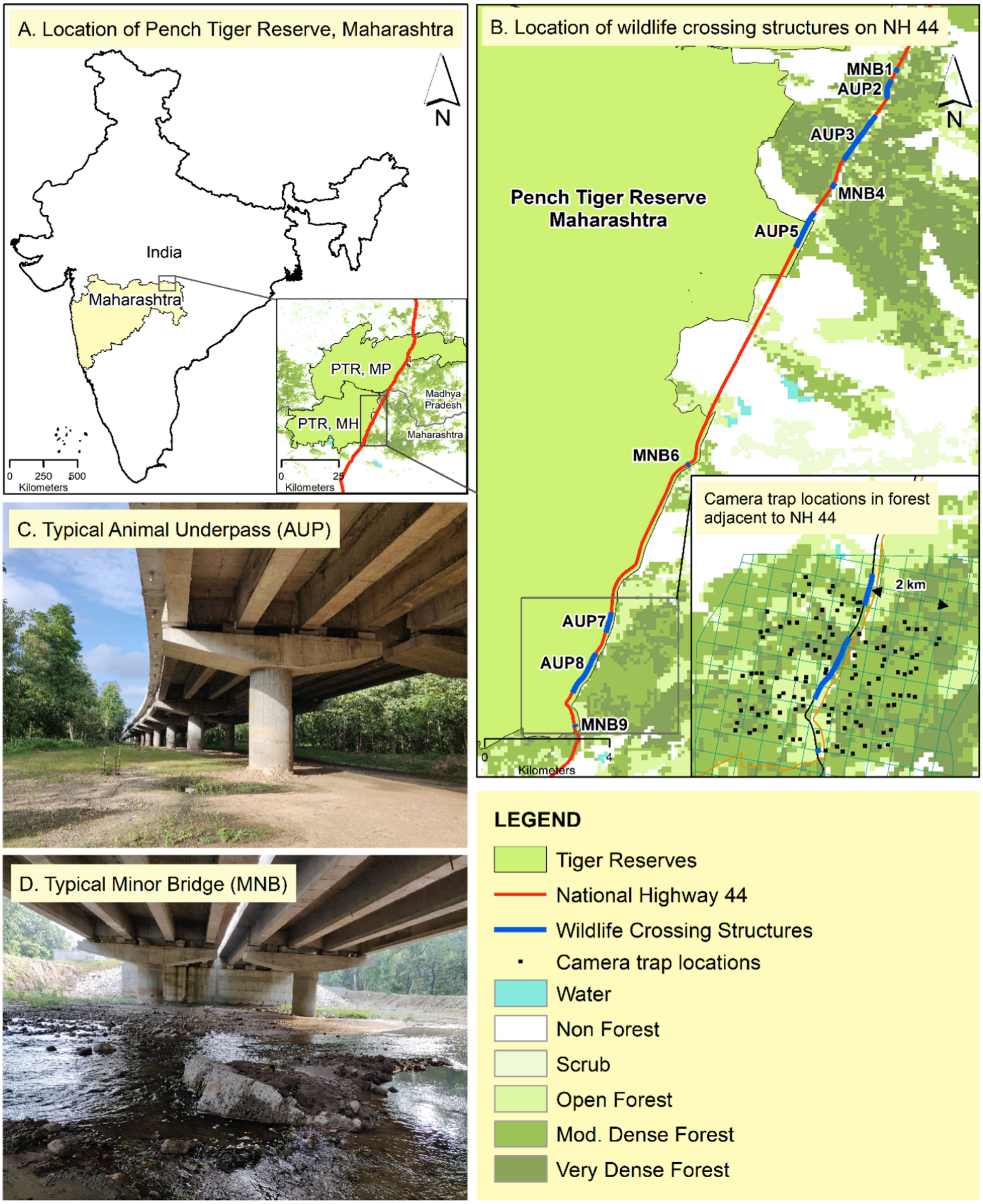

Fig. 1. Crossing structures on National Highway 44 passing through Pench Tiger Reserve, Maharashtra, India. (A) Location of Pench Tiger Reserve, Maharashtra and adjacent Pench Tiger Reserve, Madhya Pradesh; (B) Locations of the wildlife crossing structures on National Highway 44 with respect to Pench Tiger Reserve, Maharashtra; [inset] Camera trapping locations in forest adjacent to NH 44 along animal underpasses 7, 8 and 9; (C) A typical animal underpass (AUP); and (D) A typical minor bridge (MNB) on NH 44.

The Pench Tiger Reserve (PTR) is an important tiger (*Panthera tigris*) population source within the central Indian landscape, a critical tiger conservation landscape in India. Mitigation measures on National Highway 44 (previously National Highway 7; hereafter NH 44) passing through PTR in Maharashtra state are the Indian subcontinent's first dedicated measures for animal passage on any linear infrastructure. Given the scale of expected road expansion and up-gradation in tiger range countries (Carter et al., 2020), it is important to assess use of CS by wildlife on NH 44 since the study would potentially inform future mitigation strategies in the forested landscapes of the Indian subcontinent and tiger range countries, for which information is currently lacking.

Use of CS by wildlife has been found to vary with structure type (Abra et al., 2020; Denneboom et al., 2021; Mata et al., 2009, 2008; Rytwinski et al., 2016), which could be a reflection of animal behavior and preferences (González-Gallina et al., 2018; Kintsch et al., 2015). Structure characteristics viz., dimension and openness (Clevenger and Waltho, 2005, 2000) have been found to be the primary factors affecting wildlife use and diversity (Mysłajek et al., 2020) under CS. Vehicular traffic and human use of CS tend to reduce wildlife crossing events (Barrueto et al., 2014; Bhardwaj et al., 2020) particularly of carnivores (Denneboom et al., 2021), while wildlife have also been found to use CS despite co-use by humans (Bhardwaj et al., 2020; Ważna et al., 2020). Additionally, predator activity, local animal abundance, season, and structure-specific features like vegetation cover and presence of natural drainage also affect use of CS by wildlife (Ascensão and Mira, 2007; Bhardwaj et al., 2020; Brunen et al., 2020; Clevenger and Waltho, 2005, 2000; Denneboom et al., 2021; Mata et al., 2009; Schmidt et al., 2021; Wang et al., 2018; Ważna et al., 2020).

While absolute rates of CS use provide insights into comparative use amongst different structures, the effectiveness of mitigation measures can be appropriately gauged by evaluating rate of use in the context of animal movement in habitats adjacent to roads (Andis et al., 2017). Similarly comparison of animal activity in habitats near roads with that under CS can be an indicator of the level of acceptance or habituation to CS. Animal activity near roads varies with the type of road (Pourshoushtari et al., 2018) and traffic volume on the road. For example, some wild species are known to learn how to avoid peak traffic hours near roads, resulting in low mortality risk (Saxena et al., 2020; Thurfjell et al., 2015). This is also expected to be reflected in the activity of animals using CS, i.e., since traffic disturbance affects the movement and activity in the adjacent habitat as well as road crossing behavior (Kämmerle et al., 2017), similar trends are expected in the activity under CS. Both hourly traffic and human use have been found to influence animal activity under CS (Barrueto et al., 2014).

Notwithstanding the large body of available literature on factors influencing use and effectiveness of CS globally, there exists limited long-term published information on use of CS by tigers and associated species found in tiger landscapes of south and south-east Asia (Poudel et al., 2020; Zainol et al., 2021). Thereby the responses of tigers and associated species to roads and mitigation measures remains a research lacuna in road ecology.

We present results of the first two years of monitoring of the CS on NH 44 passing through PTR, Maharashtra, India. The mitigation measures comprise of a set of 9 CS with a range of sizes (50–750 m), varied levels of human use and distances from PTR, within a span of the 16 km of the highway. The habitat along the concerned section of the highway is uniform with similar species composition. This configuration of the CS provided us with a unique opportunity to test for the effect of these factors on use of CS by species across carnivore, herbivore and small mammal guilds. We examined factors affecting the use of CS by wildlife with different environmental and structure-related features. We also evaluated change in species richness with respect to undisturbed and adjacent habitat, and between CS with varying structural features. Additionally, we assessed the level of habituation of different wild species to the CS, by comparing species capture rates and hourly activities between the control habitat, habitat adjacent to the road and that under the CS. We expected similar capture rates and greater activity overlaps between adjacent habitat and CS indicating habituation. Based on the study, we discuss the factors to be considered while designing multi-species mitigation measures for tiger landscapes.

2. Materials and methods

2.1. Study area

PTR Maharashtra is spread across an area of 741.22 km^2 with 53 (SE 2.5) resident tigers and 82 (SE 8) tigers using the reserve (Jhala et al., 2020). Contiguous with PTR Madhya Pradesh (Fig. 1 A), PTR Maharashtra acts as a tiger source population for neighboring tiger habitats through the Pench-Navegaon-Nagzira-Tadoba-Indravati corridor (Qureshi et al., 2014). Besides tiger, other top predators found in the tiger reserve are leopard (*Panthera leo)*, sloth bear (*Melursus ursinus)*, and dhole or Asiatic wild dog (*Cuon alpinus*). Main herbivores and primary prey of tigers and co-predators include spotted deer or chital (*Axis axis)*, sambar (*Rusa unicolor)*, gaur (*Bos gaurus)*, wild pig (*Sus scrofa)* and nilgai or bluebull (*Boselaphus tragocamelus)*. The forests are of the southern tropical dry deciduous type (Champion and Seth, 1968).

The NH 44 is an arterial 4-lane highway that is part of the North-South transportation corridor that connects the northern and southern limits of India. The CS were incorporated into the highway as mitigation measures while being up-graded to a 4-lane highway from a 2-lane one. The prescribed speed limit on the highway is 100 kmph, with an average daily traffic volume of 5883 ± 168 vehicles as on 2019. The highway cuts through the Pench-Kanha (in Madhya Pradesh state) and Pench-Navegaon-Nagzira (in Maharashtra state) corridors for 16 km each. The study was conducted on the Maharashtra segment of the highway that passes through the eastern boundary of PTR, Maharashtra, and the Nagpur territorial forest division. Major townships along the segment are Chorbauli, Pauni and Deolapar.

In the absence of information on structure design and requirements for different target species found in the landscape (Rytwinski et al., 2016) during the conceptualization of the mitigation plan, CS dimensions were proposed so as to benefit the entire community of mammals (viz., tigers, co-predators, prey and other associated species) found in the landscape (Habib et al., 2015). The nine CS range from 50 m to 750 m in width, and comprise of 5 animal underpasses (AUPs) and 4 minor bridges (MNBs; structures with natural drainage) (Fig. 1 B, C and D; Table A.1) that have been operational since the end of the year 2018. CS width refers to the lateral length of the CS visible to the animal approaching the structure. The height of all structures is 5 m, with the exception of structure MNB9, which is ~ 4 m high. There is no fencing along the forested areas on NH 44 except for the guide walls on either side of the CS measuring

Table 1
Environmental and structure-specific variables for the nine crossing structure on National Highway 44 used in GLMM.

Variable		Name	Range/Levels
Environmental	Distance to water body (m)	near_water	793.34–10362.37
	Distance to human settlement (m)	near_stlmt	705.4–3080.5
	Distance to protected area	dist_pa	0.0–3202.09
	Season	season	Winter Summer Monsoon Post-monsoon
Structural	Distance to cover	dist_cov	16.5–62.65
	Span terrain	span_terrain	Undulating Slightly undulating Flat
	Width (m)	width	50–750
	Presence/absence of drainage	drainage	0/1
	Vehicular access	veh_access	0/1
	Number of operational camera days in session (offset)	camdays	1–23
	Terrain of CS approach	approach	Undulating Slightly undulating Flat
	Distance to next CS	dist_next	600–1854
	Capture rate of carnivores in CS	cr_carn	0.0–2.4
	Capture rate of anthropogenic activity	cr_dist	0–137.0

50–250 m (Table A.1). Fig. 1 shows examples of typical AUPs and MNBs.

2.2. *Field methods*

We used camera traps to study the use of CS as it is the most cost-effective method for long-term (>1 year) CS monitoring (Ford et al., 2009), and to enable accurate identification of user species for meaningful interpretations (D'Amico et al., 2015). The choice of camera trapping allowed us to (van Der Grift et al., 2015):

a. fulfil our initial goal of monitoring i.e., create a baseline of the use of CSs by the mammal community in the landscape,
b. monitor trends in CS use by the mammal community found in the landscape,
c. compare parameters of use viz., capture rates and activity with "control" (within Pench Tiger reserve, in the absence of road-related disturbance) and "adjacent" habitat (forest on both sides of NH 44), and
d. assess factors influencing the use of CS.

2.2.1. *Camera trapping under crossing structures*

The CSs are supported by pairs of columns/pillars separated by a distance of 20–30 m depending upon the width of the structures. We deployed single motion-triggered Cuddeback C1 ("Cuddeback, Green Bay, Wisconsin,") camera traps on each column to cover the intervening span between two consecutive columns, thus recording only those animal movements that were completely under the structures (either use or crossing). We deployed a total of 78 cameras across all CS, and the number of cameras per CS varied with the size of the CS (Table A.1). We downloaded camera trap data approximately once every fortnight (comprising one session), during the monitoring period (March 2019–December 2020).

2.2.2. *Camera trapping in habitat adjacent to NH 44*

To assess use of CS with respect to animal capture rates in habitat adjacent to the highway, we deployed camera traps (n = 104) in the forest on both sides of NH 44 on forest trails with multiple animal signs or at junctions of multiple animal trails. Single-sided camera traps were deployed at different distances to the highway up to 2000 m from NH 44 (Fig. 1 B (inset)) between mid-November and mid-December 2019.

2.2.3. *Control data*

We obtained data for natural animal capture rates from within PTR, Maharashtra, through the camera trapping exercise carried out for tiger, co-predator and prey population estimation. Data for a period of 20–25 days during the winter of 2020 was extracted from single cameras (since this exercise employs double-sided cameras i.e., two cameras facing each other). Camera trapping inside PTR is carried out in a 2 × 2 km grid framework (n = 298 camera traps).

The same camera model and settings were used for all three camera trapping exercises. The cameras were set at a height of 0.5 m from the ground. The cameras were set to capture animal photographs at a minimum lag time of 3 s.

2.3. Analytical methods

We sorted camera traps images obtained from the CS at CS ID, camera/span ID and species levels. We used function '*recordtable*' in package camtrapR (Courtiol et al., 2017) to generate record tables of species captures. We used delta time of 1 min for all species, as our aim was to assess 'use' of CSs by wildlife -including both use (animals walking parallel to the CS, grazing, resting) and crossing events (perpendicular movement i.e., crossing) as a function of the time spent under the CSs.

2.3.1. Factors affecting wildlife use of CSs

We used generalized linear mixed models with negative binomial distribution in package glmmTMB (Magnusson et al., 2020) to assess the effect of landscape and structural variables (Table 1) on use of the CS by different species. We used the number of captures of species and animal groups (carnivore, herbivore, small mammals) from a camera trap (representing use under a single span of the structure) per session as the response variable, the number of trap days (log-transformed) during a session as the offset, and the structure ID as the random effect. Number of operational camera days per session varied between CSs mainly because of battery exhaustion, theft and removal of cameras under MNBs during peak monsoon. We calculated the disturbance intensity because of livestock, humans and free-ranging dogs as the sum of their respective capture rates per session. Similarly capture rate of carnivores (tiger, leopard, sloth bear and wild dog) under the CS was calculated as the sum of their respective captures per session, and used to test whether intensity of carnivore use of CS affects use by herbivores and small mammals. We assumed the traffic volume above all CSs to be the same as there are no major intersections between the first and last CS on the stretch. We extracted the distances to human settlement, protected area (PA) and nearest CS (in m) using ArcGIS Pro Version 2.9 (ESRI Inc., 2021). We collected span-level variables such as distance to cover, approach and span terrain, and presence/absence of access roads and drainage on field. We categorized span and approach terrains as 'flat', 'slightly undulating' and 'undulating' in increasing order of steepness/ruggedness. We assessed the correlation between all continuous variables using package PerformanceAnalytics (Peterson and Carl, 2020) in R, and did not use significantly correlated variables ($r > 0.7$) in the analysis. We fit models separately for all species with > 50 captures, and evaluated models using Akaike's Information Criteria (AIC). We examined the best models for each species for over-dispersion using package 'Dharma' (Hartig, 2021). We calculated threshold values for CS widths using function *chngpt* in package 'chngpt' in R Studio ("RStudio | Open source & professional software for data science teams - RStudio," 2020) for species for which CS use was significantly affected by CS width.

2.3.2. Species richness under CS

We calculated mean species richness per CS per session as the mean number of unique mammal species recorded per session under CS, and per trap day in adjacent and control habitat for the common trapping season (winter). We also calculated species richness (absolute number of species) for all CS for the entire study duration. We examined the effect of factors (drainage, PA/non-PA, vehicular access, width, season and daily capture rate of anthropogenic activity) on the mean species richness at CS using generalized linear model with Poisson distribution, evaluated using AIC values.

2.3.3. Animal capture rates in CS, control and adjacent habitat

We calculated large mammal (excluding small mammals) capture rates (number of captures/camera day) at different sites (CS, control and adjacent habitat) using data pertaining to the same time period (November 2019–February 2020) for comparison among sites.

2.3.4. Overlap of activity among species groups and anthropogenic disturbance

We estimated large mammal (excluding small mammals) activity overlaps under CS with activity in control and adjacent habitat, and under different levels of anthropogenic activity under CS using function *overlapEst* in package 'overlap' (Meredith and Ridout, 2017) in R. We generated overlap plots between three groups using density plots in package 'ggplot2′ (Wickham, 2016) in R.

3. Results

In the 22 months of monitoring (673*78 camera days, 13.4 SD 3.8 camera days per session per camera site), we obtained 181,118 photo-captures, including captures of 21 wild mammal species ($n = 22{,}267$) i.e., 3.45 wild animal captures per camera day. The number of wild mammal species using the CS increased from 18 in 2019 to 21 in 2020. Anthropogenic activities made up for 87.7% of all captures obtained including humans (42.6%), livestock (30.6%), free-ranging dogs (14.3%) and cats (0.05%).

Wild dog, followed by tiger, was most commonly photo-captured among the six carnivore species found using the CS. Among the seven herbivores using the CS, chital followed by wild pig, was photo-captured the most. Among the eight small mammal species using the CS, black-naped hare (*Lepus nigricollis)* followed by jungle cat (*Felis chaus)* was photo-captured the most. Most wildlife captures were obtained under the two largest CSs measuring 750 m each- AUP3 (15%) and AUP8 (41.9%). Most carnivores were captured under the two CS located at the boundary of the Pauni (buffer) range of PTR (22.6% under AUP7 (100 m) and 54.9% under AUP8 (750 m)).

Data for species with < 50 captures were not used in further analysis: barking deer ($n = 4$), chausingha or four-horned antelope (*Tetracerus quadricornis)* ($n = 3$), golden jackal (*Canis aureus)* ($n = 27$), Indian pangolin (*Manis crassicaudata)* ($n = 1$), rusty spotted cat (*Prionailurus rubiginosus)* ($n = 3$), sloth bear ($n = 26$), small Indian civet (*Viverricula indica)* ($n = 40$), Indian wolf (*Canis lupus pallipes)* ($n = 14$). Additionally a large number of primate (langur (*Semnopithecus entellus)* and rhesus macaque (*Macaca mulatta)*) captures were obtained that were not analyzed.

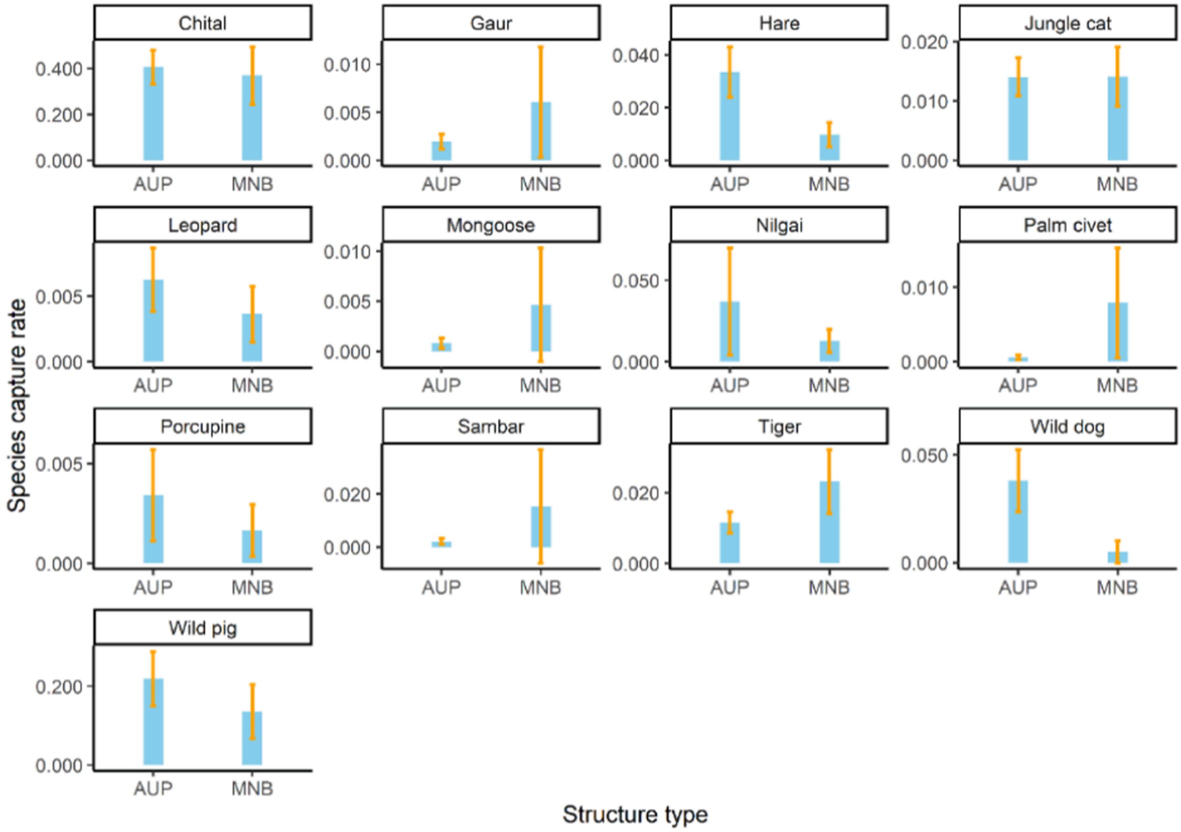

Fig. 2. Variation in use of crossing structures with respect to presence of natural drainage. Use of AUPs (animal underpasses) and MNBs (minor bridges with natural drainage) among different wild animal species as reflected by capture rates (error bars indicate 95% CI).

3.1. Factors affecting use of CSs

Distance to water and distance to settlement were negatively correlated (p = -0.78***), and distance to water was positively correlated with distance to PA (p = 0.98***). Therefore the variables distance to water and distance to settlement were not used in further analysis.

We observed significant seasonal differences in the use of CS across all wild species (Kruskal-Wallis chi-squared = 332.02, df = 3, p-value < 0.05) (Tables A.2, A.3 and A.4). Across all groups, CS were used the most during winter (mean capture rate 0.73 SD 0.86), followed by monsoon season (mean capture rate 0.50 SD 1.24). Use of CS during summer season was significantly low across all groups (mean capture rate 0.34 SD 0.81). Among carnivores, use of CS by leopard and tiger was high during winter and post-monsoon, and use by wild dog was significantly lower during summer and post-monsoon seasons. Most small mammal species showed significantly higher use of CS during post-monsoon and winter seasons, while mongoose *sp.* showed significantly low use during post-monsoon season. Season was not a significant factor influencing CS use by gaur, and winter season was positively associated with higher use by chital, sambar and wild pig. Use of CS by wild pig was negatively associated with summer and post-monsoon seasons.

3.1.1. Effect of structure-characteristics

Overall, we found that use of CS by all wildlife was significantly less in structures with drainage (Kruskal-Wallis chi-squared = 12.662, df = 1, p-value < 0.05), and MNBs were used less than AUPs. At the species level, chital, jungle cat and wild pig used both CS types equally, tigers preferred MNBs, and black-naped hare and wild dog showed a clear preference for AUPs (Fig. 2).

At the span level, presence of drainage did not affect use by leopards and wild dogs (Fig. 4(a)). Presence of drainage was negatively associated with CS use by small mammals like common palm civet and mongoose *sp.* (Fig. 4(b)), while positively affecting use by black-naped hare and jungle cat, two of the most frequent users of the CS. Presence of drainage negatively affected use by chital and wild pig (Fig. 4(c)).

While width had a weak negative effect on CS use by tiger, use of CS by wild dogs decreased with increasing widths. Significant threshold estimate of CS width for wild dogs was calculated at 100 m, while the change point for tiger was insignificant. CS width did not significantly affect use by small mammal species, with the exception of black-naped hare which showed a positive association. Significant threshold CS widths for gaur and wild pig were calculated as 300 m and 80 m respectively.

Use of CS by chital and wild pig decreased with increasing CS width (Fig. 3). High rates of use by chital were observed in CS <= 100

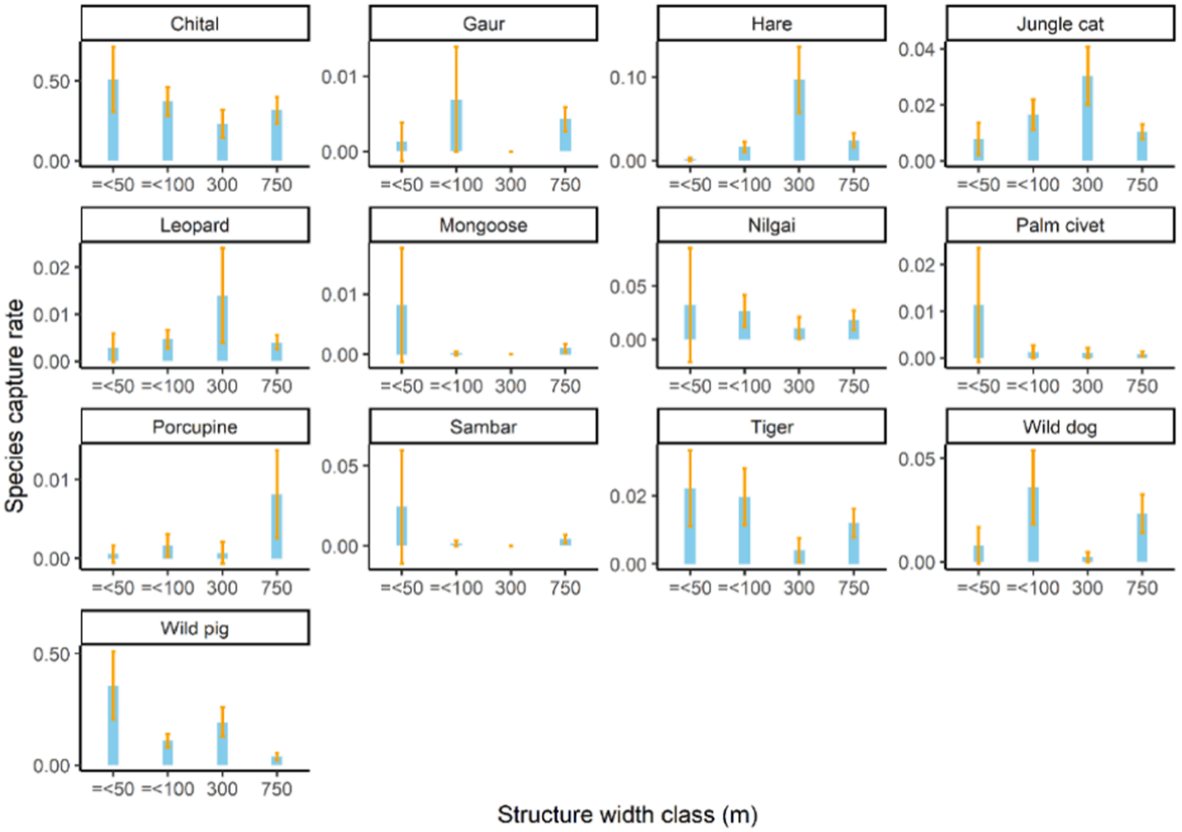

Fig. 3. Variation in use of crossing structures with respect to crossing structure width class. Large mammal movement rates as reflected by capture rates under crossing structures of different width classes (error bars indicate 95% CI).

m wide (61% of all captures). Most gaur (55%) and sambar (80%) captures were obtained under CS <= 50 m wide, followed by the largest structures (34% and 14% respectively). Nilgai showed no clear pattern of use among CS with different widths. Wild pig capture rates were highest (51% of all captures) under small structures < 50 m wide. Leopards preferred 300 m wide CS (54% of all captures). Tigers used all CS with varying intensities, and the highest use was recorded under structures =<100 m (72% of all captures). Wild dog activity was mostly concentrated under the 100 m wide structure (52% of all captures).

Terrain of the CS span significantly affected use by all wildlife (Kruskal-Wallis chi-squared = 16.54, df = 2, p-value < 0.05), with low CS use by carnivores and small mammals observed under spans with undulating terrain. Slightly undulating span terrains were positively associated with tiger and leopard use of CSs, while use by small mammals was not significantly affected. Undulating span terrain was found to positively affect gaur use.

Similarly undulating terrain of the approach to the CS significantly affected ungulate (Kruskal-Wallis chi-squared = 83.445, df = 2, p-value < 0.05) and carnivore use (Kruskal-Wallis chi-squared = 33.459, df = 2, p-value < 0.05). Use of CS by tigers was positively associated with both undulating and slightly undulating approaches, while undulating approaches were negatively associated with leopard and wild dog use. Slightly undulating terrain was positively associated with use by mongoose *sp*. and Indian crested porcupine (*Hystrix indica*), and negatively influenced jungle cat use. Undulating terrain positively affected use by mongoose *sp*. and common palm civet. While CS use by gaur and sambar was found to be positively influenced by undulating structure approach, use by wild pig was reduced in structures with undulating approach.

Overall use of CSs decreased significantly with increasing distance to the next CS for ungulates. Conversely, increasing distance to the next CS had a positive effect on tiger and leopard use. The effect was insignificant for small mammals, with the exception of mongoose *sp*. which showed a negative association. CS use by gaur increased with increasing distance to the next CS, while use reduced for sambar.

Distance to vegetation cover was an important determinant of CS use by black-naped hare, jungle cat and Indian crested porcupine, while CS use by common palm civet was positively affected by increase in distance to cover. Among ungulates, increasing distance to cover negatively affected CS use by gaur and sambar.

3.1.2. Effect of structure location

We found greater use of CS located near protected areas by ungulates and carnivores, with minor positive effect on small mammals. Among carnivores, the effect was most significant for wild dogs, and tigers. Use of CS by mongoose *sp*. decreased with increasing

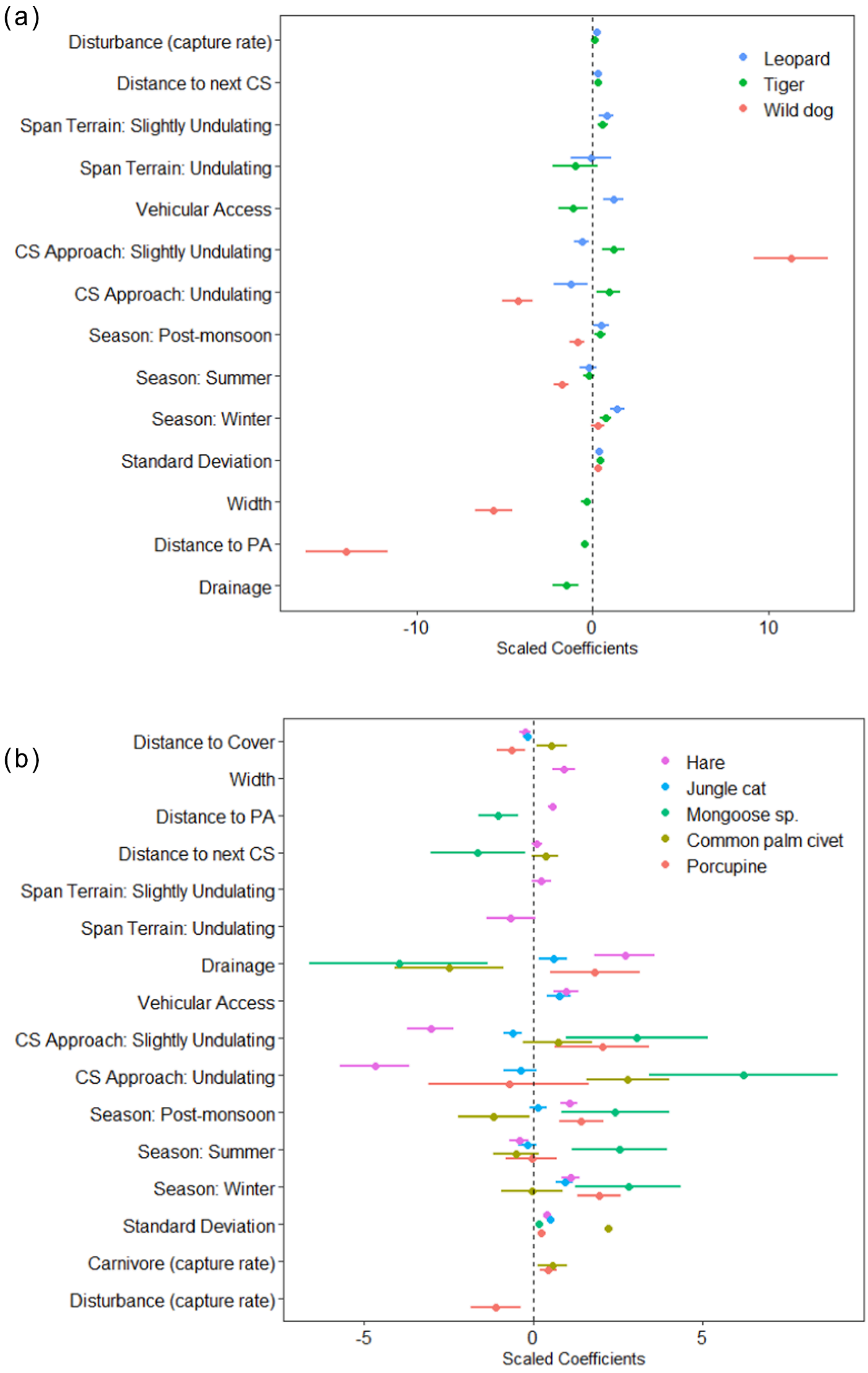

Fig. 4. Factors affecting use of crossing structures by different wildlife species. Beta coefficient estimates (dots) with 95% confidence intervals (whiskers) for carnivores (a), small mammals (b) and ungulates (c), derived from the best performing models. Confidence intervals overlapping 0 (dashed line) indicate no significant effect.

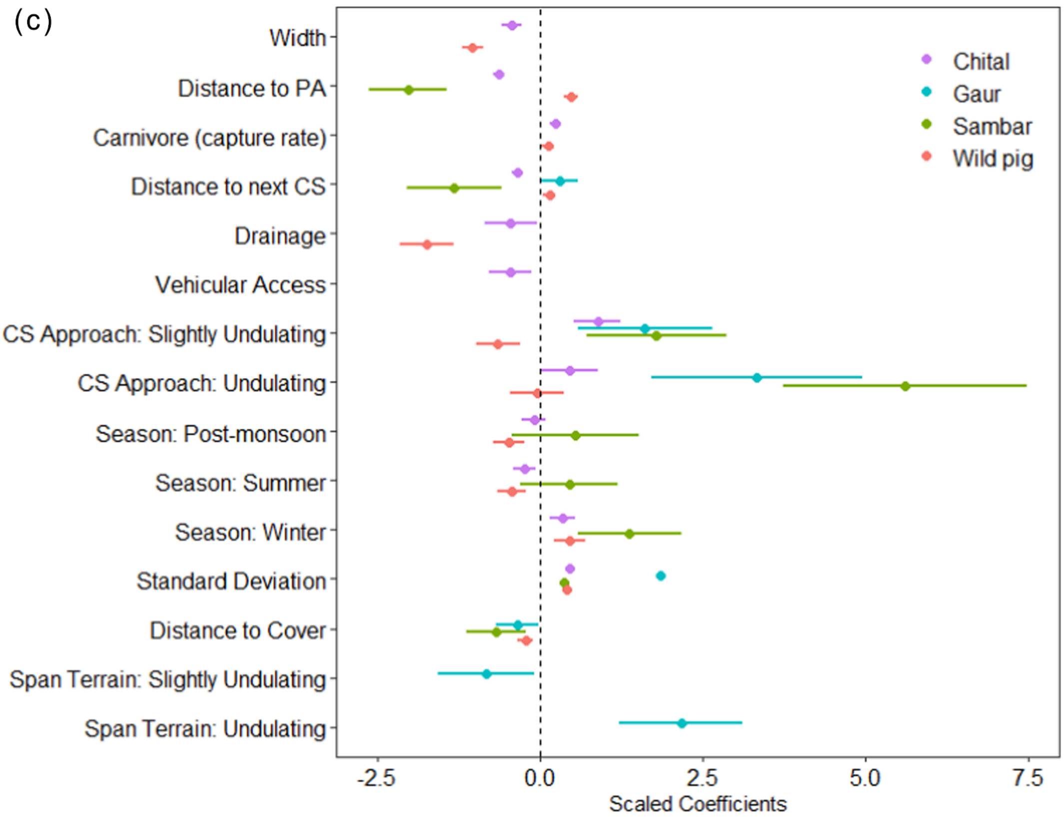

Fig. 4. (*continued*).

distance to PA while it increased for black-naped hare. Use of CS by sambar was negatively affected by distance to PA, while wild pig was found to use CS away from the PA.

3.1.3. *Effect of anthropogenic activity*

Anthropogenic use of CS did not significantly affect use by any animal group. Disturbance did not have a significant effect on any small mammal, with the exception of Indian crested porcupine, which was negatively affected.

Presence of access roads under CS spans significantly decreased use of CS by ungulates, while positively affecting use by small mammals. The effect was also negative for carnivores, with the exception of leopard that showed a positive response to presence of an access road. Presence of access road also significantly increased use of CS by black-naped hare and jungle cat. Chital, the most frequent ungulate user of CS, was found to be negatively affected by the presence of access roads.

3.2. *Species richness at CS*

Mean species richness under CS (4.8 SD 0.6) was significantly lower than that at control site (6.6 SD 0.3) (Kruskal Wallis test, $p < 0.05$, chi-squared = 111.41), but higher than that in the adjacent habitat (3.4 SD 0.3) (Fig. 5(a)). Mean species richness increased with increasing CS width (Fig. 5(b)). At CS measuring 750 m mean species richness values were found to be equivalent to that in control habitat (6.8 SD 0.5). Species richness was positively influenced by CS width and negatively with presence of drainage and distance to PA (Table A.5). We found nine common species using at least 7 CS, including tiger, leopard, chital, jungle cat, and wild pig (Fig. 5(c)).

3.3. *Animal capture rates in CS, control and adjacent habitat*

Both gaur and sambar capture rates under CS were significantly less than that in adjacent habitat (7 and 12 times respectively) and in control (11 and 19 times respectively). Chital capture rates were found to be similar across the three sites, with marginally less capture rates under CS. Nilgai capture rates in the adjacent habitat were 1.6 times higher than capture rates in control and 4 times higher than capture rate under CS. Wild pig capture rates under CS were 3 times higher than capture rates in control and 9 times higher than capture rate in adjacent habitat (Fig. 6).

Leopard, tiger and wild dog showed similar capture rates in adjacent habitat and under CS, both significantly lower (6.5 and 4 times less) than their respective capture rates in control habitat. However the capture rates of wild dogs under CS were equivalent to control capture rates as compared with that of other carnivores.

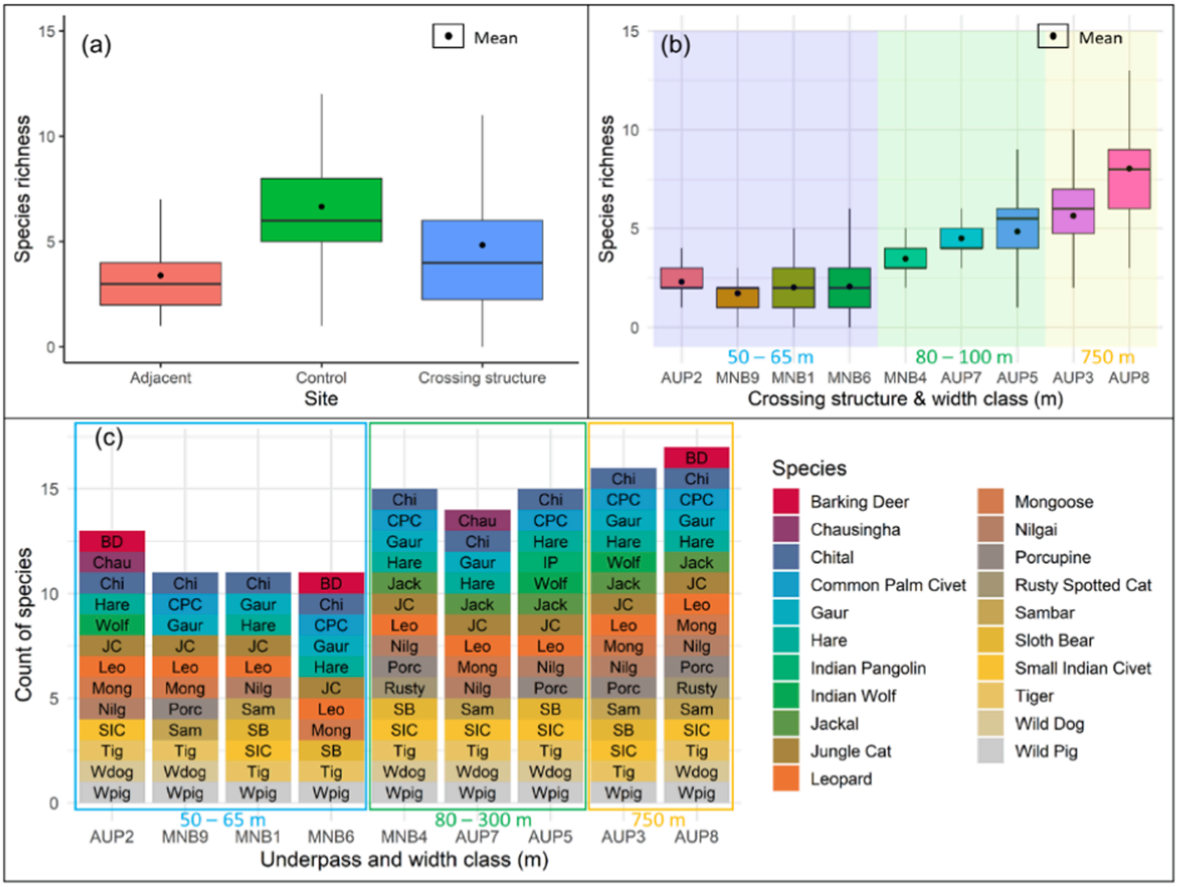

Fig. 5. Variation in species richness across sites and crossing structures. (a) Mean and median species richness across control, adjacent habitat and under crossing structure, (b) Mean and median species richness under different crossing structures arranged in increasing order of CS widths, and (c) Species richness and species recorded under crossing structures (in order of increasing CS widths).

3.4. Animal activity patterns under CS

No significant difference in chital activity between CS, control and adjacent habitat was observed (Dhat > 0.82). Wild pig activity under CS differed from activity in control (Dhat = 0.69) and adjacent habitat (Dhat = 0.39). Sambar activity adjacent to the road and under CS, although differing in activity peaks during the day, were different than that in control habitat (Dhat = 0.66 and 0.64 respectively). Gaur exhibited lesser overall activity under CS compared to control, but showed significant rise in activity during the day in the non-control areas. Nilgai activity pattern under CS was similar to activity pattern in control habitat (Dhat = 0.73). However, unlike activity in control habitat, there was a clear dip in CS activity during peak human and traffic activity hours. Leopards were found to be more active during the day in the habitat adjacent to the road than under CS (Dhat = 0.37), while activity similar to that in control habitat was observed under CS (Dhat = 0.64). Tiger activity under CS overlapped more with activity in control habitat (Dhat = 0.81), as compared with activity in adjacent habitat (Dhat = 0.57), with higher day time and late night activity under CS. Wild dog activity under CS followed a pattern of diurnal activity similar to that in control (Dhat = 0.81) and adjacent habitats (Dhat = 0.51) (Fig. 7(a)).

Most human activity under the CS, including livestock and free-ranging dog, was diurnal. For all species, we found lesser overlap with human activity in more disturbed CS as compared with CS with low human activity. We found shifts in chital, gaur, nilgai, leopard and tiger activity towards early morning or late evening hours in more disturbed CS compared with CS with lower human activity. Sambar activity under CS was more prominent during the day, with less activity recorded under CS with high human activity. There was no significant change in wild dog and wild pig activity under CS with differing levels of human activity (Fig. 7(b)).

4. Discussion

Our study demonstrates the use of CS by multiple wild mammals, and that CS are an effective mitigation strategy to restore near-natural movement near roads. We found differential effects of animal behavior on CS use. These effects were reflected in factors affecting use as well as in capture rates and activity patterns observed near roads and within CS. At the community scale, we found that the number of species using the nine CS on NH 44 increased from 18 in 2019 to 21 in 2020, indicating differential response times of

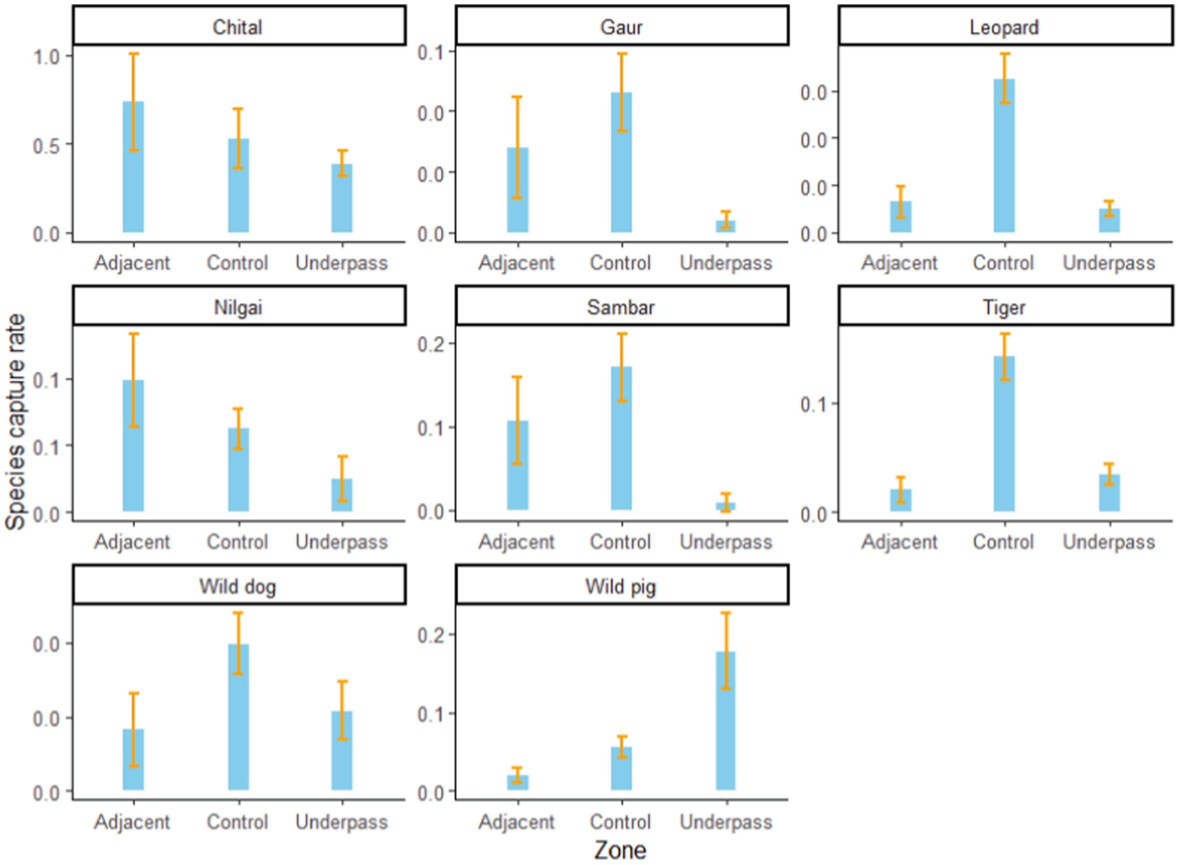

Fig. 6. Large mammal capture rates under crossing structures, control and habitat adjacent to road. Comparison of capture rates of large mammals in adjacent habitat, control and wildlife crossing (error bars indicate 95% CI).

different species to new artificial features. Inferences regarding the delayed and sporadic use of CS by some species can be made in context of their relative abundances within the tiger reserve (Jhala et al., 2020), and behavior. Sporadic captures of species such as barking deer, Indian pangolin and rusty spotted cat are a consequence of their low densities, preference for core undisturbed habitats and cryptic behavior. Indian wolves showed low use of CS as they are found in low densities in the tiger reserve and have large home ranges. Even though Indian wolves are tolerant of human disturbance (Habib et al., 2021), low (14 captures in 2020) and delayed use (first capture after a year of CS construction) may also be attributed to differential perception of human presence and vehicular traffic, the latter possibly perceived to be a greater threat. Low CS use by golden jackals, despite being habitat generalists and locally abundant, may be attributed to avoidance of the structures owing to greater CS use by large predators viz., leopard, tiger and wild dog.

While we have reported extensive use of CS by small mammals, camera traps tend to underestimate detection and effectiveness of CS use by small mammals (Jumeau et al., 2017). Therefore we refrained drawing strong inferences regarding the use of CS by small mammals.

All CS on NH44 are fairly large with regard to the minimum requirements of the ‘openness ratio’ (Reed and Ward, 1985), and vary in terms of presence of drainage, human use/activity and structural features. While these factors have been found to affect wildlife differentially, the differences can be better understood by species/guild-specific behavioral proclivities for factors such as need for cover or open spaces against predation risk as prey or as predators, and adaptability to the range of structure types (Kintsch et al., 2015).

Among prey species, anti-predation strategies and tolerance to human and road-related disturbances seem to dictate patterns in CS use. Sambar and gaur were found to prefer small-medium sized structures, spans with vegetation cover nearby, and undulating span and approach terrain. Thus they can be classified as cover obligates in terms of choice of CS that require structural or vegetation cover against predation risk (Hunt et al., 1987; Kintsch et al., 2015). However the need for cover needs to be negotiated with structure size as both animals are large-bodied and group-living, and have also been found to use larger (>100 m) structures. Chital and wild pig were found to use a variety of structures since they are structure generalists, highly abundant locally, and are possibly tolerant of human and road-related disturbance (Saxena et al., 2020).

Predictably, capture rates of tigers, leopards and wild dogs were less near the road as compared with control habitat. However, capture rates in the adjacent habitat overlap that under the CS, indicating that the structures are successful in maintaining large carnivore movement rates with respect to the surrounding habitat. Tigers and leopards were found to use a variety of CS (Ng et al.,

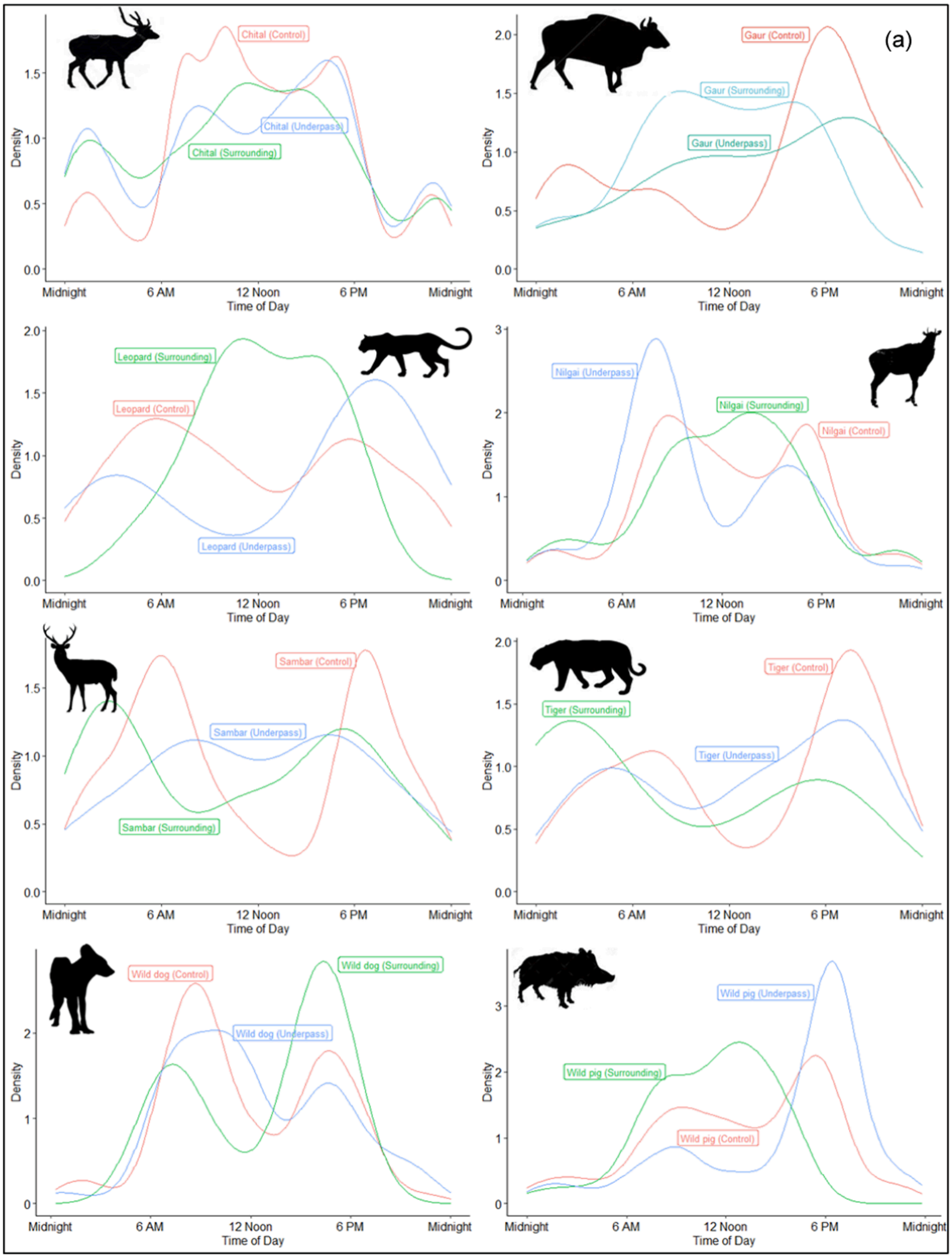

Fig. 7. Variation in large mammal activity across sites and human disturbance gradients. (a) Activity overlaps between animals in control habitat (red curves), habitat surrounding roads (green curves) and under crossing structures (blue curves). (b) Activity overlaps between species at control habitat (red curves), disturbed crossing structures (green curves), and relatively less disturbed crossing structures (blue curves). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2004). While tigers and leopards used CS with high human co-use by concentrating activity during low human use hours, wild dogs were more disturbance tolerant and were found to use CS under both high and low levels of human disturbance.

The CS on NH 44 are also one of the world's largest wildlife crossing structures on roads (ranging between 50 and 750 m), and past

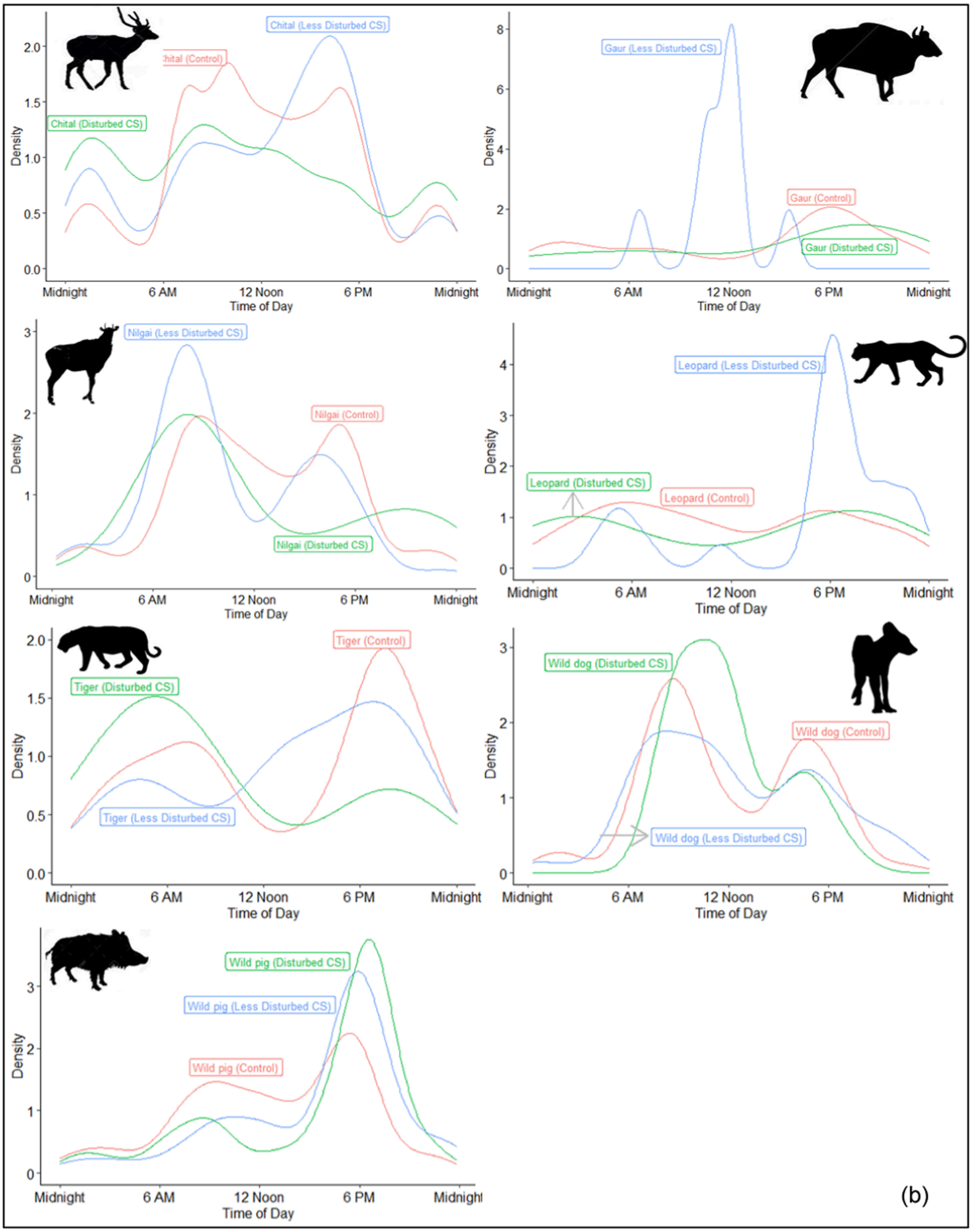

Fig. 7. (*continued*).

studies cannot be effectively compared with the results of the present study given the vast difference in CS widths (most CS monitoring studies have included underpasses and viaducts with widths ranging between 0.47 and 27.1 m (Denneboom et al., 2021), and 114 m (Mysłajek et al., 2020)). Ungulate and small mammal use of CS increased with width (Denneboom et al., 2021; Wang et al., 2018). While increasing widths decreased chital, tiger, wild dog and wild pig use of CS, the highest significant threshold estimates for CS width was calculated at 300 m (gaur).

Wild animals are known to change their activity patterns to avoid interacting with humans (Gaynor et al., 2018), and the odds of wildlife using CS with human co-use are less than structures dedicated for wildlife use (Denneboom et al., 2021). While human use was not a significant influence on CS use by wildlife, temporal patterns of avoidance of human activity were observed in most species, with the exception of chital, wild pigs and wild dogs that displayed similar activities under different levels of human use. Strategies to avoid human presence included activity shifts towards less disturbed hours (Gaynor et al., 2018), especially in CS with high human activity. Leopards were found to use CS spans with human trails mostly during late evening and early morning, indicating attempts to avoid peak human activity. Low activity overlap between sambar under CS and in proximity to roads probably indicates non-habituation of the species to the CS till the study period.

Some species are known to be flexible in their spatio-temporal use of habitat in changing environmental conditions with different levels of disturbance/threats (Johann et al., 2020). Together chital and wild pig represent prey species that increase use of risky spaces at non-risky hours (Palmer et al., 2021) i.e., at moderately disturbed spaces that may have low predator activity. Curiously, nilgai activity in the adjacent habitat was higher in comparison to both CS and control habitat. This difference in activity could indicate hesitation in using CS, as there have been more records of solitary nilgai bulls using the CS than female groups that tend to be more vigilant (Hunter and Skinner, 1998). Further studies assessing behavioral aspects such as vigilance (Seidler et al., 2018), group size and group composition of prey species would better help ascertain perceived predation risk and how it affects CS use by prey.

While culverts are known to act as CS for wildlife, particularly carnivores (Ascensão et al., 2014; Baigas et al., 2017), we found varied responses among species to the presence of natural drainage under CS (Fig. 4). Prominently, animals of open-habitat types viz., chital, black-naped hare and wild dogs, displayed marked use of AUPs against use of MNBs (Denneboom et al., 2021), while the opposite was true for moderate-dense forest-dwelling species. Therefore tolerance to water and vegetation cover among target species is an important factor to be considered while constructing CS (Brunen et al., 2020).

Greater use by leopard and wild dog was recorded under CS proximal to PTR, where CS are also closely spaced together. The other group of 4 CS (CS 1–4) is located away from the tiger reserve boundary, and the additive effect of distance to PA and high human activity could be the reason of low use by leopards. Tiger, leopard and gaur capture rates were similar across CS situated close together, while capture rates in CS located far apart were unequal. The differential use could be attributed to the proximity of the three CS (AUP7, AUP8 and MNB9) to the tiger reserve boundary, where localized activity of these animals is expected to be high.

Vegetation cover near structures was found to be an important determinant of CS use by most small mammal and major prey species (gaur and sambar) (Ascensão and Mira, 2007; Denneboom et al., 2021). Provision of vegetation cover is, therefore, an important component of CS habitat management to encourage use by prey species and to offset the perception of threat by ambush predators. Additionally anthropogenic disturbance at CS should be minimized to ensure optimum use by wildlife.

Expectedly mean species richness under CS was found to be less than that in control habitat (Shilling et al., 2020), resulting from absence of disturbance-averse animals that are not present near the road to use to CS. We recorded higher mean species richness under CS as compared to adjacent habitats, which could be because of the open nature of the CS where animal detectability was higher. Mean species richness also increased with increasing CS width (Mysłajek et al., 2020), with values comparable to control habitat at CS measuring 750 m wide. The two 750 m CS are heterogeneous in terms of approach and span terrains, and distances to vegetation cover, making different sections of these CS attractive for use by different species.

5. Conclusions

Results from the first two years of monitoring of mitigation measures on NH 44 demonstrate that CS are used by a wide variety of mammals in the landscape. Structural and environmental characteristics were found to differentially affect use by different species and guilds, while anthropogenic disturbance altered temporal use of CS by most wildlife. The CS also have the potential of maintaining near-natural species movement rates and community richness. Therefore, the success of the mitigation measures on NH 44 can potentially influence the acceptance and uptake of CS, especially larger structures, as effective mitigation measures on new and existing linear infrastructure in the Indian subcontinent, and by tiger range countries. While larger structures were found to be more accommodating of multiple species (in terms of higher species richness recorded), heterogeneity in CS design and types encourages differential use by multiple species as a function of their behavior. Therefore, based on our study, mitigation structures should be diverse in terms of their sizes, and the largest structures should cater to the needs of species with large body and group sizes in the landscape. Secondly, our study is vital for providing management recommendations that are based on interpretations of monitoring results in the context of animal behavior. Our findings are applicable for structure management measures such as habitat enrichment by increasing vegetation cover near CS and increasing below-structure heterogeneity by placing logs. These measures would enhance the use of CS by prey and small mammals. Heterogeneity and diversity in terms of availability of multiple CS of diverse designs and types (Clevenger and Waltho, 2005; Denneboom et al., 2021) would ensure that the requirements of species with varying needs are met.

Results from continuous monitoring of CS are a reflection of the initial responses of wildlife to the measures, and give useful insights for CS management. The results highlight the role of CS in mitigating the impacts of roads and traffic on wildlife by maintaining natural movement rates. The monitoring of the CS is ongoing, and we would be able to assess the effectiveness of the CS in maintaining landscape connectivity through long-term monitoring data. Such data would yield more information on inter-specific (Gagnon et al.,

2011) and species-specific demographic change (Ford et al., 2017), habituation to mitigation structures, as well as inter and intra-specific interactions (Little et al., 2002; Martinig et al., 2020; Mata et al., 2020), particularly for tiger landscapes and wild animal species of the Indian subcontinent.

CRediT authorship contribution statement

Akanksha Saxena: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Bilal Habib:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix

See Tables A.1-A.6.

Table A.1

Characteristics of crossing structures on National Highway 44 near Pench Tiger reserve, Maharashtra, including width, location, capture rate of anthropogenic activity (including human, livestock and feral dog captures), and presence of natural drainage and tarred/dirt road for vehicular access.

Crossing Structure	Width (m)	Location	Mean disturbance intensity (capture rate)	Drainage	Vehicular access
MNB1	60	Territorial forest division	5.6	1	0
AUP2	50		7.2	0	0
AUP3	750		5.5	0	1
MNB4	80		5.7	1	0
AUP5	300	Tiger reserve buffer zone	4.3	0	1
MNB6	65		2.2	1	0
AUP7	100		5.0	0	0
AUP8	750		1.3	0	0
MNB9	50		3.7	1	0

AUP = animal underpass; MNB = minor bridge.

Table A.2

Summary of fixed effect log mean estimates and standard errors for best supported models (ΔAIC values < 2) of all carnivores, leopard, tiger and wild dog use of crossing structures on NH 44, Maharashtra, India.

Predictors	**Carnivores**		**Leopard**		**Tiger**		**Wild dog**	
	Log-Mean	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*
(Intercept)	−4.14 [***]	0.20	5.86 [***]	0.22	−5.79 [***]	0.25	−21.69 [***]	1.62
Distance to cover	−0.24 [***]	0.07						
Width	−0.64 [***]	0.12			−0.35 [*]	0.15	−5.64 [***]	0.53
Distance to PA	−0.85 [***]	0.06			−0.49 [***]	0.07	−14.02 [***]	1.18
Anthropogenic capture rate	0.15 [**]	0.06	0.24[**]	0.08	0.12	0.07		
Distance to next CS	0.11	0.07	0.27 [*]	0.10	0.30 [***]	0.08		
Span terrain [slightly undulating]	0.07	0.12	0.78 [***]	0.21	0.58 [***]	0.14		
Span terrain [undulating]	−1.14 [*]	0.49	−0.09	0.60	−0.98	0.65		
Drainage [1]	−0.87 [**]	0.33			-0.152 [***]	0.37		
Vehicular access [1]	−0.62 [*]	0.24	1.19 [***]	0.30	−1.12 [**]	0.43		
Approach [sl. Undulating]	0.91 [***]	0.27	−0.62 [**]	0.20	1.18 [***]	0.33	11.30 [***]	1.08
Approach [undulating]	−0.05	0.30	−1.24 [**]	0.48	0.93 [**]	0.34	−4.28 [***]	0.43
Season [post-monsoon]	−0.21	0.12	0.47 [*]	0.24	0.44[**]	0.15	−0.87 [***]	0.22
Season [summer]	−0.91 [***]	0.12	−0.24	0.25	−0.22	0.16	−1.78 [***]	0.21
Season [winter]	0.66 [***]	0.12	1.41 [***]	0.22	0.73 [***]	0.16	0.29	0.20
Observations	4757		4757		4757		4757	

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

Table A.3

Summary of fixed effect log mean estimates and standard errors for best supported models (ΔAIC values < 2) of all small mammals, black-naped hare, jungle cat, mongoose sp., common palm civet and Indian crested porcupine use of crossing structures on NH 44, Maharashtra, India.

Predictors	**Small mammals**		**Hare**		**Jungle cat**		**Mongoose**		**Palm civet**		**Porcupine**	
	Log-Mean	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*
(Intercept)	−3.55 [***]	0.07	−2.37 [***]	0.23	−4.30 [***]	0.13	−12.55 [***]	1.28	-0.4.32 [***]	0.54	−9.06 [***]	0.73
Width	−0.24 [***]	0.05	0.90 [***]	0.16								
Distance to PA	0.09 [*]	0.04	0.58 [***]	0.07			−1.02 [***]	0.29			0.18	0.16
Carnivore capture rate	0.09 [*]	0.04							0.57 [*]	0.22	0.48 [***]	0.13
Span terrain [slightly undulating]	−0.03	0.10	0.25	0.15								
Span terrain [undulating]	−0.61 [*]	0.25	−0.65	0.37								
Drainage [1]	−0.62 [***]	0.15	2.71 [***]	0.45	0.60 [**]	0.21	−3.96 [**]	1.34	−2.48 [**]	0.83	2.03 [**]	0.70
Vehicular access [1]	1.14 [***]	0.14	0.98 [***]	0.19	0.76 [***]	0.18						
Season [post-monsoon]	0.77 [***]	0.10	1.06 [***]	0.13	0.15	0.13	2.42 [**]	0.81	−1.17 [*]	0.54	1.37 [***]	0.34
Season [summer]	−0.23 [*]	0.10	−0.41 [**]	0.14	−0.16	0.13	2.55 [***]	0.72	−0.49	0.35	−0.06	0.39
Season [winter]	1.11 [***]	0.10	1.11 [***]	0.14	0.93 [***]	0.13	2.80 [***]	0.79	−0.03	0.46	1.92 [***]	0.33
Distance to cover			−0.23 [*]	0.09	−0.16 [*]	0.06			0.55 [*]	0.24	−0.73 [**]	0.23
Distance to next CS			0.11	0.08			−1.63 [*]	0.71	0.36	0.19		
Approach [slightly undulating]			−3.03 [***]	0.35	−0.60 [***]	0.13	3.07 [**]	1.07	0.73	0.52	1.81 [*]	0.74
Approach [undulating]			−4.66 [***]	0.52	−0.38	0.25	6.20 [***]	1.42	2.80 [***]	0.62	−1.11	1.28
Anthropogenic capture rate											−1.24 [**]	0.40
Observations	4757		4757		4757		4757					

[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

Table A.4
Summary of fixed effect log mean estimates and standard errors for best supported models (ΔAIC values < 2) of all ungulates, chital, gaur, sambar and wild pig use of crossing structures on NH 44, Maharashtra, India.

Predictors	**Ungulates**		**Chital**		**Gaur**		**Sambar**		**Wild pig**	
	Log-Mean	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*	*Log-Mean*	*SE*
(Intercept)	-0.170***	0.11	−2.03***	0.15	−4.44***	0.51	−8.37**	3.34	−2.32***	0.14
Width	−0.60***	0.06	−0.43***	0.08					−1.03***	0.08
Distance to PA	−0.47***	0.03	−0.62***	0.04			−2.03***	0.30	0.48***	0.05
Distance to next CS	−0.27***	0.03	−0.34***	0.04	0.31*	0.14	−1.31***	0.37	0.15***	0.05
Carnivore capture rate	0.24***	0.03	0.24***	0.04					0.12*	0.05
Drainage [1]	−0.89***	0.16	−0.44*	0.21					−1.74***	0.21
Span terrain [slightly undulating]	0.89***	0.13	0.89***	0.18	1.62**	0.52	1.79**	0.55	−0.64***	0.17
Span terrain [undulating]	0.81***	0.18	0.46*	0.22	3.33***	0.83	5.61***	0.96	−0.04	0.21
Season [post-monsoon]	−0.11	0.08	−0.09	0.10			0.54	0.50	−0.47***	0.12
Season [summer]	−0.28***	0.07	−0.24**	0.09			0.45	0.38	−0.43***	0.11
Season [winter]	0.43***	0.08	0.35***	0.10			1.38***	0.41	0.46***	0.12
Vehicular access [1]	−0.32*	0.13	−0.46**	0.17						
Distance to cover					−0.35*	0.17	−0.68**	0.23	−0.22***	0.06
Span terrain [slightly undulating]					−0.83*	0.37				
Span terrain [undulating]					2.17***	0.48				
Observations	4757		4757		4757		4757			

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

Table A.5
Summary of factors affecting species richness under crossing structures on NH 44, Maharashtra, India.

Predictors	**Richness**	
	Log-Mean	*SE*
(Intercept)	0.92***	0.08
Drainage	−0.37***	0.07
Width	0.00***	0.00
PA_nonPA [PA]	0.20***	0.05
Season [post-monsoon]	0.18*	0.07
Season [summer]	−0.01	0.07
Season [winter]	0.40***	0.07
Observations	391	
R^2 Nagelkerke	0.715	

* $p < 0.05$**$p < 0.01$.
*** $p < 0.001$.

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