INDIAN GREY WOLF (*Canis lupus pallipes*) IN HUMAN DOMINATED LANDSCAPES: MOVEMENT, SPACE USE AND FORAGING

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

Shaheer Khan

Research Center

भारतीय वन्यजीव संस्थान
Wildlife Institute of India

Year

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भारतीय वन्यजीव संस्थान
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DECLARATION

I hereby declare that the thesis titled **"Indian Grey Wolves (*Canis lupus pallipes*) in Human Dominated Landscapes: Movement, Space use and Foraging"**, submitted by myself, Mr. Shaheer Khan (Enrolment No. 17PHD462) to Forest Research Institute (FRI), Deemed to be University, Dehradun for the award of the degree of Doctor of Philosophy in Forestry (Wildlife Science) is a record of original research work carried out by me under the supervision of Dr. Bilal Habib, Wildlife Institute of India, Dehradun., The doctoral research has not formed the basis for an award of any other degree or diploma in other university or organization. I also declare that the thesis embodies my own work, observations, and analysis, and in that respect, the investigation appears to advance knowledge in the subject. The thesis has been duly checked through URKUND, a plagiarism detection tool approved by FRI and has plagiarism to acceptable limits.

Dehradun, the August 29, 2023

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DECLARATION

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4. The Topic of research approved by the FRI University: **"Indian Grey Wolves *(Canis lupus pallipes)* in Human Dominated Landscapes: Movement, Space use and Foraging."**
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Executive Summary

This thesis presented a comprehensive investigation into the ecology of Indian wolves (*Canis lupus pallipes*) within human-dominated landscapes in Maharashtra, India. The study focused on movement patterns, den and rendezvous site selection, and food habits of Indian wolves to gain insights into their adaptation strategies and ecological interactions within changing environments.

Seven adult wolves (three males and four females) and four subadult wolves (two males and two females) were captured using soft leghold traps from 2017 - 2021. Trapped wolves were held using a double-threaded nylon hockey net and immobilized using Ketamine–Xylazine by injecting intramuscularly on their hind leg and fitted with GPS collars. A total of ten wolves from seven different packs were fitted with GPS collars, and one male was fitted with a proximity collar. The GPS collars were programmed for the different intervals between positions ranging from 0.5-5 hours per fix (median=1 hour), depending on the time of year and type of individual. I then scaled the data to 1 hour per fix for movement analysis.

The estimated average daily movement of Indian wolves was 10357.64 ± 6629.02 SD m/day (Table 2.2). The daily average movements of males were higher (12113.9 ± SD7513.68 m/d, n = 4) than those of females (9718.4 ± SD6154.66) m/d, n= 6), and the difference was found to be significantly different (F=86.33; p>0.001). The average daily movement of adults (10957.23 ± SD6999.91) was higher than that of subadults (9236.8± SD5709.60), and the difference was found to be significant (F=51.14; p>0.001). In the summer season, the wolf's daily movement was found to be highest (11875.19 ± SD6923.31 m/d), followed by pre-monsoon (10425.51 ± SD7065.23 m/d) and monsoon (9951.58± SD6166.71 m/d) and lowest in the winter season (9020.12 ± SD6276.32 m/d). The highest daily movement was found for adult males (13956.71 ± SD7500.48 m/d) followed by adult females (9800.04 ± SD6435.64 m/d) and lowest for subadult males (8211.88 ± SD5876.94 m/d). During the collaring period, two females (26138 and 26140) were breeding and delivering pups. Hence, I calculated the difference between the daily movement in the breeding and non-breeding period and found that female daily movement was lower in the breeding season (9410.83 ±

SD6512.21 m/d) than in the non-breeding season (10653.87 ± SD6638.75 m/d) and the results were found to be significantly different ($F=46.07$; $p>0.001$).

The season, age, sex, and time of day significantly impact wolf movement speed. The movement speed was significantly lower in winter ($\beta=-0.26 \pm$ SE0.03; $p>0.001$). Their movement speed decreased significantly in grassland ($\beta=-0.43 \pm$ SE0.09; $p>0.001$), and scrub forest ($\beta=-0.34 \pm$ SE0.08; $p>0.001$) and increased in agricultural lands ($\beta=0.12 \pm$ SE0.06; $p=0.08$) but the results were not found to be significant. Anthropogenic factors also influence wolf movement in the landscape. Wolves travel faster ($\beta=0.03 \pm$ SE0.003; $p>0.001$) in areas with a high human footprint. In summer season wolf moves faster during nighttime ($\beta=0.41 \pm$ SE0.03; $p>0.001$) as compared to the winter ($\beta=0.16 \pm$ SE0.03; $p>0.001$). Wolf movement speed decreased in agricultural areas during nighttime ($\beta=-0.26 \pm$ SE0.1; $p>0.01$), and the movement increased in high human footprint areas ($\beta=0.04 \pm$ SE0.003; $p>0.001$).

The average home range (95% contour) and core areas (50% contour) of the five adult wolves and five subadults from eight packs using different home range estimators were calculated. The estimators showed different home ranges and core area sizes across individuals. The home range for adult individuals was found to be 378.7, 285.4, 317.8 and 230.9 km^2 using Minimum Convex Polygon (MCP), Kernel Density Estimates (KDE), Autocorrelated Kernel Density Estimates (aKDE) and (Brownian Bridge Movement Model (BBMM), respectively. The home range for subadult individuals was found to be 71.9, 79.6, 56.7 km^2 and 37.1 km^2 using MCP, KDE, aKDE and BBMM, respectively. The core area for adult individuals was found to be 13.7, 29.1, 47.7 and 24.2 km^2 using MCP, KDE, aKDE and BBMM, respectively. The core area for subadult individuals was found to be 9.9, 4.9, 22.2 km^2 and 3.0 km^2 using MCP, KDE, aKDE and BBMM, respectively.

Resource selection function revealed a preferential selection for land use categories by the Indian wolf (Khi2L = 659.46, df = 41, $p < 0.001$). The Indian wolf preferred grassland areas (Wi = 3.49 ± 0.5SE) followed by scrub forest (Wi = 2.42 ± 1.61SE) and plantations (Wi = 2.04 ± 1.39SE). Agriculture, built-up, and waterbody were used less in proportion to their availability.

Known and probable den and rendezvous sites through local and Maharashtra Forest Department locations and from GPS locations of collared individuals were located and confirmed by scanning the site for wolf pugmarks and scats. The habitat feature, manmade linear infrastructure, and human-induced parameters associated with den and rendezvous sites were collected in the breeding season (November to February) from 2016 to 2021. A total of 32 dens (4 in Ahmednagar, 1 in Gondia, 10 in Pune, and 17 in Solapur Districts, Maharashtra, India) and 25 rendezvous sites (4 in Ahmednagar, 1 Gondia, 2 Nagpur, 5 Pune, and 13 Solapur Districts, Maharashtra, India were observed.

The data on 16 habitat and anthropogenic variables (listed below) at den and rendezvous sites and 60 contrast random locations within the 95% MCP of all the collared wolves were collected. This is referred to as third-order selection by Johnson (1980). Data were recorded for the den and rendezvous site for habitat type (Agriculture, Grassland, Plantation, and Scrub), terrain type (Flat, slope, steep and undulating), and vegetation cover in a 50 m radius circular plot centred on the den opening and rendezvous site). The vegetation cover was recorded through ocular estimation(Matteson, 1992). Distance from the nearest water source, cart road (dirt road used by locals and livestock), metal road (nearest tar road used for vehicular movement), and escape cover were recorded using Google Earth. The den substratum was classified into three categories: bund, rock crevices, and manmade structure, and the total number of den openings was also counted at each den site.

Out of 32 dens observed, the maximum dens were found in grassland (46.87% of total dens), followed by scrubland (21.87%), plantation (18.75%), and the lowest number of dens in agriculture (12.5%). I also assessed the substratum on which dens were formed and found that maximum dens (75%) were in bunds (a mound used primarily in India to separate two agricultural lands or embankments to prevent water flow between the fields), followed by rock crevices (15.62%) and manmade structure (9.37%) such as pipelines to help wolves to make dens in protected areas. Of the total dens evaluated, 23 were found with single openings, seven with two openings, and one with three and four openings. I also calculated the nearest human settlement and water source from the den site and found that the maximum dens (13 dens) were 1000-2000 meters away from any human settlement, followed by eight dens at 500-1000 meters). The maximum number of dens (n=18) were found within the 100-meter radius of dens, followed by eight dens between 100–200 meter radius.

The den sites were positively associated with the presence of water (β=-4.55 ± SE1.66; p=0.006), vegetation cover (β=1.97 ± SE0.74; p=0.008), plantation (β=1.52 ± SE0.47; p= 0.001), presence of grassland (β=1.41 ± SE0.49; p=0.004), and scrub forest (β=1.09 ± SE0.46; p=0.02). The human footprint was negatively associated with the den sites, but the estimates were not found to be significantly different (β=-0.88 ±SE0.46; p=0.054).

Out of 25 rendezvous sites observed, the maximum number of sites were found in grassland (56.0% of total rendezvous sites), followed by plantation (20.0%) and scrubland (20.0%) each, and the lowest in agriculture (4.0%). I also assessed the topographic features on which rendezvous sites were established and found that the maximum number of sites (72%) were in flat areas, followed by the slope (16.0%), and only 12% were in undulating terrain types.

The distance from escape cover (β=-5.17 ± SE2.29; p=0.02), presence of plantation (β=1.81 ± SE0.60; p=0.003), presence of grassland (β=1.46 ± SE0.56; p=0.01), presence of scrub (β=1.23 ± SE0.45; p=0.006) were positively associated with rendezvous sites and negative association with vegetation cover (β=-1.72 ± SE0.69; p=0.01).

The non-invasive technique of scat analysis was used to study the diet composition of the Indian wolves by collecting 961 scats between 2017 and 2021 throughout the study area. Paths, dirt roads, fire lines, and crossroads were prospected by walking on foot. Morphology, size, scent, colour, contents and spatial position were used to identify wolf scats. The collected scats were submitted to genetic analysis to confirm the species *Canis lupus pallipes*, avoiding misclassification of domestic dogs (*Canis lupus familiaris*) and Golden Jackal (*Canis aureus*). The Indian fox scats were smaller in size, and I did not collect any small-size scats unless it was found at confirmed wolf den sites. Out of 961 scats, DNA was extracted from only 430 scats (44.75% of the collected scats).

Species identification from faecal samples was carried out using two primers, CaCOI and WOLF4, to amplify the fragment of the control region (Vilà et al., 1999). Jackal samples were amplified only in CaCOI, while dog samples were amplified only in WOLF4. Samples that produced bands with both primers were classified as belonging to the Indian wolf. Out of 430 genetically confirmed samples, 348 scats (80%) belong to the Indian wolf, and the remaining 20% of the scats were golden jackal and feral dogs.

The most common food item in the wolf scats was bones (83.91% of total scats), followed by hairs (62.93). Feathers constituted (35.63%) the third major item in the scats. A significant proportion of scats also contain vegetative matter such as grass and leaves (18.39%), Ziziphus (6.32%) and grapes (2.59%). I also found human-related items (4.31%) in the scats, such as plastics and processed leather. Data on feeding habits obtained by analysing 348 wolf scats collected revealed that domestic prey comprised 59.38%, wild prey 23.77% and vegetable matter 14.96% of their diet. Unidentified prey remains contributed 1.89% of their food.

The most frequently occurred species in wolf scats were chicken *Gallus gallus domesticus* (27.59%) and goat *Capra aegagrus hircus* (21.84%), followed by vegetative matter (14.97%; grass, Ziziphus, grapes), sheep *Ovis aries* (9.53%), blackbuck *Antilope cervicapra* (8.69%) and chinkara *Gazella bennettii* (6.59%). Black-naped hares, reptiles, rodents, wild pigs and cattle constituted less than 2% of each. Consistent with the frequency of occurrence, the biomass model also suggested that goats (31.06%), blackbuck (21.50%), and sheep (20.98%), followed by chinkara (16.60%) and chicken (3.77%) were the principal food item of wolves across the landscape. Regarding the relative number of individuals consumed, chicken was consumed most (37.48 individuals), followed by goats, blackbuck and chinkara.

The study conducted in the same landscape by Habib in 2007 reported the frequency of different food items by analysing 3947 scats, and the scats were collected from the core areas of wolves between 2002-2005. I compared this study's results with the previously reported frequency of occurrence and found that the consumption of wild prey significantly decreased from 38.01% (Habib, 2007) to 23.77%; $P < 0.001$), and the consumption of domestic prey increased from 47.16% to 59.38% in the last 15 years. However, there was no change in the consumption of vegetative matter in the last 15 years in the Landscape. The study found that chicken consumption increased 27 times more than previously reported; results were significant ($P < 0.001$), and blackbuck consumption decreased significantly from 27.5% to 8.40%; $P < 0.001$ in these years.

Food habit analysis reveals significant dietary changes over time. Domestic prey consumption, such as goats and sheep, has increased, while the consumption of wild prey like blackbuck and chinkara has declined. Chicken consumption notably increased, possibly due to the availability of poultry waste. Dietary overlap analysis among wolf packs in different districts highlights variations in dietary preferences based on food resource availability.

This research underscores the importance of understanding wolf movement, denning ecology, and food habits for effective conservation strategies. As human populations and habitat alterations increase, studying wolf adaptation is crucial for species-specific conservation planning. The insights gained from this study contribute to informed decision-making and sustainable management of wolf populations, fostering harmonious coexistence between wildlife and human activities.

Chapter 1

Chapter 1

1.1 General Introduction

Large predators present greater conservation challenges than any other species category due to conflict and long-ranging movement. The decline of the large predator population is now a serious concern among scientists. Large predators face many pressures, including habitat loss, hunting, disease, and the worldwide commercial market for body parts. Due to this, many species face the prospect of extinction or local extermination, such as the African wild dog (*Lycaon pictus*), Asiatic wild dog (*Cuon alpinus*), Asiatic black bear (*Ursus thibetanus*), jaguar (*Panthera onca)*, tiger (*Panthera tigris*) and grey wolves (*Canis lupus*). However, due to climate change and local pressure, species often shift their formal ranges and recolonize in new areas (Kanagaraj et al., 2019). Studies from Scandinavian countries and the United States indicated that wolves have recovered and recolonised in new habitats closer to humans (Mladenoff and Sickley, 1998; Gurarie et al., 2011; Carricondo-sanchez et al., 2020). The grey wolves belong to the Canidae family, which comprises about 34-37 species in the world, including foxes, jackals, and dogs (Figure 1.1), of which at least nine of these species are threatened with becoming extinct, such as Darwin's fox (*Pseudalopex fulvipes*), red wolf (*Canis rufus*) and African wild dog (*Lycaon pictus*) (Ginsberg and Macdonald, 1990; Sillero-Zubiri et al., 2004; Wozencraft, 2005). However, many wild canids, such as the red fox (Vulpes vulpes), golden jackal (*Canis aureus*), coyote (*C. latrans*), and grey wolves (*C. lupus*), are widespread. As a result, they are often involved in contentious wildlife management issues like human-animal conflict, disease transmission, and predation on livestock. The size of canids ranges from fennec foxes, which can weigh less than 1 kg, to the grey wolf, which can weigh as large as 80 kg. However, not all grey wolves weigh 80 kg, and there has been a significant variation among subspecies levels. The variability in the body size can be explained to some extent by differences in food availability, with small canids (like the fennec fox) typically associated with arid and poor habitats where only a small body mass can be supported year-round, whereas large canids are usually associated with habitats where prey is abundant (Ginsberg and Macdonald, 1990).

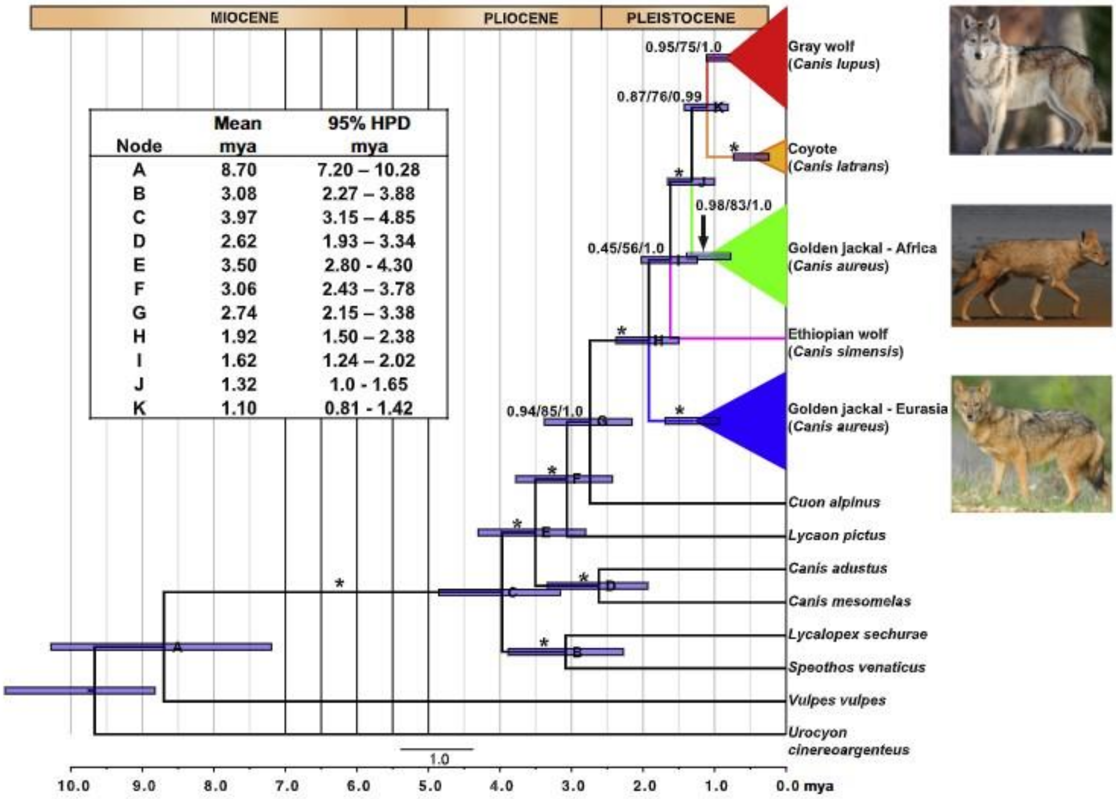

Figure 1.1: Cladogram and divergence of the grey wolf among its closest extant relatives acquired from Koepfli et al., 2015.

About the Grey Wolf

The grey wolf's range includes North America, Europe, and Asia (Mech and Boitani, 2003). Because of their adaptability, wolves can survive in various habitats, including temperate forests, mountains, tundra, taiga, grasslands, and deserts. At least 44 wolf subspecies are currently defined based on differences in morphological characteristics, behavioural patterns, and geographic distribution (Wozencraft, 2005). However, many of these subspecies' classifications are unclear and up for debate among experts (Busch, 2018), making grey wolf taxonomy highly contentious (Shrotriya et al., 2012; Pilot et al., 2014; Ersmark et al., 2016). At the species and subspecies levels, there are a number of taxonomic conclusions that are awaiting validation and revision. Amid a muddled account of the number of species and sub-species, studies suggested that wolves from the Indian regions could form the oldest lineages (Aggarwal et al., 2003; Sharma et al., 2004; Shrotriya et al., 2012; Werhahn et al., 2017, 2018; Hennelly et al., 2021).

With an adult weight range of 18 to 80 kilograms, depending on sex and geographic location, grey wolves (*Canis lupus*) are the largest wild canids. Wolves are pack hunters and are known to feed on a variety of different food items. Wolves predominantly predate upon large and medium-sized hooved mammals, including moose, elk, white-tailed deer, mule deer, blackbuck, Gazelle, and caribou (Mech and Boitani, 2003; Newsome et al., 2016; Khan et al., 2022). However, the diets of different subspecies of wolves may differ significantly in different regions. They select their prey based on availability, abundance, pack stability, season, and habitat accessibility in human-dominated landscapes (Imbert et al., 2016; Lyngdoh et al., 2019). In Asia, the unavailability of wild prey alters their diet pattern toward domestic prey and human-subsidised food (Newsome et al., 2016; Khan et al., 2022). In addition to their excellent sense of smell, wolves also have keen senses of hearing and eyesight. More than nearly any other species, wolves have a wide range of coat colours, from white to grizzled grey to brown to coal black. Worldwide, the grey wolf is categorised as the least concern by IUCN, whereas the North American red wolf, Canis rufus, is considered critically endangered.

Wolves of India

There are two major wolf populations in India, i.e., Woolly wolf/Tibetan wolf/Himalayan wolf (*C. l. chanco*) (also known as Tibetan or Himalayan wolf) and Indian wolf (*C. l. pallipes*). These wolves are supposed to have diverged from the main clade about 800,000 and 400,000 years ago, respectively (Sharma et al., 2004; Aggarwal et al., 2007; Shrotriya, Lyngdoh, and Habib, 2012; Werhahn et al., 2017; Joshi et al., 2020). However, a recent study suggested a contradictory possibility that the Indian wolf could be basal to the woolly wolf (Hennelly et al., 2021b). The study stated that Indian and Woolly wolves shared the most common ancestors with Holarctic wolves 200,000 and 500,000 years, respectively (Hennelly et al., 2021b). Some of the studies proposed that the wolves of India were not subspecies but qualified as separate species, viz. *Canis himalayensis* and *Canis indica* (Aggarwal et al., 2007). The debate regarding their taxonomic status is unsettled (Alvares et al., 2019). Nonetheless, both wolves could be presumed to be two distinct lineages (Pocock, 1941) and are geographically isolated, having allopatric distribution in India (Aggarwal et al., 2003). The Woolly wolf is found in the cold-arid zone of the upper Trans-Himalayas of India, whereas the Indian wolf is distributed primarily in the semi-arid zone of India. Although both these wolves are protected as Schedule I species under the Indian Wildlife (Protection) Act 1972. Despite protection, conserving a species residing in a human-dominated landscape and in direct conflict is challenging.

Indian wolves *Canis lupus pallipes*

The Indian wolf is believed to have evolved during the drier period of the Pleistocene and adapted to survive in the arid zones (Sharma et al., 2004; Singh and Kumara, 2006). The oldest lineage of the current grey wolf population is the Indian wolf, one of the smallest subspecies of the grey wolf (Hennelly et al., 2021). After the extinction of the Cheetah from India, it became the top carnivore species of the Indian open plains (e.g., semi-arid grasslands, scrublands, and grazing lands). The Indian wolf is distributed across 13 states of India, primarily in the semi-arid zone, with the latest population estimate of 1200– 1800 packs (Jhala et al., 2013). Indian wolves inhabit open and grassland habitats and survive primarily outside protected areas. Indian wolves are mostly found in non-protected areas with low natural prey populations (Habib, 2007; Maurya, Habib, and Kumar, 2011; Habib et al., 2021). Therefore, in most of their range in India, wolves primarily subsist on domestic livestock (Shahi, 1982; Mishra, 1997; Jethva and Jhala, 2004a; Habib, 2007; Habib et al., 2021) and are severely persecuted as a consequence. Their diet primarily comprises domestic animals or human subsidies (Jethva and Jhala, 2004b; Habib, 2007).

The former wolf range has decreased and has been locally extirpated from many places due to increasing human urban sprawl, land development, and shifting land use practices. In any scenario, fewer wolves are likely surviving now in India than the tigers (*Panthera tigris*). The Indian wolf is distributed across central India, extending up to Rajasthan in the north and Karnataka in the south (Shahi, 1982). Three biogeographic zones—the desert, the semi-arid zone, and the Deccan plateau of India—are home to the remaining wolf population (Rodgers and Panwar, 1988) and are distributed across 13 states of India. The Indian wolf is continuously distributed across Gujarat, Rajasthan, Madhya Pradesh, Maharashtra, Karnataka, and Andhra Pradesh, as per Jhala and Giles (1993).

Canis lupus has been one of the most studied among wild species (Mech, 1995). The first study of the wolf was published in 1938 on wolf behaviour. Two major long-term studies that have ever been conducted on predator-prey relationships include the wolf-moose system in Isle Royale National Park and the Superior National Forest of northeastern Minnesota (Mech, 1966, 1995; Peterson and Page, 1988). There are not many studies conducted on the Indian wolf except for a few in Velavadar National Park, Gujarat (Jhala, 1991; Jhala and Giles, 1993; Jethva, 2002; Jethva and Jhala, 2004a), the Great Indian Bustard Sanctuary, Maharashtra (Kumar and Rahmani, 1995, 1997, 2000; Habib, 2007; Habib and Kumar, 2007; Sadhukhan, 2022).

With the increasing human population, India is also home to 14 large carnivores living within and outside a protected area network. Now, 15 large carnivores, including the recently reintroduced African Cheetah *Acinonyx jubatus*. However, the protected areas are small, fragmented, and compromised functional connectivity (Mondal et al., 2016). With the population, the development and habitat are also changing very fast. The ecological impacts of this development are expected to increase, leading to the fragmentation of contiguous habitats and behavioural change of species. Therefore, studying how wolves cope with such changes is pertinent to devising suitable species and community-specific mitigation plans. Understanding movement, habitat use, den and rendezvous site selection, and food habits of wolves is key to integrating effective mitigation measures in rapidly changing habitats in India.

1.2 Literature Review

A famous old Russian saying, "*The wolf is kept fed by his feet*," describes much about the grey wolf's wide distribution and survival capabilities. Due to its wide distribution in the northern hemisphere, it is one of the most studied species (Mech, 1995). Several books, monographs, and thousands of research articles have been published describing its evolution, distribution, and different aspects of ecology, such as movement, intra-specific communications, and food habits (e.g. Mech, 1966, 1995; Jhala, 1991; Habib, 2007; Jhala et al., 2022; Khan et al., 2022). As per availability, wolves prey upon an extensive range of animals, from small-sized rodents to large ungulates, because of their ability to use large areas and digest large quantities of food in a brief time (Mech, 1970). Though the wolf is the most studied species, the wolves that lived in the Indian subcontinent are somehow neglected by scientists, and few studies have concentrated on both the subspecies, i.e., Indian wolf *Canis lupus pallipes* and Woolly wolf *C. l. chanco*.

The study on wolves in India includes the status and conservation of wolves in Rajasthan and Gujrat (Jhala and Giles, 1993), habitat, feeding habits, and population dynamics in Velvadar National Park (Jhala, 1991), conservation and status of wolves in Nannaj, Maharashtra (Kumar and Rahmani, 1995, 1997), ecology and behaviour of wolves (Kumar, 1998), study on livestock depredation in Nannaj (Kumar and Rahmani, 2000), feeding habits and habitat in Bhal area of Gujarat (Jethva and Jhala, 2003), denning behaviour in Deccan landscape (Habib and Kumar, 2007), different aspects of ecology in Maharashtra (Habib, 2007), feeding habit in Rekhuri Blackbuck Sanctuary (Maurya et al., 2011), status distribution and foraging ecology of the woolly wolf (Shrotriya, 2020), movement, ranging behaviour and habitat selection of woolly wolf (Lyngdoh, 2022) and population estimation of Indian wolf through howling survey in the semi-arid landscapes of Maharashtra (Sadhukhan, 2022).

The conservation and management of the species depend upon the information and knowledge of the species. Since the population of Indian wolves has decreased in its former range, instead of being listed as Schedule I species as per the Wildlife Protection Act 1972. Their small population shares a habitat with an ever-increasing human population. Such circumstances need careful management effort with in-depth knowledge of basic ecological parameters such as home range, dispersal, and feeding habits. Earlier studies suggested that the average home range of the Indian wolf ranges between 150 and 300 sq km depending upon prey density and availability of denning sites (Jhala, 2003; Habib and Kumar, 2007). The primary wild prey of wolves are Blackbuck (*Antilope cervicapra*), Chinkara *(Gazella Bennetti),* Black-naped hare *(Lepus nigricollis),* and also domestic prey such as goats (*Capra aegagrus hircus)* and sheep (*Ovis aries*).

Movement and Spatial Ecology

Understanding an animal's movement is critical because various management and conservation strategies may be developed depending on how it moves throughout the landscape. The majority of wolf movement research has been conducted in European and New World nations (Jedrzejewski et al., 2001; Merrill and Mech, 2003; Whittington et al., 2004; Tsunoda et al., 2009; Mech and Cluff, 2011; Tourani et al., 2014). Wolf activity and movement have been reported to vary based on their social status in the pack (Ballard et al., 1991), age and sex (Jedrzejewski et al., 2001; Schmidt et al., 2008), and dominance (Mech, 1999). Other factors that influence wolf movement include prey density (Messier, 1985), prey migration (Walton et al., 2001), the activity of neighbouring packs (Mech and Harper, 2002), and human activity (Vilà et al., 1995; Ciucci et al., 1997; Theuerkauf et al., 2003a, 2003b; Kaartinen et al., 2005; Kusak et al., 2005). Existing studies have examined how wolves avoid anthropogenic features in the landscape depending on the season and time of day (Carricondo-Sanchez et al., 2019; Carricondo-sanchez et al., 2020). Human infrastructure, such as roads and villages, is a common disturbance in wolf movement studies (Jedrzejewski et al., 2004; Zimmermann et al., 2014; Falco et al., 2019; Ciucci et al., 2020). Various studies focused on wolf movement across the range. Although it is recognised as a distinct and significant population, the movement ecology of the Indian wolf has not been studied across its range (Hennelly et al., 2021a). The space use of an animal is determined by many factors, such as age, sex, food availability, and environmental conditions (Powell and Mitchell, 2012). The home range size is among a species' most basic ecological parameters. This aspect of ecology has been studied in detail for many species (Dunn and Gipson, 1977; Obbard and Brooks, 1981; Dillon and Kelly, 2008).

The Indian wolf home ranges have been reported to range from 113.4 km^2 (Jethva, 2002) to 183.58 km^2 (Habib, 2007). These home ranges are smaller than what has been reported for the grey wolf in North America (Mech, 1970; Fritts and Mech, 1981). The home ranges of the arid region of the Middle Eastern Arabian wolf (22.0 ± 11.3 km^2) were smaller than the Indian wolf (Hefner and Geffen, 1999). The woolly wolf's 95% MCP home ranges in the Indian Himalayan area were 1044.26 ±56.27 km^2 (Lyngdoh, 2020), five times larger than the home ranges of Indian wolves. Kusak et al. (2005) reported home range sizes for the grey wolf to 150.5 km^2 (range 141-160 km^2) for two packs in Croatia from 1998 to 2001. Other studies reported 500 km^2 to 600 km^2 from Sweden (Okarma et al., 1998), 964 km^2 (range 312-3,074 km^2) home range from Northern Ontario (Anderson, 2012), 460.5 km^2 from Greece (Karamanlidis et al., 2017).

Den and Rendezvous sites selection

Any species' ability to reproduce successfully and produce offspring is essential to survival and persistence. Survival and successful reproduction are important demographic factors affecting wolf population dynamics worldwide (Boitani, 2000; Fuller et al., 2003). They often interact with humans since they are found primarily in a human-dominated landscape. Wolves survive with humans because of their ability to exploit human-modified landscapes. However, wolves also prey upon livestock, allowing the potential for conflict, especially with the shepherd community. A persistent problem is the incidence and impact of human interference on wolf dens and rendezvous sites. Reducing disturbance is difficult for wildlife management across the wolf's distribution range, particularly in a country with a high population density like India (Chapman, 1977; Paquet and Darimont, 2002; Smith et al., 2004; Habib and Kumar, 2007).

Few studies have been conducted on the den and rendezvous selection of wolves. Trapp et al. (2008) conducted a study on the den site selection of wolves in Rocky Mountain and found that wolves denned in areas with canopy cover, escape cover, herbaceous ground cover, and woody debris and were closer to water. Ausband et al. (2010) surveyed identified rendezvous sites and found that wolves preferred higher Normalized Difference Vegetation Index and surface roughness, indicating that wolves consistently used wet meadow complexes. Similarly, Iliopoulos et al. (2014) evaluated rendezvous site selection in Greece. They found wolves select rendezvous sites below 1200 asl, away from forested roads and human habitation, close to water sources and in areas with low forest fragmentation, indicating avoidance of human presence and disturbances. Benson et al. (2015) conducted the study in Algonquin Park, Canada, to understand the resource selection by wolves at dens and rendezvous sites and found that wolves selected dens closer to water, away from secondary roads, and on steeper slopes relative to rendezvous sites.

To comprehend the den shifting of Indian wolves due to human disturbance, Habib et al. conducted a study in India in 2007 on wolf denning behaviour in semi-arid landscapes in Maharashtra. Water availability and pup age were negatively correlated with wolves' tolerance for disturbances near their dens. The results indicated that in addition to the age group of pups, crucial cues for shifting dens during the early phases of pup development were the terrain, den orientation, and distance from roads.

Food Habits

Information on species' feeding habits is critical in an ecological context and in terms of conservation and management (Ciucci et al., 1997). Wolf feeding ecology is fundamental in the Indian scenario due to human-animal conflict because of livestock depredation. Rapid growing agricultural land and the expansion of human settlement forced wolves to live around human presence, ultimately increasing the human-wolf conflict. Mech (1970) explained the vast range of the wolf diet and its adaptability. As wolves live in packs and have long-distance travel habits, they can prey upon large animals.

There are numerous studies on wolf feeding ecology by various means, such as analysing stomach content, scat analysis, prey examination, and continuously tracking radio-collared wolves. Scat analysis is widely used because it is inexpensive, relatively quick to apply, and large samples can be collected without harming the animal (Floyd et al., 1978; Meriggi et al., 1996b; Klare et al., 2011). Several studies have been conducted on the wolf diet using scats analysis (Meriggi et al., 1996a; Chavez and Gese, 2005; Stahler and Smith, 2006; Hosseini-Zavarei et al., 2013; Tourani et al., 2014).

In India, several studies have been carried out on the feeding ecology of wolves. Kumar (1998) examined the kills made by wolves to assess the kill rate and livestock depredation in Solapur (Kumar and Rahmani, 2000). The minimum number of hairs per scat and the minimum number of scat samples need to be analyzed to examine the feeding ecology of wolves (Jethva and Jhala, 2003). Jethva and Jhala (2004a) evaluated biomass consumption from prey occurrence on captive wolves in Sakkarbaug Zoo, Junagarh. The diet composition of wolves was assessed in different parts of Maharashtra (Habib, 2007; Maurya et al., 2011). The previous study on the feeding ecology of wolves suggested that the wolf's preferred diet is Blackbuck, followed by livestock.

Justification of the study

With changing scenarios of land use patterns, increased human activities, and infrastructure development, the suitable areas for wolves are decreasing in India. The wolf's behaviour is to move in large areas within the human-dominated landscape. Creating protected areas for wolves in such a large landscape is impossible. India's average protected area size (173.97 km^2) (ENVIS Centre on Wildlife and Protected Areas, 2022; https://wiienvis.nic.in/) can only protect one functional pack. Due to human activities, this endangered canid is under tremendous threat and needs immediate attention. It is essential to keep track of various changes occurring in the wolf range to understand the ecology of the Indian wolves. However, the current study is crucial for monitoring the wolf population and developing management strategies for this top predator in India's semi-arid landscapes. To facilitate monitoring and research, wolves were radio-collared. These radio-collared wolves were continuously monitored to understand space use, movement, predation on ungulates, and depredation on livestock. In light of the above, this study aimed to provide information on space use, movement, den and rendezvous site selection and food habits of Indian wolves.

1.3 Hypothesis

Wildlife habitats outside designated protected area systems are declining due to the increased human population, resulting in the expansion of agricultural land and infrastructure development (Hansen and DeFries, 2007). The human population is summed up with domestic ungulates, which are attributed to habitat degradation through overgrazing, while illegal hunting of wild ungulates leads to their near replacement by livestock. Long-ranging species that share a habitat with humans are more prone to be affected negatively by these factors, which are more prominent in developing countries like India. On the one hand, living in a human-dominated landscape can harm the population due to anthropogenic activities; on the other hand, it also provides optional food subsidies and inflated livestock densities. Some species living in the fragmented human-dominated landscape have developed behavioural adaptations to exploit easy food substitutes and find suitable areas to reproduce and shelter. Both humans and wildlife are known to adapt to local conditions to exploit the landscape, resulting in competitive exclusion. Indian wolves share their habitat with humans and predate mainly on livestock. I hypothesize that for wolves to be successful in such habitats, they need to optimize between negative and positive benefits associated with human-dominated landscapes. Given the above, I tried to answer the following questions.

- How do wolves move in the human-dominated landscape?
- Which biological, habitat and anthropogenic factors affect wolf movement in the landscape?
- What is the current home range size of wolves in Maharashtra?
- What are the essential characteristics of denning and rendezvous sites critical for survival in the human-dominated landscape?
- What are wolves' current food habits, and how have they changed in the landscape in the last 15 years?

1.4 Objectives of the study

A. To understand the space use and movement of Indian wolf in the human-dominated landscape

B. To understand the characteristics of denning and rendezvous sites in the human-dominated landscape

C. To evaluate the diet of Indian wolves in the human-dominated landscape

1.5 Study Area

In India, the Indian wolf is distributed across Rajasthan, Haryana, Uttar Pradesh, Madhya Pradesh, Gujarat, Maharashtra, Karnataka, Kerala, and Andhra Pradesh. The study was conducted in one of the strongholds of the Indian wolf population, i.e., Maharashtra. Maharashtra is a state in the western peninsular region of India. In Maharashtra, the Indian wolves were collared from three adjoining districts, i.e., Ahmednagar, Pune, and Solapur Districts, for the study (Figure 1.2). Primary habitats are tropical deciduous forests and semi-arid and coastal areas. It has a coastline stretching 840 kilometres along the Arabian Sea. The State lies between 15°35' N to 22°02' N latitude and 72°36' E to 80°54' E longitude. The two major rivers in the state are Godavari and Krishna. The State has a limited area under irrigation, low natural fertility of soils, and large areas prone to recurrent drought. Due to this, Maharashtra's agricultural productivity is generally low compared to the national averages for various crops.

Maharashtra is also the second-most populous and second-highest forested area, with 20.13% of the total state area under forest cover. The recorded Forest Area in the State is 159,489 km^{2}, of which 128,324 km^2 are reserved forests, 17,438 km^2 are protected forests and 13,727 km^2 is unclassed forests. According to the Champion and Seth classification, Maharashtra has five types of forests:

- Southern Tropical Semi-Evergreen forests are found in the western ghats at 400–1000 meters elevation.
- Southern Tropical Moist Deciduous forests, a mix of Moist Teak bearing forests (Melghat) and Moist Mixed deciduous forests (Vidarbha and Thane district). Commercially important Teak, Delbergia, and bamboo are found in these forests.
- Littoral and Swamp forests are mainly found in the Creeks of Sindhudurg and Thane districts of the coastal Konkan region.
- Southern Tropical Dry Deciduous forests occupy a significant part of the State. The main species is Tectona grandis (Teak). These forests produce medium- and small-sized timber.

- Southern Tropical Thorn forests are found in the low-rainfall regions of Marathwada, Vidarbha, Khandesh, and Western Maharashtra.

Most of the Indian wolf population of the State is found in Southern tropical dry deciduous and thorn forests, majorly in Nashik, Aurangabad, Beed, Ahmednagar, Solapur, Pune, Satara, Sangli and Kolhapur Districts. They are also often sighted in Nagpur, Amravati and Chandrapur Districts.

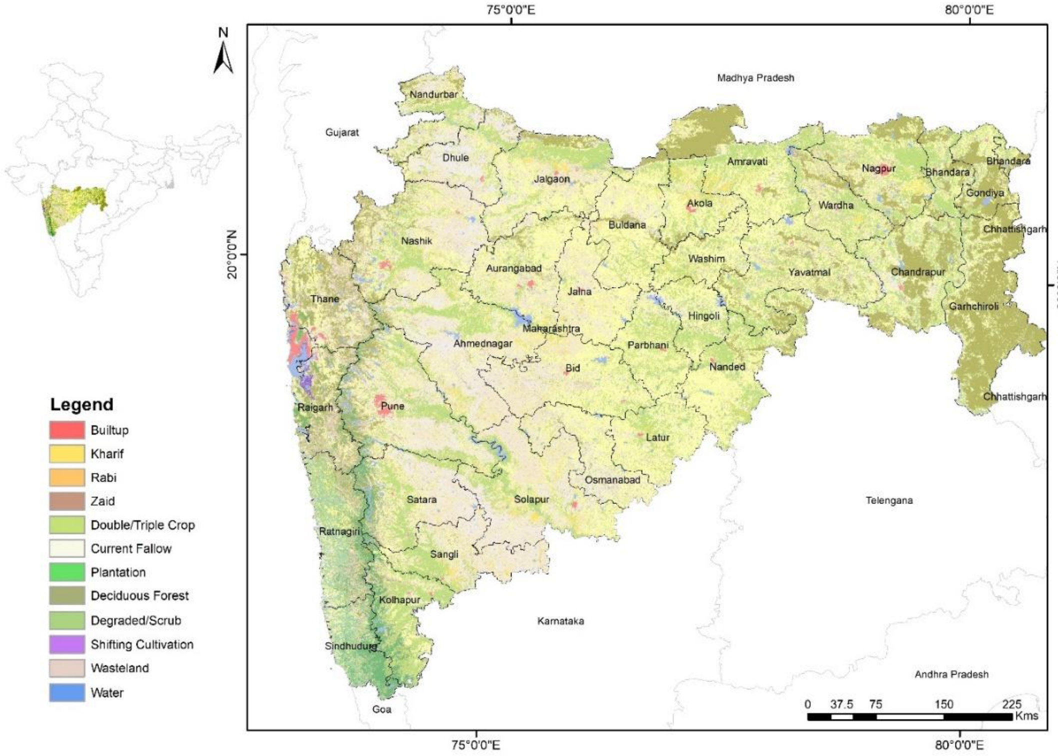

Figure 1.2: Land use land cover map of Maharashtra obtained from Bhuvan NRSC.

Climate

Maharashtra experiences a tropical monsoon climate with hot, rainy, and cold weather seasons and dry summers. The month of March marks the beginning of the summer, and the temperature rises steadily until June. Maharashtra is one of the warmest regions in India, with an average daily high temperature of 33^0 C. During the summer, the temperature rises from 40 °C to 49 °C. The rainfall patterns in the State vary by the topography of different regions. The southwest monsoon usually arrives in July and lasts till September. Maharashtra has many of the 99 Indian districts identified by the Indian Central Water Commission as drought-prone. The Eastern Vidarbha landscape receives good rainfall from July to September. The western districts of

Maharashtra receive heavy rains of an average of 2,000 to 2,500 mm. In contrast, the central and southern districts of Nashik, Pune, Ahmednagar, Dhule, Jalgaon, Satara, Sangli, Solapur, and Osmanabad receive an average of 500 mm annually. These low rain-fed areas are mainly the stronghold of the Indian wolf population.

Soil

The soil substrate in Maharashtra's Central and southern regions is comprised of half-decomposed basalt rock formations. The soil is derived from the igneous rock called basalt or black soil. The soil is low in organic carbon. Moreover, the soil expands in volume when moist and shrinks when dry, producing deep cracks. The infiltration rate is moderately slow. Crack development accelerates the process of soil moisture loss. Two major rivers, Krishna tributaries, Bhima and Sina, flow through this area.

Topography

The terrain in the Central and Southern Maharashtra region gently undulates with mild slopes and flat-topped hillocks with intermittent shallow valleys. These valleys have black cotton soils that are cultivated under the rain-fed regime. Grasslands are distributed in disjunct, fragmented patches, forming a mosaic of grazing, agricultural lands, and human settlements. Most of these grasslands are present on cultivable slopes and the top of hillocks. These grasslands are government-owned or private and mainly for the grazing of livestock.

Road Network

India has a network of over 6,215,797 km of roads and is the second-largest road network globally. Adjusted for its large population, India has approximately 1.90 km of roads per square km, much higher than China's 0.54 km of roads per square km (Ministry of Road Transport and Highways, 2021). In the last three decades, India's road network expanded drastically to connect major manufacturing, commercial, and cultural centres. According to the Ministry of Road Transport and Highways, as of March 2020, India had about 138,531 km of national highways and expressways, plus another 176,818 km of state highways. Moreover, in the upcoming years, the government of India has already planned for Bharatmala Priyojana to build 83,677 km of roads (Ministry of Road Transport and Highways, 2021). Out of the total states, Maharashtra ranked first in having the largest network of roads. It constitutes 20115.04

km of highways, 48842.21 km of primary roads and 96186.00 km of minor roads (Figure 1.3). The State of Maharashtra's National Highways was 6,249.2 km long before 2014. The length of the NH was extended to 17,749 km in 2018 (NIC 2018). Additionally, 4,687 km of in-principle NHs have been sanctioned by the Govt of India. In 4 years, form 2014 to 2018 the National Highway length increased by three times. This rapidly increasing road network poses a serious threat to local wildlife, especially the species that share their habitat with humans.

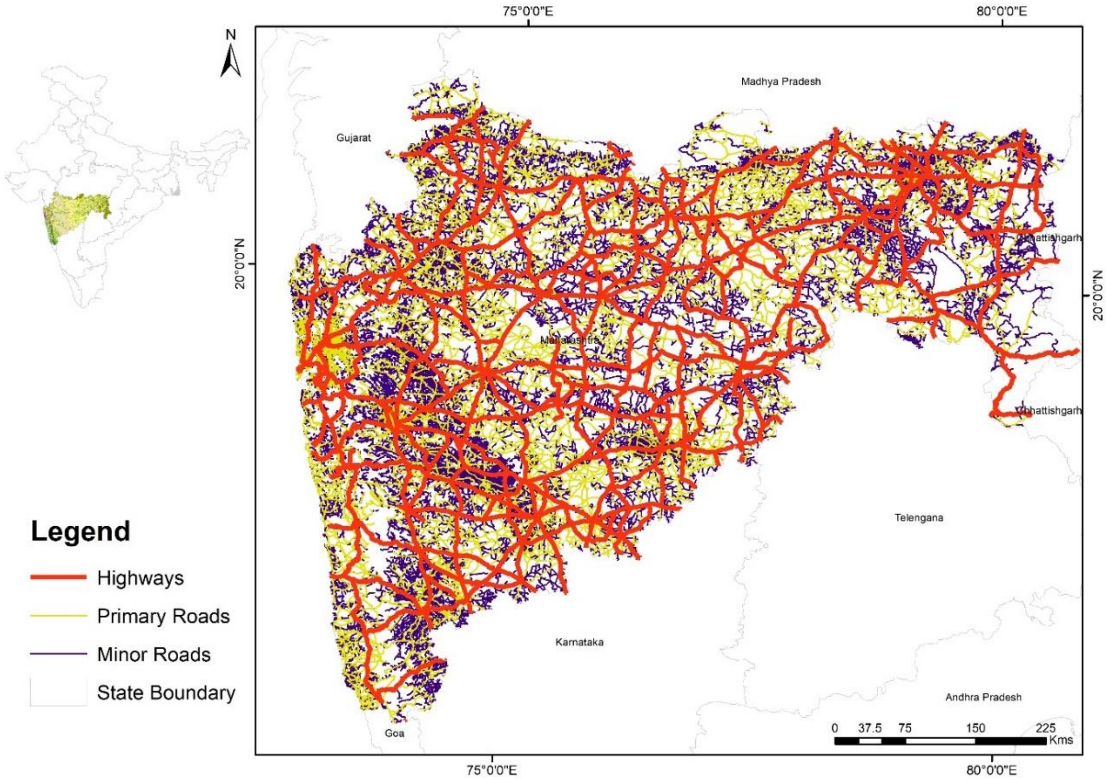

Figure 1.3: Map showing the highway, primary and minor road network of Maharashtra

Flora

The flora of wolf-bearing areas of Maharashtra is unique. Most of the plants in the wolf-bearing areas are classified as "monsoon ephemerals", as most depend on the rainwater. Alone Great Indian Bustard Sanctuary, spread across Solapur and Ahmednagar Districts, has a rich diversity of plants. The plant community was represented by 259 genera of 436 taxa (Janakiraman and Jalal, 2015). The common grasses are

Heteropogon contortus, Lophopogon tridentatus, Aristida funiculate, A. stocksii, Chysopogon fulvus, Melanocenchris jacquemontii, Oropetium thomaeum and *Sehima nervosum*. The *Acacia leucophloea, A. nilotoca, Cassia articulate, Tephrosia purpurea,* etc., were among the few shrubs and trees present in the landscape (Rahmani, 1989) with patchy plantation of *Gliricidia sepium* and *Azadirachta indica* by the forest department.

People

Since wolves share their habitat, it is critical to comprehend how people feel about the surrounding wolf population. The wolf was admired by ancient Indians for its ability as a predator and its commitment to the welfare of the pack, serving as a model of social behaviour for contemporary humans. For generations, wolves and people have coexisted together in this area. However, as people expanded in number, they needed additional space for farming and raising livestock. This expansion resulted in habitat degradation, ultimately affecting the wild prey population. The conflict between wolves and people arises due to the decline in the natural prey population as they shift their diet to livestock. On the opposite side, In the Indian states of Maharashtra, Karnataka, Goa, Madhya Pradesh, and Uttar Pradesh, there is a herding caste known as the Dhangar. In southern Maharashtra, Goa, and northern Karnataka, they are known as Gavli. According to the Dhangars, the wolf removes their diseased or weak animals, which helps to thin down the herd. Additionally, the loss is insignificant, which is only 5-7 sheep each year and is therefore tolerable for them. There is no confrontation, just coexistence, because the wolf keeps the livestock on their toes.

Chapter 2: Movement Ecology and Space Use

Chapter 2: Movement and Space Use

2.1 Introduction

Various events in animal life history are necessary for survival, and movement is one of the primary activities underlying many ecological systems (Nathan et al., 2008; Kays et al., 2015; Hays et al., 2016). Understanding animal movements provides a variety of information about a species and its natural history (Turchin, 1998), and research into such movements has recorded considerable progress. Large predators are often regarded as the most charismatic but also considered fragile components of their ecosystems worldwide (Miquelle et al., 2005). They shape the entire community at the top of the food chain and influence all trophic levels (Ripple et al., 2014). Large predators naturally occur at low densities due to their wide range of requirements (Woodroffe and Ginsberg, 1998). However, the ideal contiguous landscapes are essential for the long-term survival of such species that are increasingly threatened by human demands for space. Moreover, their presence in the area is frequently coinciding with livestock depredation. Such unique circumstances result in perceived or potential human-animal conflict, jeopardising ecological balance in the area.

The Wolf (*Canis lupus*) is a widely distributed species throughout the northern hemisphere (Mech 1970; Mech and Boitani 2003). Due to its wide distribution, it is one of the most studied species (Mech 1995). However, most wolf movement studies have been confined to European and New World countries (Merrill and Mech, 2000; Jedrzejewski et al., 2001; Whittington et al., 2004; Tsunoda et al., 2009; Carricondo-sanchez et al., 2020; Smith et al., 2022). Wolf movement behaviour is often determined by their requirements to search for prey and mark their territories (Mech 1970). As various management and conservation strategies may be developed based on how an animal moves across the landscape, it is vital to understand their movement. During breeding, wolves congregate near dens and rendezvous sites and restrict their movement. Usually, males travel away from these sites to search for food (Mech and Boitani 2003). In addition to the breeding male, the non-breeding members of the pack provide food to the nursing mother and pups (Harrington and Paquet 1982; Mech 1999). This alloparental care also affects the breeding pair movement. Wolf activity and movement have been found to vary depending on their social status in the pack (Ballard and Dau, 1983), age, and sex (Jedrzejewski et al., 2001; Schmidt et al., 2008), and dominance (Mech 1999). The other documented factors that affect wolf movement are prey density (Messier, 1985), prey migration (Walton et al., 2001), the activity of neighbouring packs (Mech and Harper, 2002), and human activity (Vilà et al., 1995; Ciucci et al., 1997; Theuerkauf et al., 2003a, 2003b, 2007; Kusak et al., 2005).

Recent studies have examined wolf avoidance of anthropogenic features in the landscape dependent on season and day or night (Carricondo-sanchez et al., 2020). Human infrastructure, such as roads and settlements, is a nearly universal disturbance in wolf movement studies (Zimmermann et al., 2014; Falco et al., 2019; Habib et al., 2021a). In Poland, Theuerkauf et al. (2003a, 2003b) noted that the spatiotemporal segregation of wolves and humans is an adaptation of wolves that promotes coexistence while allowing wolves to acquire food. Indeed, human-induced mortality was identified among the most critical variables in driving wolf activity patterns (Theuerkauf, 2009). Many studies concentrated on movement across wolf distribution. However, the movement ecology of the Indian wolf has not been studied despite being acknowledged as a distinct and important population (Hennelly et al., 2021b). A few VHF telemetry studies have been conducted in Gujarat, Rajasthan (Jhala and Giles, 1993), and Maharashtra (Habib, 2007). Only one study using GPS telemetry on the woolly Wolf (*C. l. chanco*) in India, a distinct subspecies of wolf found in the Himalayas (Habib et al., 2021b). However, two recently published studies broadly discussed the movement of Indian wolves using GPS telemetry (Habib et al., 2021a; Khan et al., 2022). Studying the Indian wolves' movement can provide crucial insights into their conservation.

Another critical question is how a wolf utilises space-use or home range in a landscape. A species' home range is the region where it can meet all its biological requirements. Seasonal feeding habitat, security, travel, denning, and birth and rearing of young ones are all critical life requirements. How these habitats are exploited and distributed affects home range size and local and regional population distributions. This understanding contributes to the development of a species-specific conservation management approach. Many studies have found that wolf packs have stable home ranges that are exclusive territories (Mech, 1970; Messier, 1985). Territorial behaviour is assumed to be a spacing mechanism that regulates wolf numbers to food availability. However, in other cases, home ranges are dynamic and nonexclusive. The causes of this instability are unknown, although they are most likely related to food supply.

Wolves, in general, seem to cognitively map their territories and localise their home ranges in locations where appropriate food is available and human disturbance is limited (Mladenoff et al., 1995). Wolves utilise areas within their home ranges to maximise prey encounters (Huggard, 1993). Topographic complexity influences the selection of home ranges and transit routes in mountainous environments (Paquet et al., 1996). The abundance of wintering ungulate prey and snow depth in these locations correspond to wolf utilisation of the valley bed and lower slopes (Paquet et al., 1996; Khan et al., 2022). According to Mech (1970) and Ballard et al. (1997), wolves living on the tundra and relying on migrating caribou range across a broader region than wolves residing in wooded areas and depending on resident prey.

Several approaches to describing the size of the home range have been developed (Worton, 1989; Erran Seaman and Powell, 1996), and several simulation studies have shown that some home range estimates represent the home range much better than the others (Worton, 1987; Nilsen et al., 2008). Borger et al. (2006) recently evaluated the performance of the kernel density estimates (KDE) and minimum convex polygon (MCP) in an empirical context and verified the findings of simulation studies; the KDE method performed significantly better than the MCP method. The MCP approach (Mohr, 1947, 1990) is the most widely used home range estimator in ecological research (Laver and Kelly, 2008). MCP defines an animal's home range as the smallest convex polygon that contains X% of locations from the original data set. Despite its limitations (Worton, 1987; Harris et al., 1990; Powell, 2000; Börger et al., 2006; Nilsen et al., 2008), particularly its inability to differentiate between areas of high and low use by the subject animal, MCP is still one of the most widely used methods of calculating home range (Powell, 2000).

On the other hand, Kernel estimators employ nonparametric statistics to assess the likelihood of locating an individual in a certain place (Worton, 1989). The Brownian Bridge Movement Model, BBMM (Bullard, 1999), evaluates the home ranges of all collared individuals. BBMM is nowadays a widely used method that estimates the path of an animal's movement probabilistically from data recorded at brief intervals. BBMM quantifies the utilization distribution of an animal-based on movement paths and accounts for temporal autocorrelation and high data volumes (Fischer et al., 2013). The model approximates the movement path between the two following locations by applying a conditional random walk. Although many home range estimators exist

(Horne et al., 2020), autocorrelated kernel density estimation (aKDE) was the first to explicitly account for temporal autocorrelation in the data (Fleming et al., 2015; Fleming and Calabrese, 2017). Whether explicitly stated or not, all home range estimators make an assumption about the underlying movement process. For most estimators in the literature, including all those described above, that assumption is simply that the data were sampled from an IID (independent and identically distributed) process. However, while all methods assume the movement process, only some explicitly separate the movement modelling and home range estimation steps. The aKDE is a generalization of the Gaussian reference function KDE that operates under the principle that autocorrelation structure in the data can first be estimated and then conditioned upon when optimising the bandwidth (Fleming et al., 2015).

In a country like India, where the human population is at its maximum, the wolf's habitat is under extreme pressure with changing land use patterns and urbanisation. It is crucial to keep track of various changes occurring in the wolf range and its capability of adaptation to save this species. It is vital to gain insights into their movement ecology and space use to ensure this distinct and important subspecies continued survival and recovery in the landscape. This study used GPS telemetry to understand how Indian wolves' daily movement varied between individuals, time of the day, sexes, and age class. I examined how wolves adapted to the human-dominated landscape by changing their movement speed to different land use classes and human disturbances. Also, I examined wolf space use using different approaches across sexes and age classes. This information can aid in developing effective conservation strategies and implementing measures to protect the species.

2.2 Methodology

Capturing and Collaring of Wolves

Seven adult wolves (three males and four females) and four subadult wolves (two males and two females) were captured using soft leghold traps from December 2017 to January 2021. Traps (n = 25) were set up in a circle, placed ~20 cm away from each other, and coyote and wolf gland lure No. 100 (Stanley Hawbaker and Sons, Fort London, Pennsylvania) were used to attract the wolves toward the traps. Fresh scats from different packs were also used and placed around the traps. The traps were connected to the based device "MinkPolice" product by Alert House ApS. This device operates with a magnetic switch triggered every time an animal steps on the traps and sends alert messages to registered email or phone numbers. Trapped wolves were held using a double-threaded nylon hockey net and immobilized using Ketamine–Xylazine by injecting intramuscularly on their hind leg (Habib, 2007) and fitted with GPS collars manufactured by Vectronic Aerospace, Germany. The collars registered and stored data, including date, time, location, and altitude. A total of ten wolves from seven different packs were fitted with GPS collars, and one male was fitted with a proximity collar (Table 2.1; Figure 2.1). The GPS collars were programmed for the different intervals between positions ranging from 0.5-5 hours per fix (median=1 hour), depending on the time of year and type of individual. I then scaled the data to 1 hour per fix for movement analysis.

All the individuals were captured following standard and approved protocols after due permission from the Ministry of Environment, Forests and Climate Change, Government of India, and Maharashtra Forest Department. The Wildlife Institute of India Animal Ethics Committee reviewed and approved all capturing and handling of the animal.

Understanding the movement ecology of Indian wolves

I calculated movement parameters such as displacement per hour daytime and nighttime displacement per hour with the help of trajectory details using the ArcMET path statistics tool in ArcGIS. Since the GPS fixes were collected as different intervals, varying interfix intervals across individuals were made uniformly by postprocessing all data into an hourly data format for analysis (Leblond et al., 2016; Abrahms et al., 2017). I considered the daily movement as the sum of linear distances obtained from each consecutive GPS fix from the first and last locations of the same day (i.e. from 00h to 24h). All movement parameters and analyses were carried out using adehabitatLT (Calenge, 2015b) and animal movement tool (Signer et al., 2019) in program R 4.0.3 (R Core Team, 2022) and ArcMET tool of ArcGIS 10.6 (Wall, 2014). Each individual's daily movements were compared during seasons, age, and sex of the individual.

Effect of variables on the movement speed

I also assessed the effect of biological, habitat, and human-induced parameters on wolves' movement speed (displacement per hour) in the landscape. I measured 13 biological (age, sex, season, breeding, non-breeding phase, and time of the day), habitat (agriculture, plantation, scrub, grassland, water, and NDVI), and human-induced parameter (human footprint) at the starting point of each step length of all the collared wolves to understand the effect of these on movement speed. The landuse landcover data were extracted from Bhuvan NRSC data. The normalized difference vegetation index (NDVI) data was used to evaluate the effect of vegetation cover on movement speed. NDVI datasets were obtained from Google Earth Engine™ (GEE) between 2017 and 2021 at a spatial and temporal resolution of 30 m and 32 days, respectively (Gorelick et al., 2017). The day and nighttime movements were also evaluated across individuals by classifying locations based on the time of the day using the animal movement tool (amt). The human footprint data was extracted from the raster layer developed by Venter et al., 2018. To model the human footprint, Venter et al., 2018 used data on human pressures and included: 1) the extent of built environments, 2) population density, 3) electric infrastructure, 4) croplands, 5) pasture lands, 6) roads, 7) railways, and 8) navigable waterways. The tool "extract values to raster" was used to extract values in ArcGIS 10.6.

I used Generalised Linear Models (GLMs, McCullagh and Nelder, 1989) to obtain a mathematical description of movement speed with various parameters. GLMs allow for appropriate error formulations from the exponential family distributions, avoiding restrictions of traditional regression models. The error and link functions depend on the nature of the data. The six candidate models were then fitted to the movement speeds with negative binomial GLM with log link, and the best model was chosen based on the lowest like-likelihood value (Tables 2.2 and 2.3). I used the lme4 package in program R 4.1.0 to perform GLM (R Core Team, 2022), and plots were created using GGplot and SjPlot packages in R 4.1.0 (R Development Core Team 2023, Vienna, Austria).

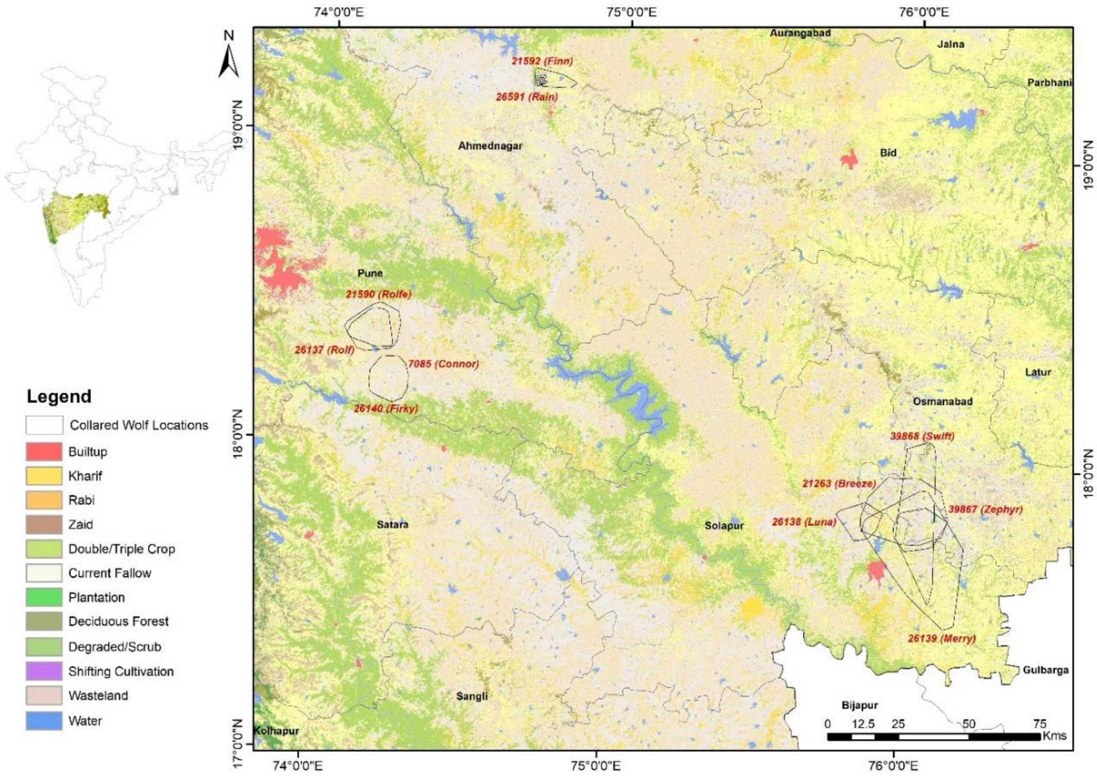

Figure 2.1: Map Showing the collar wolves' locations collared from three Districts (Ahmednagar, Pune, and Solapur) of Maharashtra. Each polygon depicts an individual wolf range in the landscape.

Table 2.1: Details of collared wolves with the tracking period, collar type and capture location in Maharashtra (AF: Adult Female; AM: Adult Male; SAF; Subadult Female; SAM: Subadult Male).

Collar ID/Name	Sex/ Age	Tracking period used in the analysis	Collar type	Area
26139/Merry	AF	25.12.17-21.09.19	GPS, Activity	Gangewadi, Solapur
21263/Breeze	AM	29.12.17-01.08.18	GPS, Activity	Gangewadi, Solapur
26140/Firky	AF	22.12.17-17.09.19	GPS, Activity	Morgaon, Pune
7085/Connor	AM	22.12.17-17.09.19	Proximity, VHF	Morgaon, Pune
21592/Finn	SAM	22.06.19-15.11.19	GPS, Activity	Ahmednagar
21591/Rain	SAF	24.06.19-14.08.20	GPS, Activity	Ahmednagar
21590/Rolfe	SAF	26.06.19-29.06.20	GPS, Activity	Saswad, Pune
26137/Rolf	SAM	27.06.19-11.11.19	GPS, Activity	Saswad, Pune
26138/Luna	AF	05.12.20-23.12.21	GPS, Activity, Dropoff	Nannaj, Solapur
39867/Zephyr	AM	03.01.21-21.01.22	GPS, Activity, Dropoff	Gangewadi, Solapur
39868/Swift	SAF	03.01.21-26.03.21	GPS, Activity, Dropoff	Gangewadi, Solapur

Understanding space use of Indian wolves

In this chapter, I represented frequently used home range estimators such as Minimum convex polygon (MCP), Kernel density estimators (KDE), Autocorrelated Kernel Density Estimators (aKDE), and Brownian bridge movement model (BBMM) to understand the Indian wolf space use. The following estimators include the most commonly used home range estimators in the ecological literature (Horne et al., 2007; Laver and Kelly, 2008; Kie et al., 2010).

Home range areas were estimated using the MCP and KDE implemented in the R package adehabitatHR (Calenge et al., 2005), aKDE through the R package ctmm (Calabrese et al., 2016) and BBMM using R package BBMM (Nielson et al., 2012). 95% contour was considered the overall home range, and 50% contour was the core area of the animal home range (Fischer et al., 2013). All GPS locations collected from Dec 2017 – Feb 2021 were analyzed to understand the home-range pattern of wolves in the human-dominated landscape.

Habitat Preferences and Use by Indian Wolves

The land use data for the states of Maharashtra was acquired from Bhuvan's open-source website (NRSA, 2016) and was used to understand the habitat preferences of Indian wolves. Habitat use and preference of the Indian wolf were analyzed using Manly's resource selection function (Manly et al., 2002). The design-III study framework of habitat use, where the animals are identified individually, and the use and availability were measured for each individual (Thomas and Taylor, 1990). The data on "use" was calculated from the number of GPS fixes, and the "availability" of land-use categories was calculated within the 100% MCP home range. All the measurements of MCP and analyses were carried out using the package adehabitatHR (Calenge et al., 2005) and "adehabitatHS" version 0.3.15 (Calenge, 2015a) in program R 4.0.3 (R Core Team, 2021).

2.3 Results

Movement Ecology of Indian Wolves

The estimated average daily movement of Indian wolves was 10357.64± 6629.02 SD m/day (Table 2.2). The highest daily movement was found for ID 38687 (14332.54 ±7044.68 SD m/day), followed by ID 21263 (13308.89 ± 8233.58), and the lowest was found for ID 21592 (6081.254± 5014.05), and the difference between the individual was found be significant (F= 42.43; p>0.001) (Figure 2.2a). The daily average movements of males were higher (12113.9 ± SD7513.68 m/d, n = 4) than those of females (9718.4 ± SD6154.66) m/d, n= 6), and the difference was found to be significantly different (F= 86.33; p>0.001) (Figure 2.2b). The average daily movement of adults (10957.23 ± SD6999.91) was higher than that of subadults (9236.8 ± SD5709.60), and the difference was found to be significant (F= 51.14; p>0.001) (Figure 2.2c). In the summer season, the wolf's daily movement was found to be highest (11875.19 ± SD6923.31 m/d), followed by pre-monsoon (10425.51 ± SD7065.23 m/d) and monsoon (9951.58 ± SD6166.71 m/d) and lowest in the winter season (9020.12 ± SD6276.32 m/d) (Figure 2.2d). However, a Tukey posthoc test showed that the difference between the summer and monsoon, pre-monsoon, post-monsoon, and winter was significantly different, and the difference between monsoon, post-monsoon, and winter and post-monsoon were not significantly different. The highest daily movement was found for adult males (13956.71 ± SD7500.48 m/d) followed by adult females (9800.04 ± SD6435.64 m/d) and lowest for subadult males (8211.88 ± SD5876.94 m/d) (Figure 2.2e). However, a Tukey posthoc test showed that the difference between all the age classes was significantly different except for the subadult female and male (p=0.83). During the collaring period, two females (26138 and 26140) were breeding and delivering pups. Hence, I calculated the difference between the daily movement in the breeding and non-breeding period and found that female daily movement was lower in the breeding season (9410.83 ± SD6512.21 m/d) than in the non-breeding season (10653.87 ± SD6638.75 m/d), and the results were found to be significantly different (F= 46.07; p>0.001) (Figure 2.2f).

Table 2.2: The overall, daytime and nighttime movement per hour and daily movement of collared wolves in Maharashtra, along with the details of the number of tracking days and location acquired, were provided. Collar ID with asterisks (*) denotes the subadult individuals.

Collar ID	Daily Displacement (meters)	Daytime displacement per hour (meters)	Nighttime displacement per hour (meters)	Displacement per Hour (meters)	Number of Tracking days	Number of Locations
21263 Breeze	13308.9	500.88	979.34	727.42	217	2112
26139 Merry	10729.2	609.11	665.72	637.99	615	7585
26140 Firky	8607.67	483.63	627.45	549.76	604	8320
26138 Luna	10069.89	476.58	413.47	445.77	383	9048
39867 Zephyr	14332.54	714.06	514.86	615.53	383	5863
21592 Finn*	6081.25	254.69	312.12	282.29	141	3229
21591 Rain*	7962.66	252.06	529.68	385.96	416	3070
26137 Rolf*	10482.46	304.2	640.18	467.81	371	8722
21590 Rolfe*	11227.16	294.9	789.22	533.88	137	6677
39868 Swift*	10301.43	281.96	665.7	473.62	82	1854
Overall Mean	**10310.32**	**417.21**	**613.77**	**512.81**		
Adult Mean	**11409.64**	**556.85**	**640.17**	**595.29**		
Subadult Mean	**9210.99**	**277.562**	**587.38**	**428.71**		

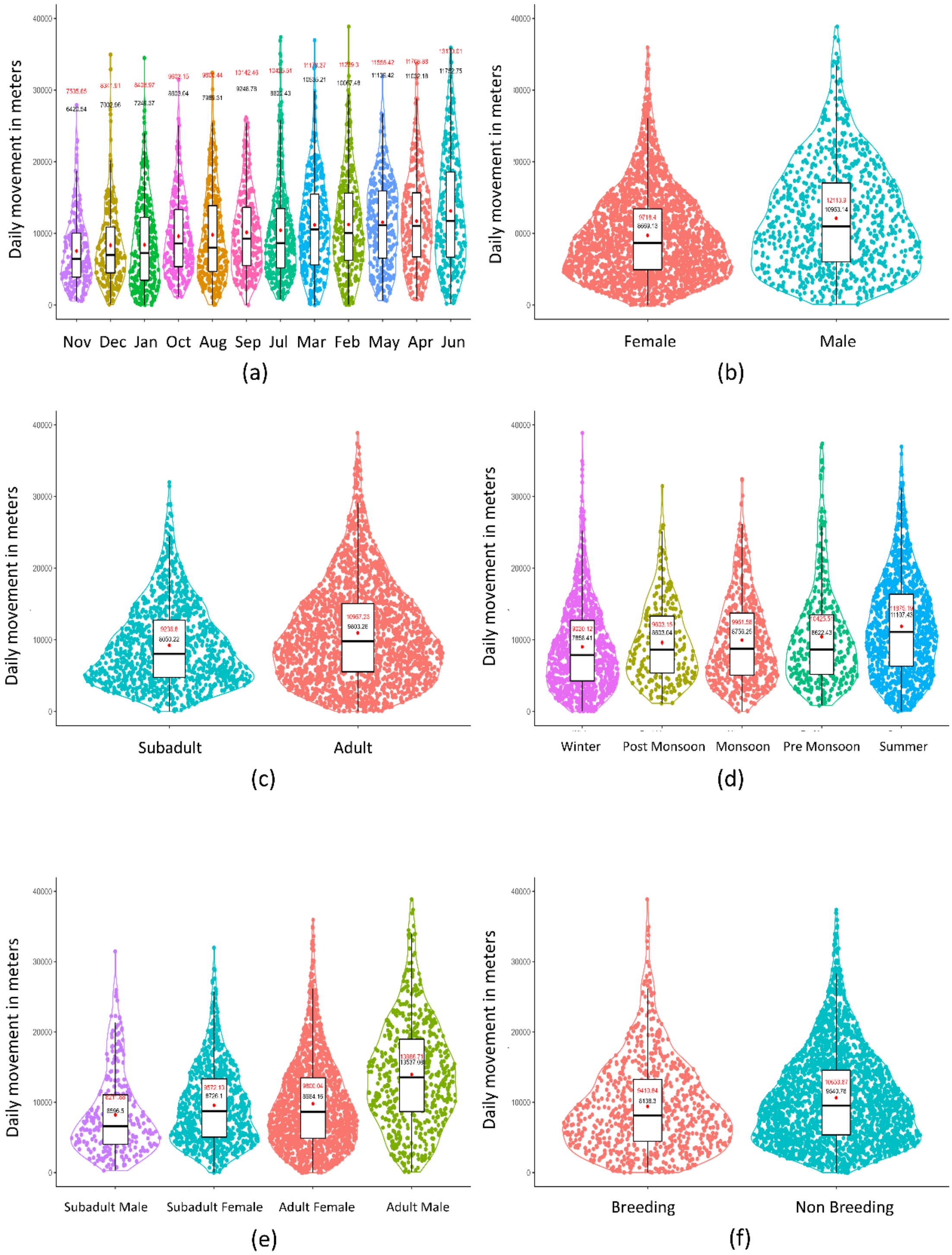

Figure 2.2: Violin plots showing the estimated daily movement (a) of collared individual Indian wolves (b) of male and female (c) of adult and subadult (d) in different seasons (e) of different ages and classes (f) of breeding females (ID 26140 and ID 26138) in the state of Maharashtra, India. Values on the box plot denote the median in black and the mean in red. Each dot inside the violin plot represents the daily displacement.

Effect of biological, habitat, and anthropogenic parameters on the movement of wolves

The movement speed on different biological, habitat, and anthropogenic parameters was best predicted in model 5 with the lowest logLik value (-364607.8) and AICc value (729251.7) (Table 2.3).

The season, age, sex, and time of day significantly impact wolf movement speed. The movement speed was significantly lower in winter (β=-0.26 ± SE0.03; p>0.001). Their movement speed decreased significantly in grassland (β=-0.43 ± SE0.09; p>0.001), and scrub forest (β=-0.34 ± SE0.08; p>0.001) and increased in agricultural lands (β=0.12 ± SE0.06; p=0.08) but the results were not found to be significant. Anthropogenic factors also influence wolf movement in the landscape. Wolves travel faster (β=0.03 ± SE0.003; p>0.001) in areas with a high human footprint. In summer season wolf moves faster during nighttime (β=0.41 ± SE0.03; p>0.001) as compared to the winter (β=0.16 ± SE0.03; p>0.001). Wolf movement speed decreases in agricultural areas during nighttime (β=-0.26 ± SE0.1; p>0.01), and the movement increases in high human footprint areas (β=0.04 ± SE0.003; p>0.001) (Figure 2.3).

Table 2.3: Log-likelihood (LogLik), number of parameters (K), Akaike's Information Criterion value (AIC), change in AIC value (ΔAIC), and Akaike's weight (***ωi***) of models for movement speed of Indian wolves, Maharashtra, India.

Model Description	LogLik	K	AIC	AICc	ΔAIC	*ωi*
Null Model Intercept only	-366041.0	2	732085.9	732085.9	2818.26	0
Biological Parameters **Model 1: Sex + Age + Time of the day (TOD) + Season + Breeding + Non-Breeding Period**	-365501.5	8	731019.0	730950.8	1751.31	0
Habitat Feature **Model 2: Agriculture + Plantation + Scrub + Water + Grassland + NDVI**	-365395.1	8	730806.1	730806.1	1538.45	0
Anthropogenic parameters **Model 3: Human Footprint**	-365799.2	3	731604.4	731604.4	2336.75	0
Biological, Habitat and Anthropogenic parameters **Model 4: Sex + Age + Season + Time of the day + Season + Breeding + Non-Breeding Period + Scrub + Grassland + NDVI + Human Footprint**	-364736.8	12	729497.5	729345.4	229.84	0
With interaction between variables **Model 5: Age + Scrub + NDVI + TOD*Grassland + TOD*Human Footprinnt + TOD*Agriculture + TOD*Sex + TOD*Season**	-364617.8	16	729252.0	72967.7	0.00	1

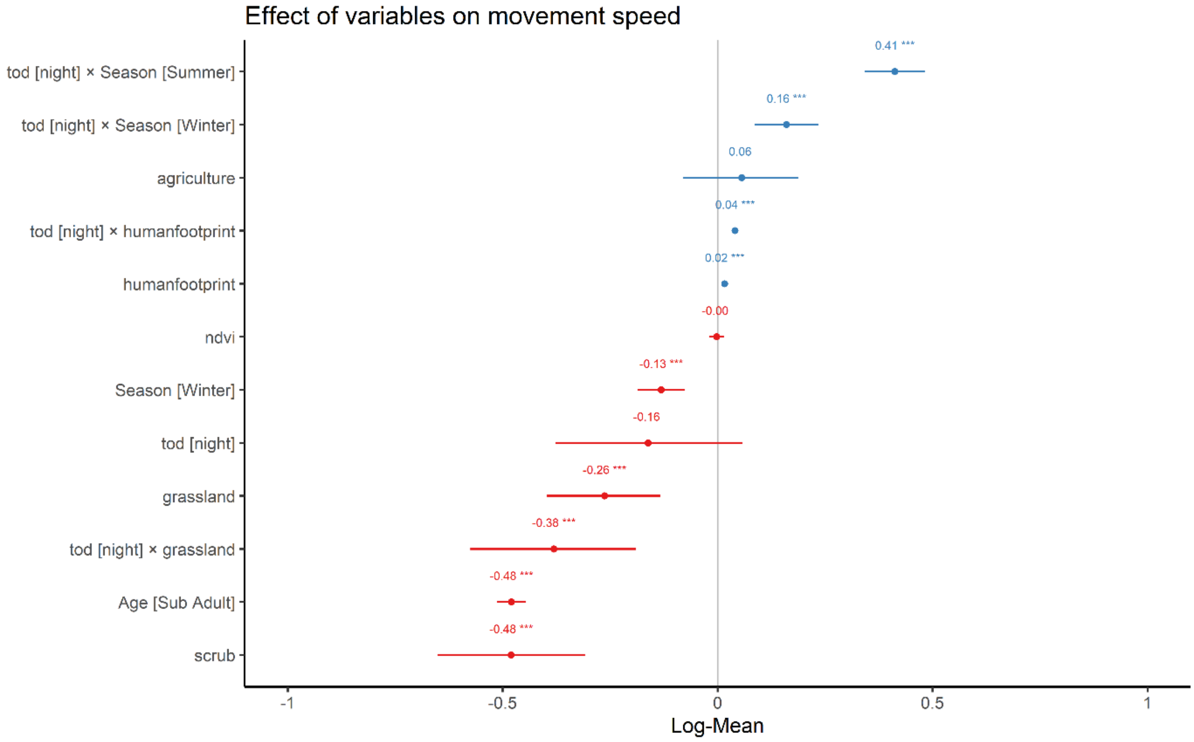

Figure 2.3: Scaled coefficients with a significance level of variables from generalized linear model estimates for the movement speed of Indian wolves. The horizontal bars represent the 95% confidence interval for each variable.

Home-range estimation

Using different home range estimators, I calculated the average home range (95% contour) and core areas (50% contour) of the five adult wolves and five subadults from eight different packs. The different estimators showed different home ranges and core area sizes across individuals. The home range for adult individuals was found to be 378.7, 285.4, 317.8 and 230.9 km^2 using MCP, KDE, aKDE and BBMM, respectively. The home range for subadult individuals was found to be 71.9, 79.6, 56.7 km^2 and 37.1 km^2 using MCP, KDE, aKDE and BBMM, respectively. The core area for adult individuals was found to be 13.7, 29.1, 47.7 and 24.2 km^2 using MCP, KDE, aKDE and BBMM, respectively. The core areas for subadult individuals were found to be 9.9, 4.9, 22.2 km2, and 3.0 km2 using MCP, KDE, aKDE, and BBMM, respectively (Table 2.4).

Table 2.4: The home ranges and core area sizes of ten GPS-collared wolves in Maharashtra

Individual wolf (sex)/ Area	50% MCP (km^2)	50% KDE (km^2)	50% aKDE (km^2)	50% BBMM (km^2)	95% MCP (km^2)	95% KDE (km^2)	95% aKDE (km^2)	95% BBMM (km^2)
Breeze (M)/ Gangewadi	99.0	73.9	109.2	31.6	519.7	557.3	614.4	399.6
Merry (F)/ Sangdari	51.05	46.5	97.3	19.0	981.5	579.7	686.7	325.9
Firky (F)/ Morgaon	3.07	3.7	5.4	54.4	110.6	89.7	90.5	284.1
Luna (F)/ Nannaj	3.04	2.3	3.7	3.1	69.3	52.0	46.2	38.8
Zephyr (M)/ Gangewadi	43.35	19.2	22.8	12.7	212.4	148.3	151.1	106.3
Swift (F)*/ Gangewadi	5.97	4.7	5.7	2.5	19.6	22.6	23.4	14.5
Finn (M)*/ Ahmed nagar	0.53	1.9	0.8	0.6	4.9	4.8	5.9	4.7
Rain (F)*/ Ahmed nagar	0.71	0.2	1.2	1.7	13.2	6.9	12.5	14.4
Rolfe (F)*/ Saswad	4.05	12.1	15.8	7.2	180.5	138.9	140.8	97.7
Rolf (M)*/ Saswad	3.46	5.5	87.7	3.1	141.5	93.6	101.1	54.4
Overall Average	**21.4**	**17.0**	**35.0**	**13.6**	**225.3**	**169.4**	**187.2**	**134.0**
Adult Average	**13.7**	**29.1**	**47.7**	**24.2**	**378.7**	**285.4**	**317.8**	**230.9**
Subadult* Average	**9.9**	**4.9**	**22.2**	**3.0**	**71.9**	**53.4**	**56.7**	**37.1**

Habitat Preferences and Use

Resource selection function revealed a preferential selection for land use categories by the Indian wolf (Khi2L = 659.46, df = 41, $p < 0.001$). The Indian wolf preferred grassland areas (Wi = 3.49 ± 0.5SE) followed by scrub forest (Wi = 2.42 ± 1.61SE) and plantations (Wi = 2.04 ± 1.39SE). Agriculture, built-up, and waterbody were used less in proportion to their availability (Figure 2.4). When I split the data into adult and subadult wolves, Plantation (Wi = 3.89 ± 2.37SE) was the most preferred land use class, followed by grasslands (Wi = 3.11 ± 0.48SE) by adult wolves (Figure 2.5), whereas for subadult wolves' grasslands (Wi = 3.90 ± 0.99SE) were the most preferred class followed by scrub forest (Wi = 1.65 ± 2.08SE) (Figure 2.6).

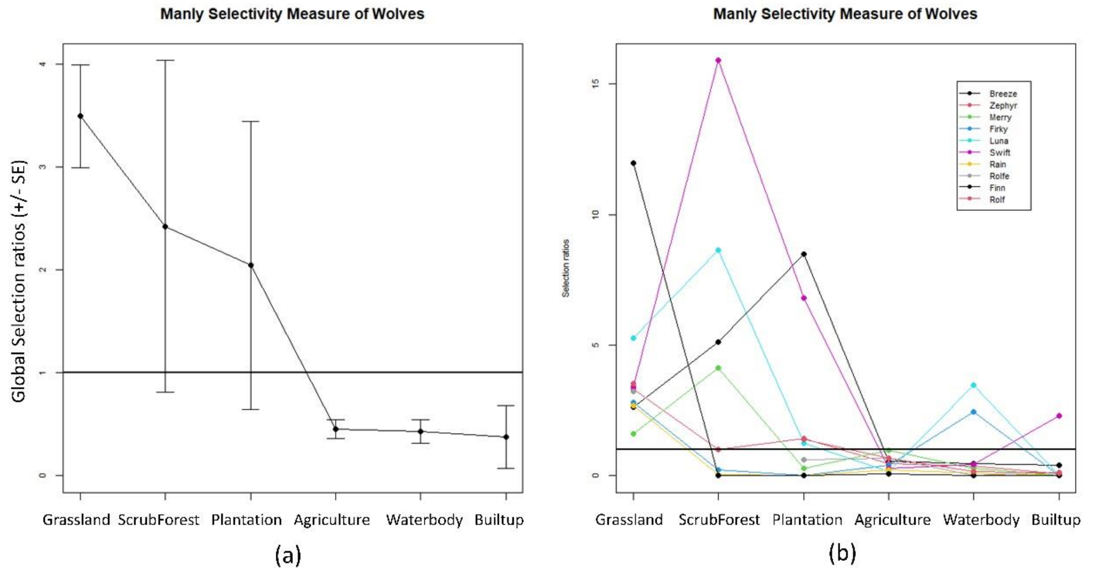

Figure 2.4: Land use proportion in relation to availability vs. used based on Manly's test for Indian wolf (a) overall and (b) individual-wise habitat selection.

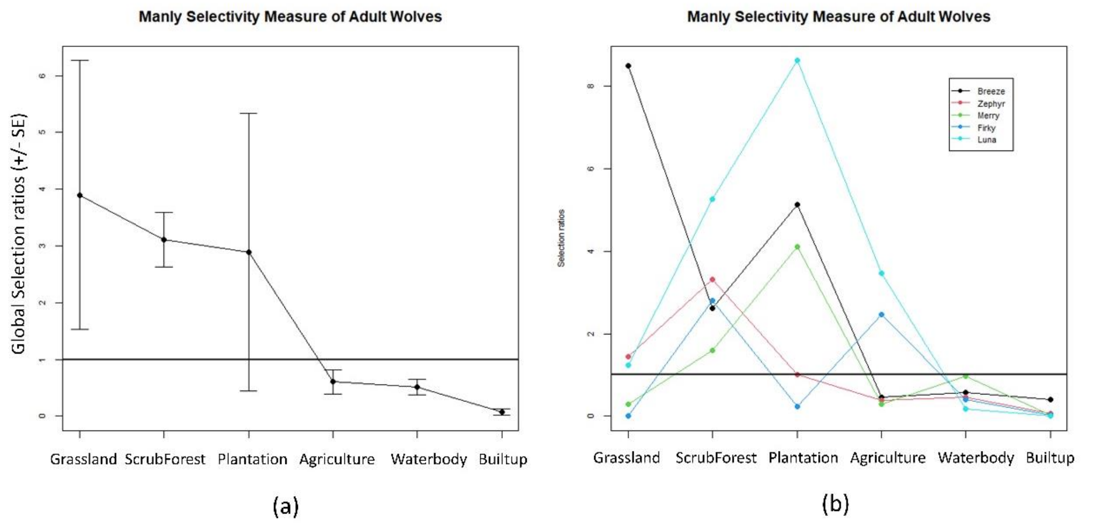

Figure 2.5: Land use proportion in relation to availability vs. used based on Manly's test for adult Indian wolf (a) overall and (b) individual-wise habitat selection.

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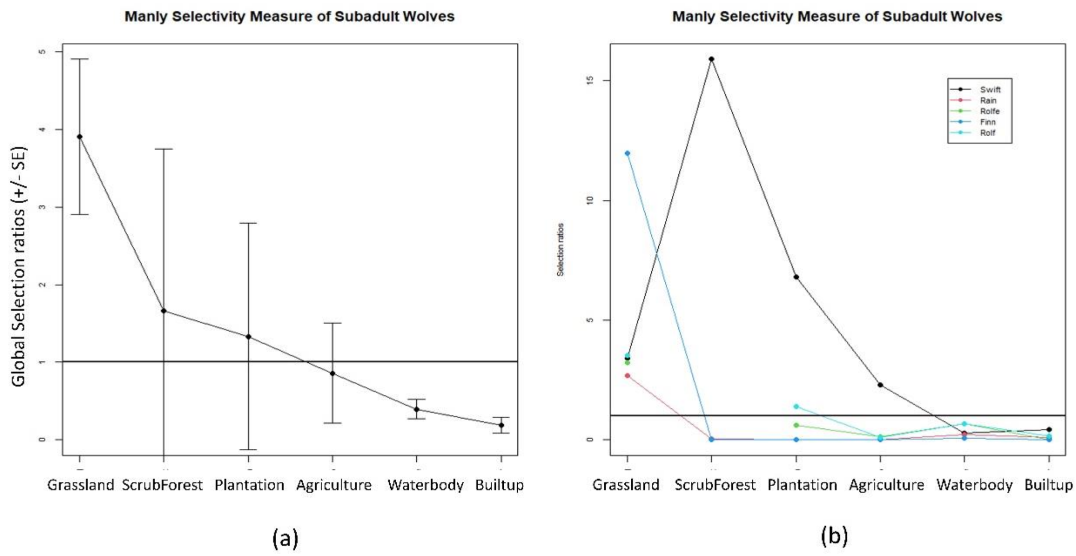


Figure 2.6: Land use proportion in relation to availability vs used based on Manly's test for subadult Indian wolf (a) overall and (b) individual-wise habitat selection.

2.4 Discussion

In this study, I found the average daily movement of Indian wolves was 10357 ± SD6629 m/d, and the individuals showed a high variation in their daily movements, ranging from 6081 m/d to 14332 m/d. The variation observed in the movement is due to the variable age and sex of the collared wolves. Depending on prey density and vulnerability, wolves can travel up to 80000 m/d (Mech et al., 2016). Under different ecological conditions in North America, with high ungulate density, wolves move between 1600 and 9000 m/d (Kolenosky and Johnston, 1967). Wolf movements in the temperate lowland forest of Poland, with a rich population of ungulates, were estimated at 4400 m/d (Jędrzejewski et al., 2002). In areas where wolves rely primarily on human food subsidies and do not need to traverse large areas, such as Dalmatia or central Italy, distances are considerably shorter (3300 m/day) (Ciucci et al., 1997). The observed average daily movement of wolves in different studies varied greatly, ranging from 3300 to 80000 m/d (Ciucci et al., 1997; Mech et al., 2016). The interval between two consecutive fixes is crucial in calculating daily movement, and a small fix interval is subjected to provide accurate movement (Merrill and Mech, 2003; Reshamwala et al., 2022). In our study, the GPS fix interval varied from 1-5 hours per fix (median=1 hour) as small GPS fix intervals require more battery consumption and shorten the collar life. The shorter GPS fix interval may change the observed daily movement, as suggested by other studies (Wysong et al., 2020; Reshamwala et al., 2022). Studies with larger samples are needed to improve our understanding of wolves' maximum daily movement.

The male wolves showed 19.17% higher movement than the females. I believe the differences in movement behaviour between males and females were influenced by their different roles in the pack and the biparental care of pups. The adult individuals' movements (male and female) were 15.7% higher than those of the subadult that remained with the natal pack even after a year. Indian wolf packs were mainly comprised of alpha pair and their offspring. Most offspring disperse within a year, but few remain with the natal pack to help rear the new litter. While alpha pairs go out hunting, these previous years' siblings take care of young pups and occasionally take part in hunting, too. So, their movement is mainly confined near the rendezvous sites. These factors could be why there is less movement of subadult individuals than adults.

This study confirms the hypothesis of decreased female movement during the denning season for reproductive females (Alfredéen, 2006). Mostly, females nurture the pups and keep the den clean and dry (Packard et al., 2003). Our study found that female movement decreased by 36.94% during the breeding season compared to the non-breeding season. The study conducted by Aberdeen reported a decrease in the movement by reproducing females as high as 200% (Aberdeen 2006). However, the decline in movement in our study was small compared to Aberdeen's 2006 study. The pack size in Indian wolves is small, and to provide food to pups, females also need to contribute to the hunt. This might be why females also contributed to hunting while rearing pups, showing a smaller difference in breeding and non-breeding seasons than previously reported movement differences. In India, the denning season begins in December; during this month, days are slightly warmer, and the nights are cooler (the average temperature in winter is 24^0 C) in our study sites. The female occasionally left the den, mainly during the day, suggesting that she stayed with the pups to keep them warm during the cooler period and to guard den sites against threats such as dogs. Breeding males, on the other hand, visit the den site less frequently than adult females (Harrington and Paquet, 1982; Kusak, 1991; Potvin et al., 2004) but contribute by feeding the female (Mech, 1999) and therefore spend most of their time hunting away from the den (Harrington and Paquet, 1982; Kusak, 1991). Many other studies also reported the same that adult females with pups were less active during the denning season (Kusak, 1991; Vilà et al., 1995; Theuerkauf et al., 2003b; Schmidt et al., 2008; Tsunoda et al., 2009).

Indian wolves showed seasonal variation in their movement, which was higher in summer, followed by pre-monsoon, and lowest in winter. The winter coincides with the denning season, and a nomadic community known as the "Dhangar" visits this landscape yearly to use grasslands for livestock grazing and spends a month or two in these areas. The arrival of the Dhangar community in wolf-bearing areas allows the wolves to feed on them. Hence, they restrict their movement to a particular place. Also, winter coincides with the breeding season of the Indian wolf. However, food is scarce in the summer, with less water in the landscape. To fulfil their daily requirements, wolves tend to move more. Also, wolf attacks on livestock are more common during the summer (Kusak, 2002). These might be caused by increased food demand for growing pups and the scarce availability of livestock on open pastures throughout the summer or due to food scarcity. Wolves had to wander from retreat areas, where they spent days, to areas closer to humans, where they sought food. Moreover, water is also scarce in the summer, so wolves tend to move more to obtain it.

Wolves are generalist species and utilize all available landscape features (Mladenoff et al., 1995; Gurarie et al., 2011). However, their movement speed was governed by various biological, habitat, and anthropogenic factors. The movement speed decreases in grassland and scrub forests and increases in agricultural lands (Figure 2.7a-c). Wolves also increase their movement in areas with a high human footprint (Figure 2.7d). As I hypothesized, the time of the day is critical in affecting wolf movement in the landscape, as humans were very active during the daytime. Wolves must segregate themselves temporally to avoid human interactions. However, in our study, the wolves showed no difference in the daytime (444.35 m/h) and nighttime (535.0 m/h) movement speed when I compared the overall movement of all seasons. The overall results aligned with Droghini and Boutin's 2018 study, which found no difference in day and nighttime movement speed. However, the time of the day influences movement based on sex, age, and season. The male individual's movement was significantly higher at night (Figure 2.8a), and no difference in female daytime and nighttime movement. The observed disparity in movement speed between male wolves during daytime and nighttime, but not in females, suggests potential sex-specific behaviours. Males may exhibit nocturnal activities related to hunting, territorial defence, and reproductive strategies. However, I found a small difference in male-female daytime and nighttime movement speed while seeking differences between adult and subadult individuals (Figure 2.8b). Our result showed that Indian wolves' movement speeds were significantly higher at night during summer (Figure 2.8c). This may be due to the study area's high daytime temperature, which reaches 50^0 C. In hot climates, wolves may be more active at night to avoid heat stress during the day. Additionally, prey species may be more active in cooler nighttime temperatures, prompting wolves to adjust their hunting schedules. Understanding sex-specific ecological roles and behaviours is vital for interpreting these patterns, highlighting the nuanced dynamics within wolf populations during different times of day.

Moreover, the human and livestock frequency increases at waterbodies during the daytime during summer. So, wolves tend to move more at night for their daily activity, hunting, and waterbody use. High daytime temperatures explain higher wolf movement at night during summer versus daytime. Previous studies identified the same pattern in different regions around the globe. During the summer, wolves were active at night in Alaska (Ballard et al., 1991). Dalmatian wolves also travel and hunt for food, mostly at night in summer (Kusak et al., 2005). Nocturnal wolf activity enhanced movement by allowing the wolves to traverse and visit sites extensively utilised by humans. Theuerkauf et al. 2003 showed that wolves in Białowieza were active throughout the day, with peaks at dusk and dawn related to wolf hunting activity. Wolves have demonstrated a remarkable ability to adapt to human-dominated landscapes. They can become accustomed to human activity, noise, and structures. Some individuals may even learn to navigate high human footprint areas. I have found that wolf movement usually utilises high human footprint areas at night with increased movement speed (Figure 2.8d).

The size, shape, and spatial distribution of wolf home ranges and core areas are also crucial for conservation and management activities. This study gives an idea about the home ranges and their core areas of ten individuals from seven packs based on data collected from Dec 2017 to Feb 2021 using the GPS collars. The home range of adult wolves was found to be 378.7 km^2 using 95% MCP and 230.9 km^2 using 95% BBMM, whereas the core area size of adult wolves was found to be 13.7 km^2 (95% MCP) and 24.2 km^2 (95% BBMM). The home range of subadult wolves was found to be 71.9 km^2 using 95% MCP and 37.1 km^2 using 95% BBMM, whereas the core area size of subadult wolves was found to be 9.9 km^2 (95% MCP) and 3.0 km^2 (95% BBMM). The size of a pack's home range varies considerably between individuals and different areas. Territory and home range sizes are closely related to pack size, prey density, and human disturbances (Peterson et al., 1984; Messier 1985). Indian wolves exhibit varied home range sizes across different areas, and this may be due to ecological factors and prey availability. Areas with abundant prey might support smaller home ranges as wolves have ample resources (Peterson et al., 1984). Conversely, in areas with sparse prey, wolves may need larger territories to meet their dietary requirements. Habitat type and human activities also influence home range sizes. The differences in home ranges highlight the adaptability of Indian wolves to diverse environments, emphasising the intricate interplay between ecological factors, prey dynamics, and anthropogenic influences in shaping their spatial requirements. Territories tend to be smaller in summer when packs are tied to the home sites (den and rendezvous sites) (Mech 1977a). This contrasts with my study, as Indian wolves' breeding season is in winter, and they tend to use more areas in summer to overcome food scarcity and avail water in the landscape. In Algonquin Park, where the principal prey is deer, territories ranged from 104 to 311 km^2 (Pimlott et al., 1969). In the mountain zone, home ranges in the Rocky Mountains range from 1058 to 3374 km^2 (Paquet 1993) and in the Yukon from 583 to 794 km^2 (Hayes et al., 1991). In the Arctic region, home ranges on Ellesmere Island were >2500 km^2 (Mech 1987, 1988). Winter-territory size in Minnesota averaged 78–153 km^2 (Fuller 1989). However, different methods have been used to estimate home ranges for all the above-mentioned studies. Still, we can get a general idea about the home range sizes of different subspecies of wolves.

The MCP method provides a general indication of range use based on the GPS movement data. MCPs for long-ranging animals such as wolves must be viewed cautiously. Given their ability to travel considerable distances, their MCP may appear quite large when, upon further analysis, they utilize a significantly smaller portion of their range during critical seasons. As I found in this study for the home range of Merry/ID26139, the 95% MCP was 981.5 km^2, 95% aKDE was 686.7 $km^{2,}$ and 95% BBMM was found to be 325.9 km^2. Here, I presented a home range of wolves based on various estimators, the MCP, KDE, AKDE, and BBMM methods to understand the wolves' home range and core area and conclude that recently developed estimators like aKDE and BBMM provide better estimates of home ranges that can be used for wolves' conservation and devising management plan.

The choice between the BBMM and the aKDE for home range estimation depends on several factors, including the characteristics of the data, research objectives, and personal preferences. The BBMM is based on the concept of Brownian motion, assuming that an animal's movement follows a random walk pattern. It estimates the animal's home range by constructing a continuous utilization distribution surface that considers the temporal order of the animal's locations. BBMM considers the autocorrelation between consecutive locations and provides a more realistic representation of animal movement. It can be particularly useful for studying fine-scale movement patterns and habitat selection. The aKDE is a density estimation method incorporating autocorrelation to estimate the animal's home range. Considering the autocorrelation structure between points, a smooth probability surface is created based on the observed locations (Calabrese et al., 2016). In summary, BBMM and aKDE offer different approaches to home range estimation. BBMM considers the temporal order of locations and assumes a Brownian motion model (Horne et al., 2007), while aKDE focuses on spatial autocorrelation to create a smooth probability surface (Fleming et al., 2015).

The wolves preferred the grasslands and used the grassland patches more than their availability (Pocock, 1941; Mech, 1970). Avoidance of waterbodies by the Indian wolf could be better explained by the association of water presence with the proximity of humans in the peninsular Indian landscape. The Indian wolves strongly avoided human-influenced areas such as agriculture and built-up. Paquet et al. (1996) found that mountain wolves had few options to avoid humans due to the selection of valley habitats that humans often use. The Indian wolf also faces higher human pressure because of the plains' higher population density (Habib, 2007).

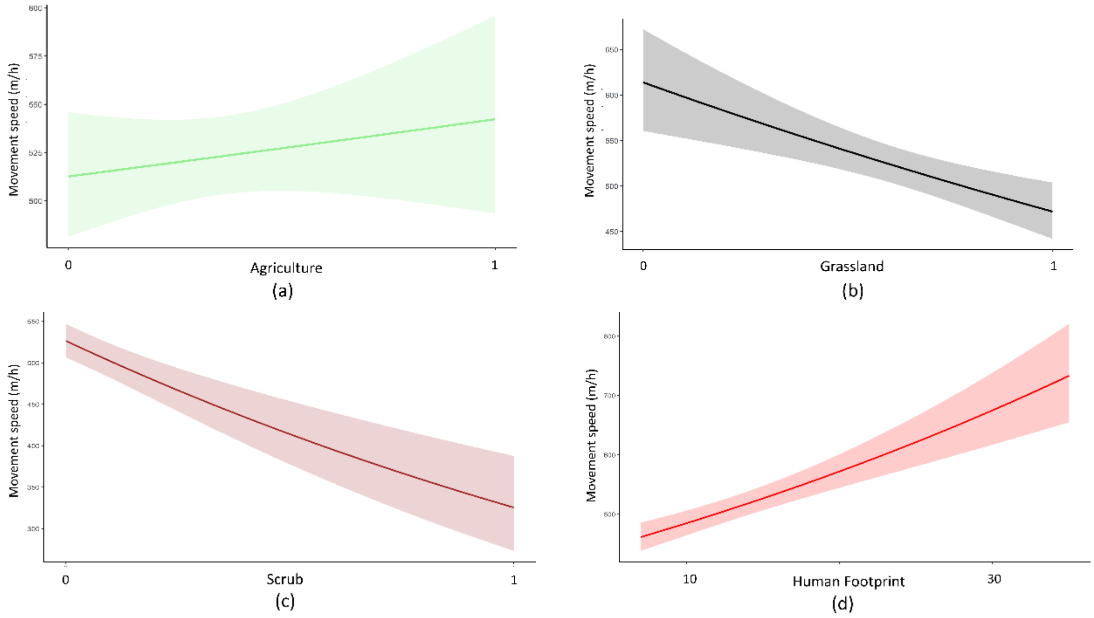


Figure 2.7: The effect plot of various habitat types and the human footprint on wolf movement speed: (a) effect of the presence of agricultural areas, (b) grassland, (c) Scrub forest, and (d) human footprint

Although studies have emphasised population uniqueness and suggested that these wolves are the most basal, studies on Indian wolf ecology across their distribution range are limited. This chapter aimed to understand the wolf movement ecology and space use as it provides various information about ecosystem functioning and various landscape-level management can be drawn by understanding movement. Our results reveal how the Indian wolf's movement differs based on age, sex, and other biological parameters. This is the first study presenting the fine-scale movement behaviour of Indian wolves. Here, I understand how Indian wolves adjust fine-scale movement behaviours temporally to exploit available habitats and to reduce their risk of encountering human disturbance, which helps to explain wolves' continued survival in the Anthropocene's shared landscapes.

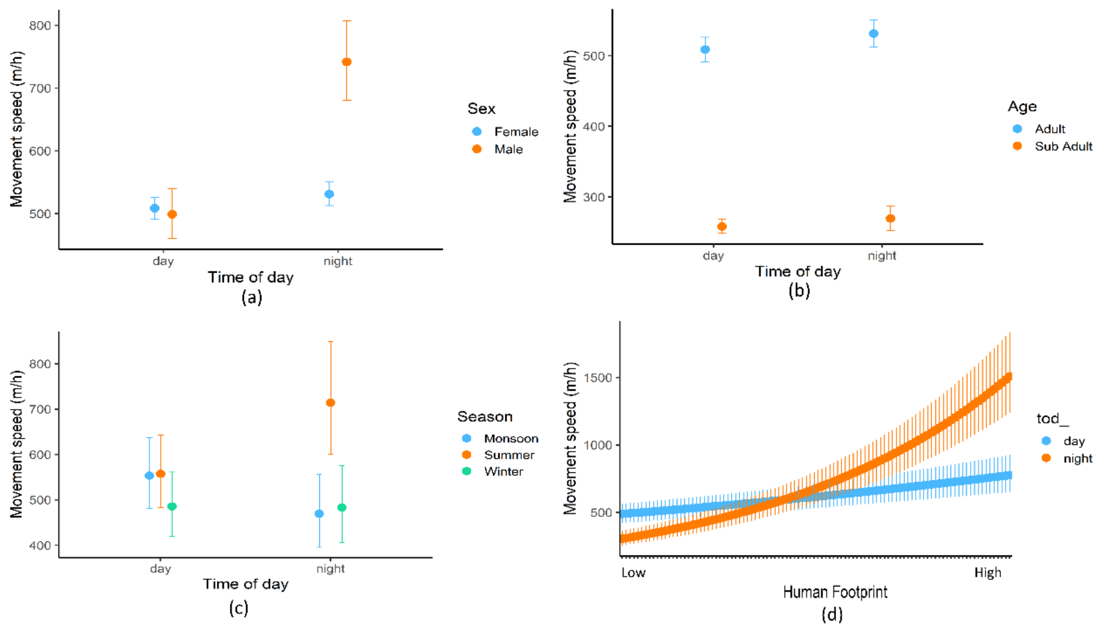


Figure 2.8: Effect of time of the day on various biological and human footprints on the movement speed of wolves: (a) effect on male and female, (b) on adult and subadults, (c) seasons, and (d) human footprint.

Chapter 3: Den and Rendezvous Site Selection

Chapter 3: Den and Rendezvous Site Selection

3.1 Introduction

Large carnivores, naturally occurring in low numbers due to energy constraints, have a significantly greater impact on the community structure through resource facilitation and trophic cascades (Fortin et al., 2005; Ripple et al., 2014). Most large carnivores are endangered worldwide because of habitat degradation and fragmentation, poaching, the illegal trade of their body parts, decreased prey, and conflict with humans (Karanth and Chellam, 2009). The viability of large carnivore populations in landscapes that are progressively dominated by human activities is essentially linked to their dependence on conservation initiatives. (Weber and Rabinowitz, 1996; Linnell et al., 2001), Identifying key breeding areas is necessary (Kenney et al., 2014). For the prolonged survival of large carnivores in these landscapes, conservation strategies should prioritise protecting key breeding areas.

The Indian wolf *Canis lupus pallipes* is found in various habitats across human-dominated areas. They are social animals and use dens and rendezvous sites for rearing pups. They often interact with humans since they are found primarily in a human-dominated landscape. Wolves survive with humans because of their ability to exploit human-modified landscapes (Habib, 2007). However, they also prey upon livestock, allowing the potential for conflict, especially with the shepherd community. A persistent problem is the incidence and impact of human interference on wolf dens and rendezvous sites (Iliopoulos et al., 2014). Reducing disturbance is difficult for wildlife management across the wolf's distribution range (Chapman, 1977; Darimont and Paquet, 2002), particularly in a country with a high population density like India (Habib and Kumar, 2007).

Although wolves are a generalist species that move over large areas and can survive in many different environments, tolerating various levels of human disturbance (Mech and Boitani, 2003; Sillero-Zubiri, Hoffmann, and Macdonald, 2004), they are conscientious at den and rendezvous site selection. The site selection for denning and rendezvous sites is crucial for survival. Their reproduction and denning behaviour have been studied extensively outside of India (Mech, 1970; Ballard and Dau, 1983; Fuller, 1989; Ciucci and Mech, 1992; Heard and Williams, 1992; Matteson, 1992; Unger, 1999). However, given the extensive land use change in India, it is crucial to frequently study denning and rendezvous site selection behaviour. Wolves only use dens when young pups cannot travel with the pack (Boitani, 2000; Fuller et al., 2003).

Wolf dens are usually located near water and dug into well-drained soil or between rock splits. They can be dug under a boulder, among tree roots, or in cut banks, hollow logs, or other sturdy natural structures. Wolves often enlarge existing fox or porcupine dens. The den and rendezvous sites are comparatively small areas where reproductive activities occur. Pups are born, fed, raised, and protected in the den sites and a series of rendezvous sites. These site selection and activity around the den can have an impact on the pack's ability to reproduce because the majority of pup deaths occur during the first six months (Harrington and Mech, 1982), and movements away from these sites are limited during the first six weeks after birth (Fuller et al., 2003; Mills et al., 2008).

Many studies identified resource availability as the main factor determining wolf reproductive success (Fuller, 1989; Fuller et al., 2003), while others showed wolf human-caused mortality as an essential inhibitor of wolf reproduction and population recovery (Liberg et al., 2012). Homesite selection by wolf packs can be closely related to both these factors. It can directly influence access to food resources by reproductive wolf packs (Frame et al., 2008) and disturbance to nurturing adults and pups from humans (Habib and Kumar, 2007; Argue et al., 2008; Nonaka, 2011).

Anthropogenic and habitat characteristics associated with den and rendezvous sites have not been well documented for Indian wolves. However, wolf dens and rendezvous sites were well explored in other subspecies of wolves (Joslin, 1967; Unger, 1999; Theuerkauf et al., 2003a). Unger (1999) found wolves in Wisconsin and Minnesota, USA, selected wetland habitats for rendezvous sites and hypothesized this was because young pups cannot travel far and require ample water to process a diet high in protein. Unger (1999) also hypothesized that dense grasses in wet meadows decreased the detection of pups by intruders. Conceivably, wolves could also select wet meadows because they provide abundant small mammal and insect prey for pups.

Conservation of wolf populations is dependent on informed management of wolf habitat. I hypothesized that wolves in India would follow the same pattern as other wolf subspecies. The goals of the present study were to 1) provide a general description of habitat type, substratum, number of openings, distance from the nearest human settlement, and topographic features and identify important factors associated with the den and rendezvous site selection. The increasing omnipresence of humans and their associated disturbances within animal niches makes this research of broad significance. The information produced in this study will help devise a better management plan for the survival of the Indian wolves in human-dominated landscapes.

3.2 Materials and Methods

Field data collection for den and rendezvous sites

Known and probable den and rendezvous sites through local and Maharashtra Forest Department locations and from GPS locations of collared individuals were located and confirmed by scanning the site for wolf pugmarks and scats. The habitat feature, manmade linear infrastructure, and human-induced parameters associated with den and rendezvous sites were collected in the breeding season (November to February) from 2016 to 2021. Probable den sites were integrated into the study only after confirming recent use by wolves.

The data was collected after ensuring that wolves were not present, or often after waiting until wolves were vacating the den sites, to minimise our influence on wolf den sites. Since wolves often use the same dens in subsequent years (Ballard and Dau, 1983; Mech and Packard, 1990), I took precautions not to modify the den and collected the data without disturbing the site. I collected data at 32 dens (4 in Ahmednagar, 1 in Gondia, 10 in Pune, and 17 in Solapur Districts, Maharashtra, India) and 25 rendezvous sites (4 in Ahmednagar, 1 Gondia, 2 Nagpur, 5 Pune, and 13 Solapur Districts, Maharashtra, India (Figure 3.1). I also collected data from 25 rendezvous sites. The rendezvous sites were identified after sighting wolves with pups older than eight months at least three times. As a single pack can use the same rendezvous site for several years (Capitani et al., 2006), to avoid overestimating the important characteristics, I did not collect the data if the site is within 800 meters from any of our previously recorded rendezvous sites.

I measured 16 habitat and anthropogenic variables (listed below) at den and rendezvous sites and 60 contrast random locations (Figure 3.1) within the 95% MCP of all the collared wolves. This is referred to as third-order selection by Johnson (1980). In contrast to presence-absence models, I designed a use versus availability method with the advantage of not presuming that individuals never use certain places (Boyce et al., 2002; Pearce and Boyce, 2006). This method assumes that the observed occurrences represent a sample of the locations that may contain information on animal preferences (Manly et al., 2002). Moreover, while generating the contrast random locations, the points that fall on water bodies, human settlements, and roads were excluded from the analysis.

Data were recorded for the den and rendezvous site for habitat type (Agriculture, Grassland, Plantation, and Scrub), terrain type (Flat, slope, steep and undulating), where terrain type were considered relatively. Flat terrain was considered the surface with 0^0 to 5^0 relief, slope terrain where the areas the dens were made slope more than 5^0 to 30^0, steep terrain were the area with more than 30^0 to 90^0 relief, and undulating terrain where the dens were made on mostly flat land with some gentle upsurge. The vegetation cover was also recorded in a 50 m radius circular plot centred on the den opening and rendezvous site. The vegetation cover was recorded through ocular estimation (Matteson, 1992). Distance from the nearest water source, cart road (dirt road used by locals and livestock), metal road (nearest tar road used for vehicular movement), and escape cover were recorded using Google Earth. The den substratum was classified into three categories: bund, rock crevices, and manmade structure, and the total number of den openings was also counted at each den site. The above variables were selected based on their ecological importance and previous studies conducted on other subspecies of wolves for denning and rendezvous site selection (Kusak, 1992; Trapp et al., 2008; Benson et al., 2015).

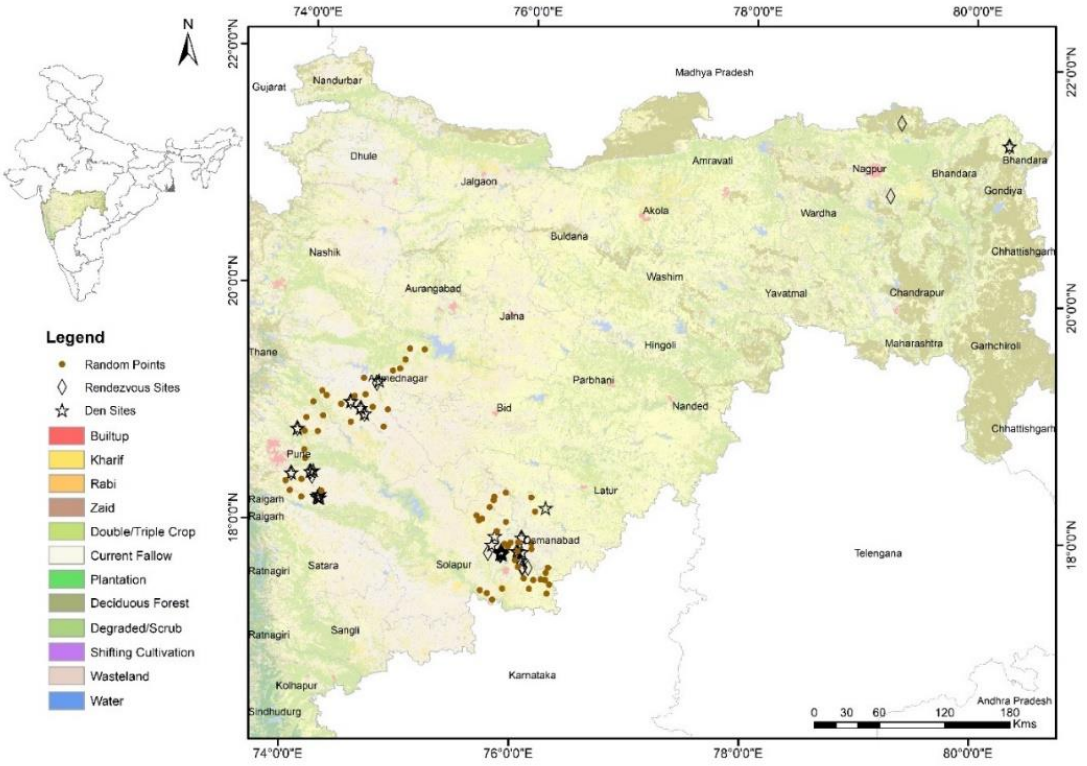


Figure 3.1: Study area showing den (star symbol), rendezvous sites (diamond symbol), and contrast random locations (solid dots) points on LULC datasets in Maharashtra. The LULC data were obtained from Bhuvan's NRSA LULC. Inset: Location of the study area in India.

Data extracted using GIS for each den and rendezvous site

The distance from the primary road, human population density, and human footprint were extracted using extract values to the point tool in ArcGIS 10.6. The primary road was assessed using open-source OpenStreet Map (OSM) 2016 data. OSM road type shapefile was used to prepare Euclidean distance from the primary road. The human population density 2020 map (Stevens et al., 2015) and human footprint 2009 (Venter et al., 2018) and the tool extract values to raster were used to extract values in ArcGIS 10.6.

Data Analysis

I first used a correlation test to check for the correlation between the used variables. Prior to building the candidate models, I did a Pearson correlation test between the 16 variables and eliminated highly correlated variables (>0.7). Thus, I finalized 11 variables for the final analyses and removed human population density and three topographic features (flat, steep, and undulating parameters) from the analyses as they were correlated with the other variables (Figure 3.2). I used Generalised Linear Models (GLMs, McCullagh and Nelder, 1989) to obtain a mathematical description of site selection by wolves in an attempt to avoid the covariance of explanatory variables. GLMs allow for appropriate error formulations from the exponential family distributions, avoiding restrictions of traditional regression models. The error and link functions depend on the nature of the data. A logit link function was used since the den and rendezvous sites (a binary response variable: 1=presence, 0=absence) followed a binomial distribution (McCullagh and Nelder, 1989). The seven postulated candidate models were then fit to the den and rendezvous sites using GLM with probit link, and the best model was selected based on the lowest like-likelihood value (Tables 2 and 3).

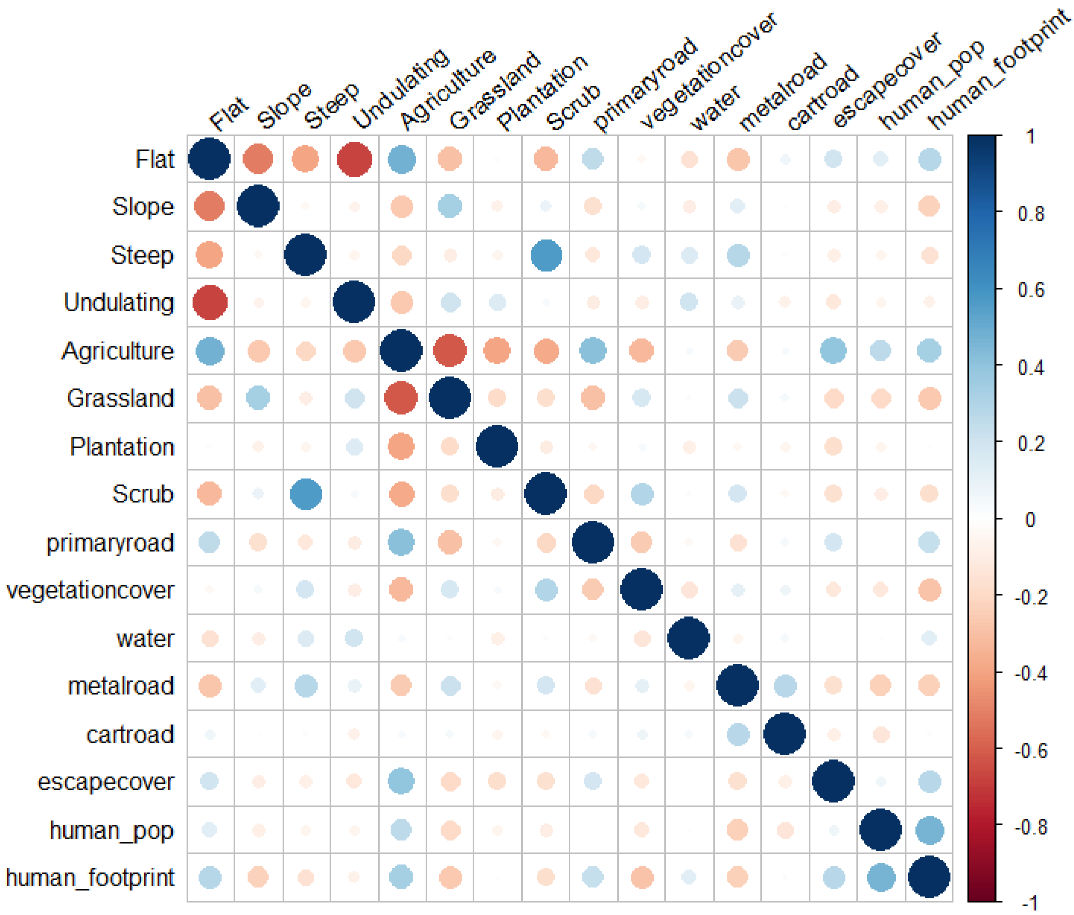


Figure 3.2: Correlation plot between the 16 variables and the positive and negative values of more than 0.7 were eliminated from the candidate models. The drop variables were flat, steep, undulating terrain types, agricultural lands and human footprints were removed.

All statistical analyses were performed using the R statistical software V. 4.1.0 (R Development Core Team 2023, Vienna, Austria), GLM were fitted using the MuMIn package, and plots were created using GGplot and SjPlot packages in R 4.1.0 (R Development Core Team 2023, Vienna, Austria).

3.3 Results

Den site characteristics and habitat selection

Out of 32 dens evaluated, the maximum dens were found in grassland (46.87% of total dens), followed by scrubland (21.87%), plantation (18.75%), and the lowest number of dens in agriculture (12.5%) (Figure 3.3a). I also assessed the substratum on which dens were formed and found that maximum dens (75%) were in bunds (a mound used primarily in India to separate two agricultural lands or embankments to prevent water flow between the fields), followed by rock crevices (15.62%) and manmade structure (9.37%) such as pipelines to help wolves to make dens in protected areas (Figure 3.3b). Of the total dens evaluated, 23 were found with single openings, seven with two openings, and one with three and four openings (Figure 3.3c). I also calculated the nearest human settlement and water source from the den site and found that the maximum dens (13 dens) were 1000-2000 meters away from any human settlement, followed by eight dens at 500-1000 meters (Figure 3.3d). The maximum number of dens (n=18) were found within the 100 meter radius to the nearest water source, followed by eight dens between 100–200 meter radius (Figure 3.3e).

The presence of the den sites was best predicted in model 6 with the lowest logLik value (-18.90) and AICc value (51.79) (Table 3.1). The den sites were positively associated with the presence of water (β=-4.55 ± SE1.66; p=0.006), vegetation cover (β=1.97 ± SE0.74; p=0.008), plantation (β=1.52 ± SE0.47; p= 0.001), presence of grassland (β=1.41 ± SE0.49; p=0.004), and scrub forest (β=1.09 ± SE0.46; p=0.02). The human footprint was negatively associated with the den sites (β=-0.88 ±SE0.46; p=0.054) (Table 3.2, Figure 3.4).

Table 3.1: Log-likelihood (LogLik), number of parameters (K), Akaike's Information Criterion value (AIC), change in AIC value (ΔAIC), and Akaike's weight (***ωi***) of models for den site selection of Indian wolves, Maharashtra, India.

Model Description	**LogLik**	**K**	**AIC**	**AICc**	**ΔAIC**	*ωi*
Null Model **Intercept only**	-59.44	1	120.88	120.92	64.79	0.000
Habitat Feature **Model 1: Slope + Grassland + Plantation + Scrub + Vegetation Cover**	-28.09	6	68.18	69.17	16.03	0.000
Distance to Water and Escape Cover Model 2: Dist to Water + Dist to Escape Cover	39.98	3	85.96	86.23	33.10	0.000
Linear Infrastructure **Model 3: Cart Road + Metal Road + Primary Road**	-55.66	4	119.33	119.79	66.66	0.000
Anthropogenic parameters **Model 4: Human Footprint**	-51.52	2	107.04	107.18	54.04	0.000
Habitat features, Linear Infrastructure and Distance to Water and Escape Cover **Model 5: Grassland + Plantation + Scrub + Dist to Escape Cover + Vegetation Cover + Dist to Water + Primary Road**	-19.46	8	54.93	56.66	3.53	0.146
Habitat, Distance to Water and Escape Cover and Anthropogenic parameters **Model 6: Grassland + Plantation + Scrub + Vegetation Cover + Dist to Water + Human Footprint**	-18.90	7	51.79	53.13	0.00	0.854

Table 3.2: Generalised Logistic Regression model predicting Indian wolf den sites vs. contrast sites in Maharashtra. Model 6 was selected based on the lowest Log-likelihood, and AICc values were selected to summarise the results. The beta coefficients of the variable used for all the models and the standard errors, z value, p values, and VIF (Variance Inflated Factor) value are provided. The VIF value measures the amount of multicollinearity in a set of variables. The VIF value equal to 1 represents no correlation: values between 1 and 5 represent moderate correlation, and values greater than 5 represent a high correlation between the variables.

	β estimates (±SE)	**p-value**	**z value**	**VIF**
(Intercept)	-2.101 (±0.63)	0.001	-3.297	
Grassland	1.416 (±0.49)	0.004	2.868	1.558
Plantation	1.527 (±0.47)	0.001	3.230	2.072
Scrub	1.090 (±0.46)	0.020	2.323	1.166
Vegetation Cover	1.979 (±0.74)	0.008	2.671	1.722
Water*	-4.551 (±1.66)	0.006	-2.736	1.174
Human Footprint	-0.888 (±0.46)	0.054	-1.928	1.086

*the water variable data was calculated as the distance from the den location. So here, the negative value of the estimate represents the association of the den site with water.

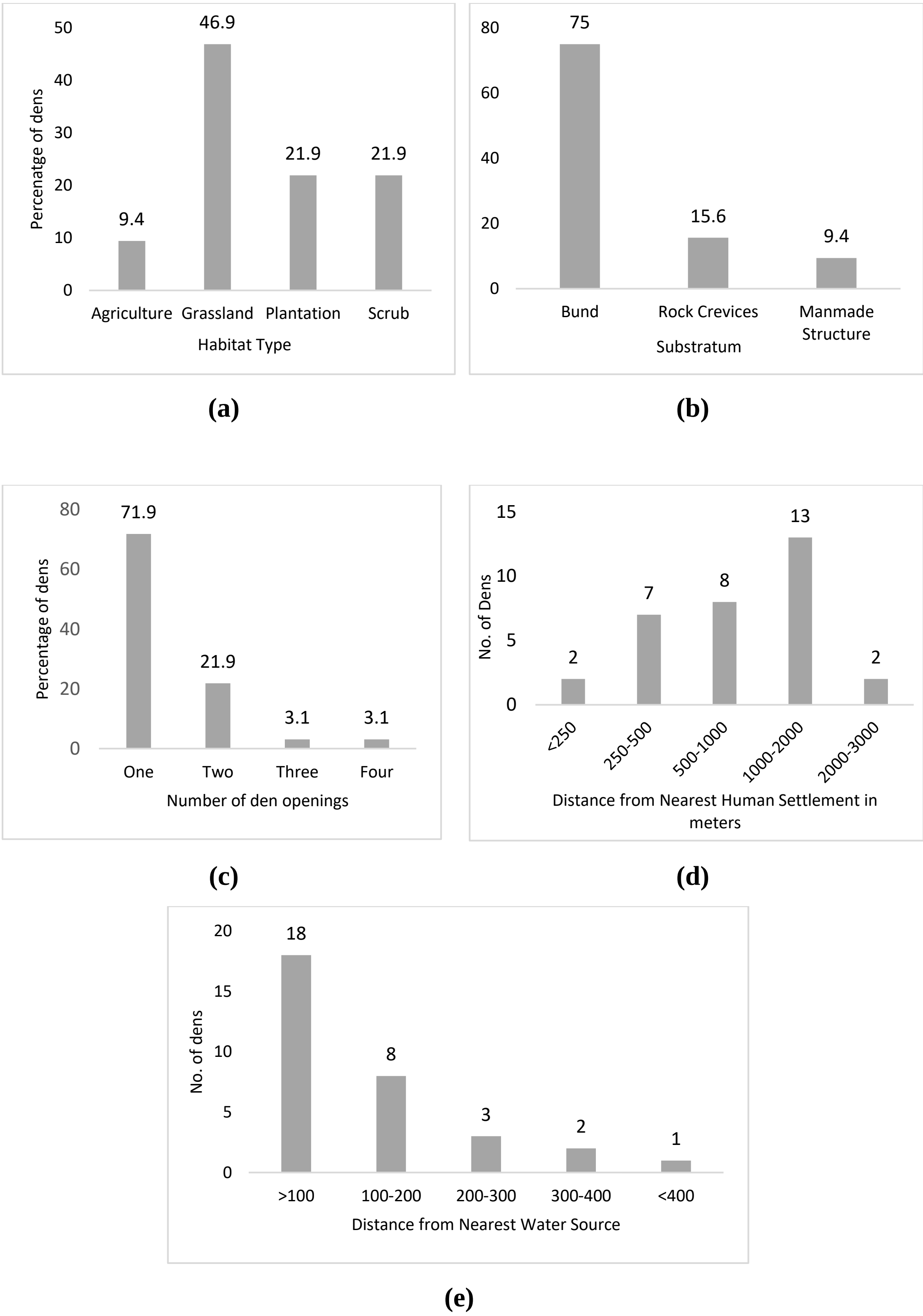


Figure 3.3: Key characteristics of den sites of Indian wolves in Maharashtra, (a) habitat type, (b) substratum, (c) the number of openings, (d) distance from nearest human settlement, and (e) distance from nearest water source from dens.

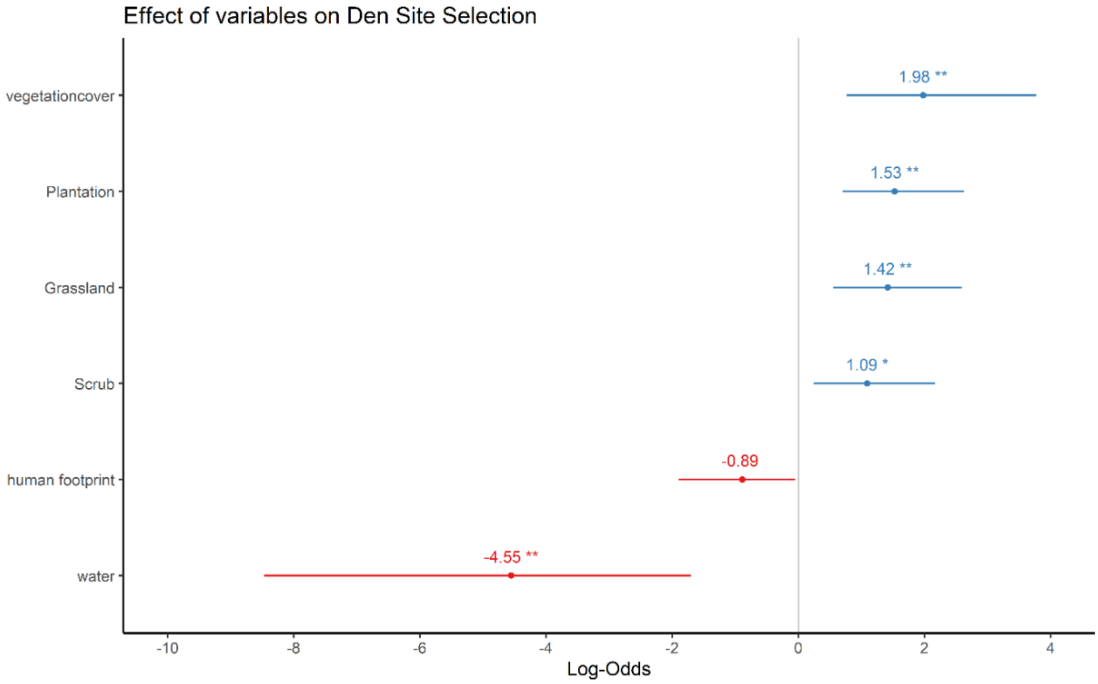
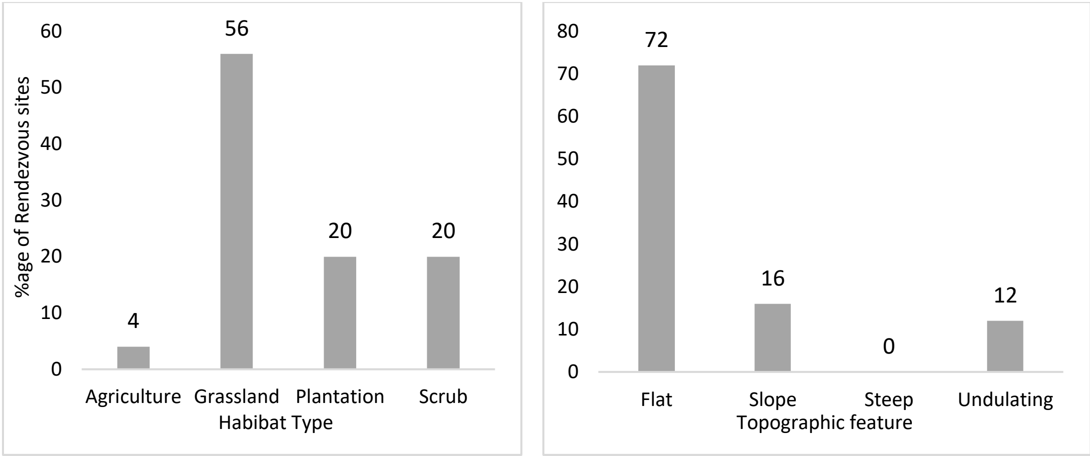


Figure 3.4: Scaled coefficients with a significance level of variables from generalized linear model estimates for the den site of Indian wolves. Horizontal lines depict the 95% confidence interval of each variable. Data for the water variable was calculated as the distance from the den location. So here, the negative value represents the association of the den site with water.

Rendezvous site characteristics and habitat selections

Out of 25 rendezvous sites evaluated, the maximum number of sites were found in grassland (56.0% of total rendezvous sites), followed by plantation (20.0%) and scrubland (20.0%) each, and lowest in agriculture (4.0%) (Figure 3.5a). I also assessed the topographic features on which rendezvous sites were established and found that the maximum number of sites (72%) were in flat areas, followed by the slope (16.0%), and only 12% were in undulating terrain types (Figure 3.5b).

The presence of a rendezvous site was best predicted in model 6, with the lowest LL value (-16.64) and AICc value (46.51) (Table 3.3). The distance from escape cover (β=-5.17 ± SE2.29; p=0.02), presence of plantation (β=1.81 ± SE0.60; p=0.003), presence of grassland (β=1.46 ± SE0.56; p=0.01), presence of scrub (β=1.23 ± SE0.45; p=0.006) were positively associated with rendezvous sites and negative association with vegetation cover (β=-1.72 ± SE0.69; p=0.01) (Table 3.4, Figure 3.6).



(a) **(b)**

Figure 3.5: Key characteristics of rendezvous site (a) habitat type and (b) topographic feature at each rendezvous site of wolves in Maharashtra.

Table 3.3: Log-likelihood (LL), number of parameters (K), Akaike's Information Criterion value (AIC), change in AIC value (ΔAIC), and Akaike's weight (***ωi***) of models for rendezvous site selection of Indian wolves, Maharashtra, India, 2016–2021.

Model Description	**LL**	**K**	**AIC**	**AICc**	**ΔAIC**	***ωi***
Null Model **Intercept only**	-47.73	1	97.47	97.53	51.01	0.000
Habitat Feature **Model 1: Slope + Grassland + Plantation + Scrub + Vegetation Cover**	-20.68	6	53.36	54.60	8.08	0.013
Distance to Water and Escape Cover Model 2: Dist to Water + Dist to Escape Cover	39.32	3	84.65	84.99	38.47	0.000
Linear Infrastructure **Model 3: Cart Road + Metal Road + Primary Road**	-42.45	4	92.90	93.47	46.95	0.000
Anthropogenic parameters **Model 4: Human Footprint**	-47.26	2	98.52	98.69	52.17	0.000
Habitat feature, Linear Infrastructure, and Distance to Escape Cover **Model 5: Grassland + Plantation + Scrub + Dist to Escape Cover + Vegetation Cover + Primary Road**	-16.58	7	47.16	48.84	2.32	0.235
Habitat, Distance to Water and Escape Cover, and Anthropogenic parameters **Model 6: Grassland + Plantation + Scrub + Vegetation Cover + Dist to Escape Cover**	-16.44	6	45.28	46.51	0.00	0.751

Table 3.4: Generalised Logistic Regression model predicting Indian wolf rendezvous sites vs contrast sites in Maharashtra. Model 6 was selected based on the lowest Log-likelihood, and AICc values were selected to summarise the results. The beta coefficients of the variable used for all the models and the standard errors, z value, p values, and VIF (Variance Inflated Factor) value are provided.

	β estimates ±SE	p-value	z value	VIF
(Intercept)	-3.557 ±1.168	0.002	-3.045	
Grassland	1.468 ±0.566	0.010	2.592	2.031
Plantation	1.816 ±0.604	0.003	3.005	2.268
Scrub	1.238 ±0.455	0.006	2.723	1.786
Escapecover*	-5.173 ±2.290	0.024	-2.259	1.130
Vegetation Cover	-1.722 ±0.694	0.013	-2.482	1.872

*the escape cover variable data was calculated as the distance from the rendezvous site location. So here, the negative value represents the association of the rendezvous site with the escape cover.

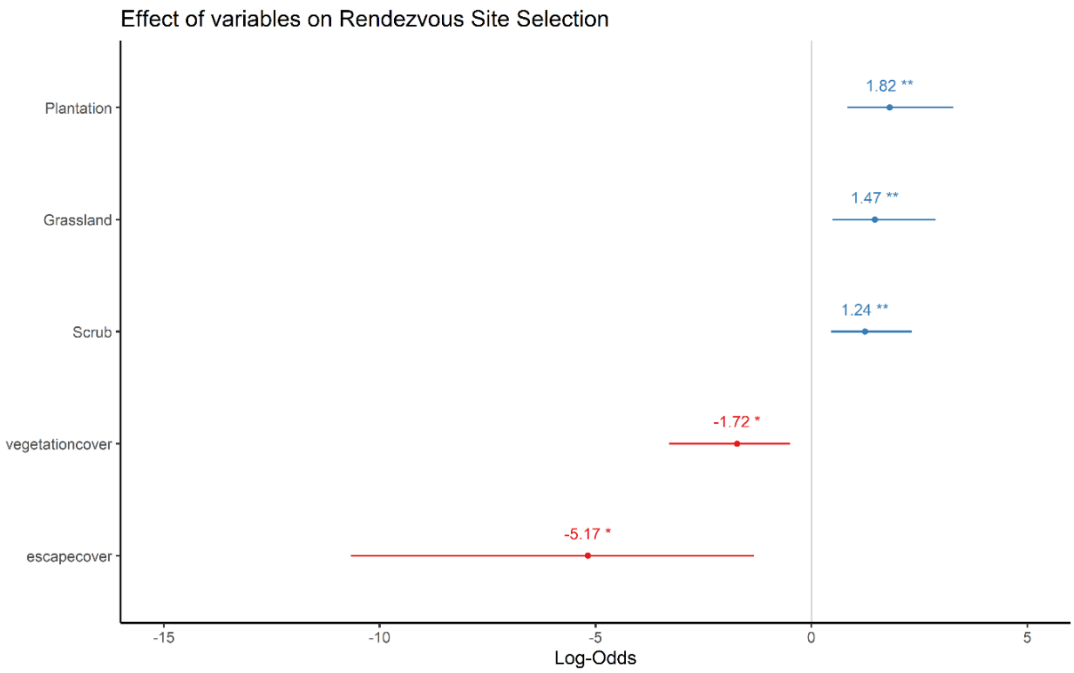


Figure 3.6: Scaled coefficients with a significance level of variables from generalized linear model estimates for the rendezvous site of Indian wolves. Horizontal lines depict the 95% confidence interval of each variable. Data for the escape cover variable was calculated as the distance from the rendezvous site location. So here, the negative value represents the association of the rendezvous site with the escape cover.

3.4 Discussion

The results suggested that the presence of the grassland, plantation, and scrub forest were significantly important factors for den and rendezvous site selection. Moreover, vegetation cover ($\beta=1.97$; $p=0.008$) and proximity to the water ($\beta=-4.55$; $p=0.006$) were also significant contributing factors for the den site selection. However, proximity to escape cover was significantly associated, and vegetation cover was negatively associated with the rendezvous sites. Escape cover here includes dense vegetation, plantation, and rugged terrain, providing concealment and refuge. These environments facilitate evasion from human threats. At the rendezvous site, young wolves learn various life history lessons in open habitats. These areas are often very near to such escape covers so that in response to any threat coming towards them, they take refuge in such areas. These landscape features enhance their survival by providing shelter and minimising visibility. In ecosystems where wolves reside, the availability of such escape cover is crucial for maintaining a balance between predation and predator avoidance in their ecological niche. Most rendezvous sites (n=18) were also reported from flat topography (Figure 3.5b). The findings were similar to that of the study of Sidorovich et al., 2017, where they reported that wolves prefer small grassy areas for den sites and rendezvous sites are characteristically centred near open areas bordered by tree cover or thickets near the site (Pimlott et al., 1969; Ballenberghe et al., 1975). These open areas are generally less disturbed and are used for livestock grazing. The livestock grazing in these areas also allows wolves to depredate on them. Of total dens, 75% of dens were made on the bund.

The bunds are pile foundations that line the edge of agricultural fields and are made of soil and sometimes stones. Their advantage is that water is confined inside the field, which helps retain rich soil and maintain soil moisture for longer while reducing soil erosion in the low rain shed areas. The wolves use these bunds to build dens in the landscape. Most dens were found with a single opening followed by two openings. Two dens were found with three and four openings, respectively, corroborating the findings of Matteson's 1992 study in Montana. Of the total den sites observed, 13 dens were found 1000-2000 meters away from any human settlement, and as the distance decreases, the number of dens also decreases (Figure 3.3d). As human settlement implies increased disturbance, den sites were located away from it, supporting results from studies in Greece (Iliopoulos et al., 2014), Italy (Ciucci et al., 1997; Capitani et al., 2006), Poland (Theuerkauf et al., 2003a).

According to Karlsson et al. (2007), the presence of humans close to den sites might cause wolves to avoid a particular area. In contrast to what I found, Thiel et al. (1998) recorded multiple cases of wolves establishing dens near human activity and explained the connection to human-induced subsidies. The proximity to the water source was also an important variable. Most of the dens (n=18) were within 100 meters of a water source. Similar results have been presented in many research conducted on the den site selections in different regions (Joslin, 1967; Voigt, 1973; Carbyn, 1974; Unger, 1999; Habib and Kumar, 2007; Ausband et al., 2010; Benson et al., 2015). This demonstrates the significance of the water near the den sites. Proximity to water sources reduces the need for adults to travel longer distances and, therefore, expose the dens unattended for a longer duration to drink water, which is essential for their survival. Because canid milk is relatively diluted and lactating females need to consume a lot of water to make milk, proximity to water appears to be a significant determinant at this time (Habib and Kumar, 2007). The vegetation cover at the den site is an important factor. The cover at our den sites was 46.97 ±20.78%, which was lower than the study conducted in northwest Montana and southern Canadian Rockies (66.1 ± 27.3%) (Matteson, 1992), in northwestern Wisconsin and east-central Minnesota (70 ± 24%) (Unger, 1999) and Montana, Idaho, and Yellowstone areas (72 ± 24%) (Trapp et al., 2008). Since our study area falls under the semi-arid landscape of Maharashtra, the low availability of vegetation cover in the area may explain the reason behind the use of low vegetation cover den sites.

The den provides a crucial function for the first few weeks of the pup's life by protecting the young from the environment and potential threats. Compared to the outside world, the den's temperature and humidity are typically moderate and steady (Paquet and Carbyn, 2003). Wolf dens continue to serve as the hub of activity after pups sneak out of the den and start to consume semisolid food that parents have regurgitated at 3–4 weeks (Mech, 1970). Followed by the use of the rendezvous sites, areas where pups are left, usually with a subadult, while pack members forage. Rest and play dominate the activities at rendezvous sites (Theberge and Falls, 1967).

Recently, several studies have related the choice of home sites by wolves to variables such as climate, soil type, vegetation type, tree cover, human disturbance, and prey availability. However, most of these studies have been in North America and Europe (Ballard and Dau, 1983; Norris et al., 2002; Theuerkauf et al., 2003a; Capitani et al., 2006). Also, there have been multiple reports of repeated use of established natal dens and rendezvous sites (Voigt, 1973; Carbyn, 1974; Paquet and Carbyn, 2003). According to Voigt (1973), one rendezvous site was used at least five times for nine years. In the given scenario, the identified den and rendezvous sites need to be monitored to ensure no changes in these sites and better species protection in the non-protected human-dominated landscape.

The increase in human population, habitat degradation, changing land use patterns, and low wild prey abundance have decreased the former range of wolves and even its local extinction (Jhala, 2003). In addition, the expansion of agricultural activities into marginal areas, including open plains, resulted in the loss of habitat and reduced their geographic range drastically (Mech, 1970). This is the first study where I presented an Indian wolf den and rendezvous site selection in human-dominated landscapes of India. However, researchers have observed frequent use of secondary dens sites (Chapman, 1977; Habib and Kumar, 2007), but our study only focuses on natal dens (Banfield, 1954). I presented the key characteristics of natal den and rendezvous sites to identify important features associated with these sites. However, our results are preliminary, and more study is required to understand these features more robustly with more data sets. This study has potential and could serve as baseline information that could aid in Indian wolf conservation in the country.

Chapter 4: Food Habits of Indian Wolves

Chapter 4: Food Habits

4.1 Introduction

The demand for land has increased in the setting of the Anthropocene, which is characterised by increasing human populations and their expanding requirements such as agriculture, industry, and infrastructural development. As a result of this growing land use change, global wildlife habitats are being fragmented (Fischer and Lindenmayer, 2007; Haddad et al., 2015), and animal species have been forced to live in close proximity to human settlements (Woodroffe and Ginsberg, 1998; Inskip and Zimmermann, 2009). The consequences of this cohabitation between humans and wildlife are multifaceted. Direct consequences for carnivorous species residing in such settings encompass threats like poaching, retaliatory killing, habitat fragmentation due to anthropogenic barriers or fencing, and raod-related mortalities (Mech and Boitani, 2003; Liberg et al., 2012). Concurrently, more indirect impacts manifest, including the transmission of diseases, depletion of prey resources, and other ecological perturbations.

Furthermore, certain carnivorous species have demonstrated behavioural plasticity by capitalising on human-associated food subsidies (Meriggi and Lovari, 1996; Vanak and Gompper, 2010; Reshamwala et al., 2021). Consequently, the dynamics of carnivore survival and sustenance within human-dominated landscapes necessitate the employment of diverse strategies. One such example is the Indian wolf *Canis lupus pallipes,* one of the world's most endangered populations. These wolves are genomically distinct from Holarctic wolves and are considered ESUs (Evolutionary Significant Units) (Hennelly et al., 2021b). The Indian wolf is believed to have evolved during the Pleistocene epoch to exploit a comparatively vacant dry zone niche (Sharma et al., 2004). It became the top predator species of the Indian open plains (semi-arid grasslands, scrublands, grazing areas). Their importance as an ecological regulator via trophic cascades is well recognised (Smith et al., 2004; Ripple and Beschta, 2007).

The wolf consumes many food items throughout their distribution and maintains the ecological balance (Mech and Boitani, 2003). The food habits of the grey wolf have been extensively investigated in North America and Europe (e.g., (Ciucci et al., 1996;

Jędrzejewski et al., 2002; Mech and Boitani, 2003; Capitani et al., 2004). However, this important ecological component of wolves has yet to receive much attention in Asia, notably India (Lyngdoh et al., 2019; Khan et al., 2022). Although wolves in India have been reported to feed on a wide variety of food items, such as carrion and agricultural products (Khan et al., 2022), their main prey in most areas are large and medium-sized ungulates which depend on the composition of the regional ungulate community (Jethva and Jhala, 2004b; Singh and Kumara, 2006; Habib, 2007; Shrotriya, 2020; Khan et al., 2022). Most studies in India demonstrated that Indian wolves consume various domestic prey (Jethva and Jhala, 2004b; Singh and Kumara, 2006; Habib, 2007; Maurya et al., 2011; Khan et al., 2022). Domestic animal predation is a critical factor in wolf-human conflicts (Kaczensky, 1998) that leads to wolf persecution (Meriggi and Lovari, 1996; Habib and Kumar, 2007; Cortés et al., 2016). Furthermore, such interactions negatively affect individuals' opinions and compromise their tolerance level (Habib and Kumar, 2007; Majić and Bath, 2010; Rigg et al., 2011). Inadequate knowledge of the ecological and social factors underlying human-carnivore interactions frequently impedes the improvement of effective management strategies (Bagchi and Mishra, 2006).

Understanding wolf food habits is important not solely from the ecology perspective but also from an economic and conservation perspective (Ciucci et al., 1997), especially given the increasing human-wolf conflict in India due to livestock depredation (Habib, 2007). Rapid population growth and urbanisation reduce wild prey availability globally (Ripple et al., 2014). The Deccan landscape alone has reported a 40-50% prey decrease (Wolf and Ripple, 2016), forcing wolves to shift to livestock. The previous systematic study conducted on the Indian wolf diet was in 2007 (Habib, 2007), and after that, no studies have been conducted in the landscape. Here, I tried to understand wolves' present food habits and explored the change in the diet of wolves in the landscape. Moreover, a recent study stated that Indian wolves are the most ancient lineage of wolves (Hennelly et al., 2021b). Understanding these wolves' food habits and developing a proper management plan for the remaining population has been essential.

In human-dominated areas, they choose prey depending on availability, abundance, pack stability and season (Imbert et al., 2016). Due to the availability of blackbuck (*Antilope cervicapra*), chinkara (*Gazella bennettii*), and livestock such as sheep (*Ovis aries*) and goats (*Capra aegagrus hircus*), the Indian wolf preyed mostly on medium-sized animals (Khan et al., 2022). The goat and sheep numbers in India's wolf-bearing states (Rajasthan, Andhra Pradesh, Maharashtra, and Telangana) are the highest (20th Livestock Census: All India Report, 2019). I hypothesise that the wolf in semi-arid areas of Maharashtra is a generalist feeder and feeds on various food items. I also hypothesised that wolves in Maharashtra's semi-arid landscape became more dependent on livestock as the wild prey population declined drastically.

From an applied perspective, livestock depredation and perceived human competition have led to a global decrease and local extinction of carnivore species (Treves and Karanth, 2003), underlining the importance of systematically identifying the species' food habits. Therefore, understanding site-specific food habits and changes in diet composition is vital to conservation as it influences population structure and determines ecological interactions.

4.2 Materials and Methods

Scat Collection

Diet analysis based on studying animal faecal matter has long been an essential component of carnivore ecology and natural history studies (Floyd et al., 1978; Meriggi et al., 1996b; Klare et al., 2011). To study the diet composition of the Indian wolves, I used the non-invasive technique of scat analysis by collecting 961 scats between 2017 and 2021 throughout the study area. Paths, dirt roads, fire lines, and crossroads were prospected by walking on foot. Morphology, size, scent, colour, contents and spatial position were used to identify wolf scats. Scats collected along the trails were stored in ziplock bags, labelled with the date and Global Positioning System (GPS) location, and sun-dried for 5–10 days if required. The wolf-bearing areas also harbour feral dog populations in plenty. The scats are often misidentified with them. The collected scats were submitted to genetic analysis to confirm the species *Canis lupus pallipes*, avoiding misclassification of domestic dogs (*Canis lupus familiaris*) and Golden Jackal (*Canis aureus*). The Indian fox scats were smaller in size, and I did not collect any small-size scats unless it was found at confirmed wolf den sites.

Identification of scats

I tried to scrape all the collected scat samples for species identification. However, I could only collect DNA from 430 samples (44.75% of the collected scats) for species identification.

I did species identification from scats using molecular tools. DNA was extracted from faecal samples using the Guanidine iso-thiocyanate method (Boom et al., 1990) in a room dedicated to low-copy DNA extraction. Negative controls composed of reagents, only without samples, were included for every extraction to monitor for contamination. Species identification from faecal samples was carried out using two primers: CaCOI (forward sequence 5′-AACAGACCGTAATCTTAATACGACATTTTTC-3′, reverse sequence 5′-GTAAGTGACAATGTGAGAAATTATTCCGAAC-3) and WOLF4 (forward sequence 5′-GATATCCCTACTTACACTAGGA-3′, reverse sequence 5′-ATGAAAAGAACTATCCCCGTAC-3′) to amplify the fragment of control region (Vilà et al., 1999). Polymerase chain reactions (PCR) were carried out in a volume of 10 μL including 4μL Hotstar-Taq Master Mix, 3.5μL BSA, 0.4μL each of forward and reverse primer, 0.5μL RNAse free H_2O, and 1.2μL DNA, with thermocycling conditions as detailed in Sharma et al. (2004) on Indian canids. Following the amplification of the target DNA, the PCR products were loaded in 2% agarose gel electrophoresis and identified based on bands. Jackal samples were amplified only in CaCOI, while dog samples were amplified only in WOLF4. Samples that produced bands with both primers were classified as belonging to the Indian wolf. To our knowledge, I only collected confirmed wolf scats from the field, and later, with the help of genetics, I found that 80% (N=348) of scats belonged to Indian wolves; the remaining 20% of the scats were golden jackals and feral dogs (Figure 4.1).

Later, each sample was weighed, washed in running water, and dried in an oven at 40°C for 24–48 hours to prepare reference slides to identify mammalian medullary hair patterns (Bahuguna et al., 2010). All the down feathers in the scats were identified to order level using reference material prepared during this study and existing literature (Dove and Koch, 2011).

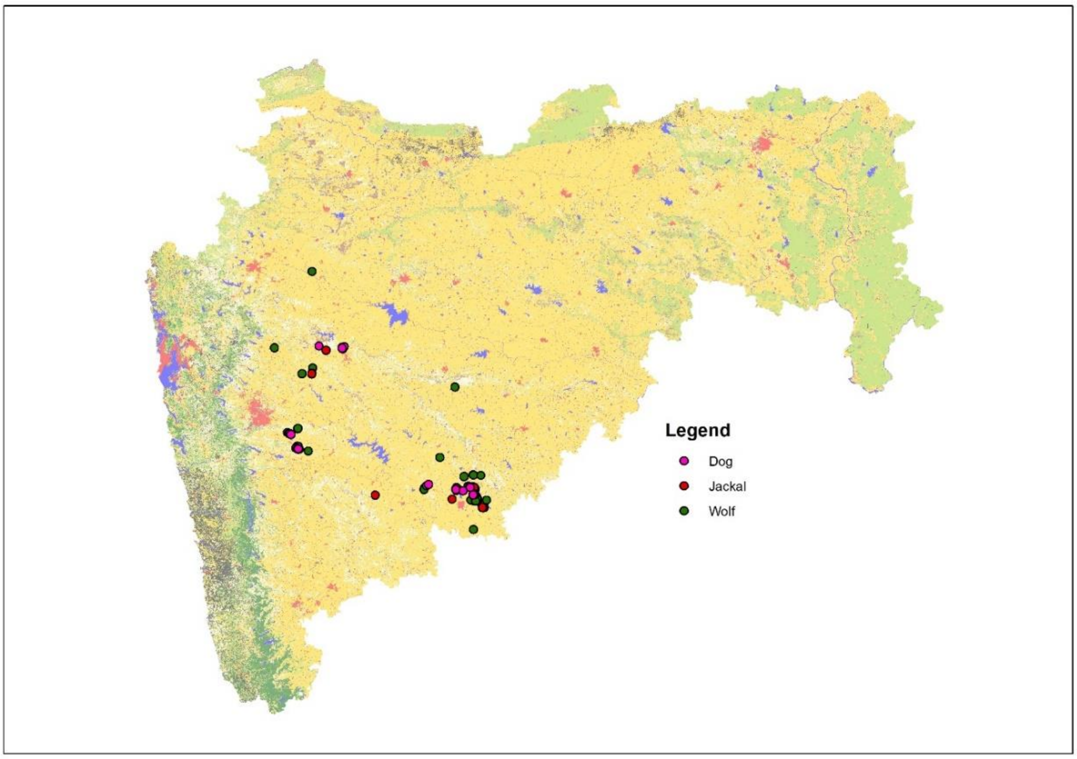


Figure 4.1: Location of identified scat samples (N=430) collected from the human-dominated landscape of Maharashtra. Out of 430 scats, 348 scats belong to Indian wolf, 56 scats belong to Golden Jackal, and 26 Scats belong to Feral dogs.

Diet Analysis of Wolves

I calculated the frequency of occurrence of prey or food items in the scats. Given the high digestibility of larger prey species compared to small prey species and the low occurrence of hair in the scats, interpretations of prey consumption are often misleading (Karanth and Sunquist, 1995). Smaller prey may be overrepresented because they create more scats per kilogram of flesh ingested than larger species. By accounting for the body mass of prey species, relative biomass models help to overcome this bias (Ciucci et al., 1996; Ghaskadbi et al., 2022). Previous research used a correction factor created for grey wolves Canis lupus (Floyd et al., 1978) with modifications (Weaver, 1993) to evaluate the relative significance of the prey species. Wachter et al. (2012) enhanced the linear regression biomass model by proposing an exponential model that accounts for a species' maximum consumable biomass. Models with an asymptote on the graph of consumable biomass are more accurate and ecologically significant (Chakrabarti et al., 2016; Lumetsberger et al., 2017). I adopted the non-linear model for our analysis since biomass consumed compensates for the differential digestibility of food items (Klare et al., 2011) and is regarded as the most significant ecological parameter:

$$Y = 1.382\ (1 - \exp(-0.021X))$$

Where Y is the biomass of prey consumed (kg) to produce a single field collected scat, and X is the prey species' mean body weight (kg). The mean weight of potential prey species ingested by wolves was derived from previously released data on wolf food preferences in the same landscape (Habib, 2007). I also estimated the fraction of relative biomass (D) and the relative number of individuals (E) consumed by the wolf using the species-specific adjustment factor (Y):

Frequency of occurrence= (Total number of a particular prey/Total number of scats) x 100

Relative biomass of prey species D = (A x Y) / Σ (A x Y) x 100

Relative number of individuals consumed E = (D / X) / Σ (D / X) x 100

where Y is a correction factor, X is the average weight of prey, and A is the frequency of occurrence.

To calculate the food item selectivity, I used the Ivlev Electivity Index

Ivlev Index = ri - pi / ri + pi

Where ri is the proportion of food items in scats and pi is the availability of the particular food item in the area (relative biomass/sq.km)

To calculate the dietary overlap between the collared wolf pack, I used Pianka's index (Pianka, 1974):

$$o_{jk} = \frac{\sum p_{ij}\ p_{ik}}{\sqrt{\sum p_{ij}{}^{2}\ \sum p_{ik}{}^{2}}}$$

Where O is the index ranging from 0 to 1 of the amount of overlap between *j* and *k* packs, and p_i is the occurrence of each food item.

4.3 Results

The most common food items in the wolf scats were bones (83.91% of total scats), followed by hairs (62.93%). Feathers constituted (35.63%) the third major item in the scats. A significant proportion of scats also contain vegetative matter such as grass and leaves (18.39%), Ziziphus (6.32%) and grapes (2.59%). I also found human-related items (4.31%) in the scats, such as plastics and processed leather (Figure 4.2). Data on feeding habits obtained by analysing 348 wolf scats collected revealed that domestic prey comprised 59.38%, wild prey 23.77% and vegetable matter 14.96% of their diet. Unidentified prey remains contributed 1.89% of their food.

The most frequently occurred species in wolf scats were chicken *Gallus gallus domesticus* (27.59%) and goat *Capra aegagrus hircus* (21.84%), followed by vegetative matter (14.97%; grass, Ziziphus, grapes), sheep *Ovis aries* (9.53%), blackbuck *Antilope cervicapra* (8.69%) and chinkara *Gazella bennettii* (6.59%). Black-naped hares, reptiles, rodents, wild pigs and cattle constituted less than 2% of each (Figure 4.3). Consistent with the frequency of occurrence, the biomass model also suggested that goats (31.06%), blackbuck (21.50%), and sheep (20.98%), followed by chinkara (16.60%) and chicken (3.77%) were the principal food item of wolves across the landscape (Table 4.1). Regarding the relative number of individuals consumed per 100 scats, chicken was consumed most (37.48 individuals), followed by goats, blackbuck and chinkara (Table 4.1). I calculated Ivlev's electivity index scores of 6 species whose densities were available from the landscape. The density of cattle, goats, sheep and chicken was acquired from livestock census data 2019, and the density of chinkara and blackbuck was obtained from Habib et al. (2018). Based on Ivlev's electivity index score, wolves significantly preferred to prey upon chinkara (0.998) and blackbuck (0.947) (Figure 4.4). Along with these, three domestic species, chicken (0.796), sheep (0.553), and goat (0.373), were found to be the preferred food of wolves at the landscape scale. There was an avoidance of cattle (−0.963), including *Bubalus bubalis* and *Bos taurus,* by wolves (Figure 4.4).

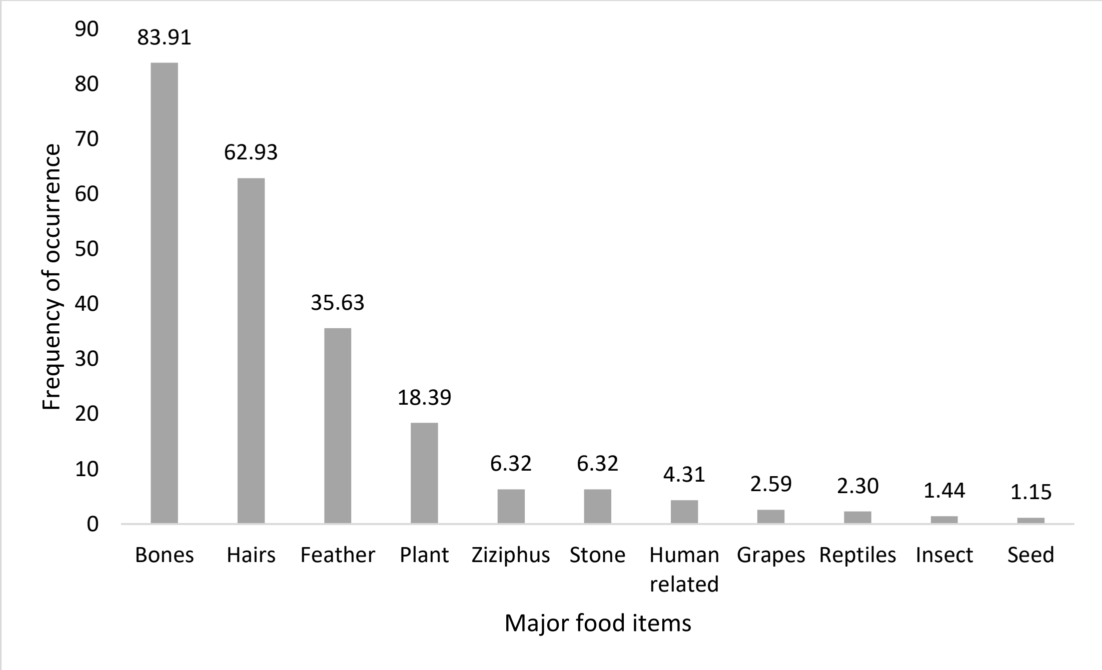


Figure 4.2: The percentage of occurrence of major food items observed in the scats of the Indian wolf

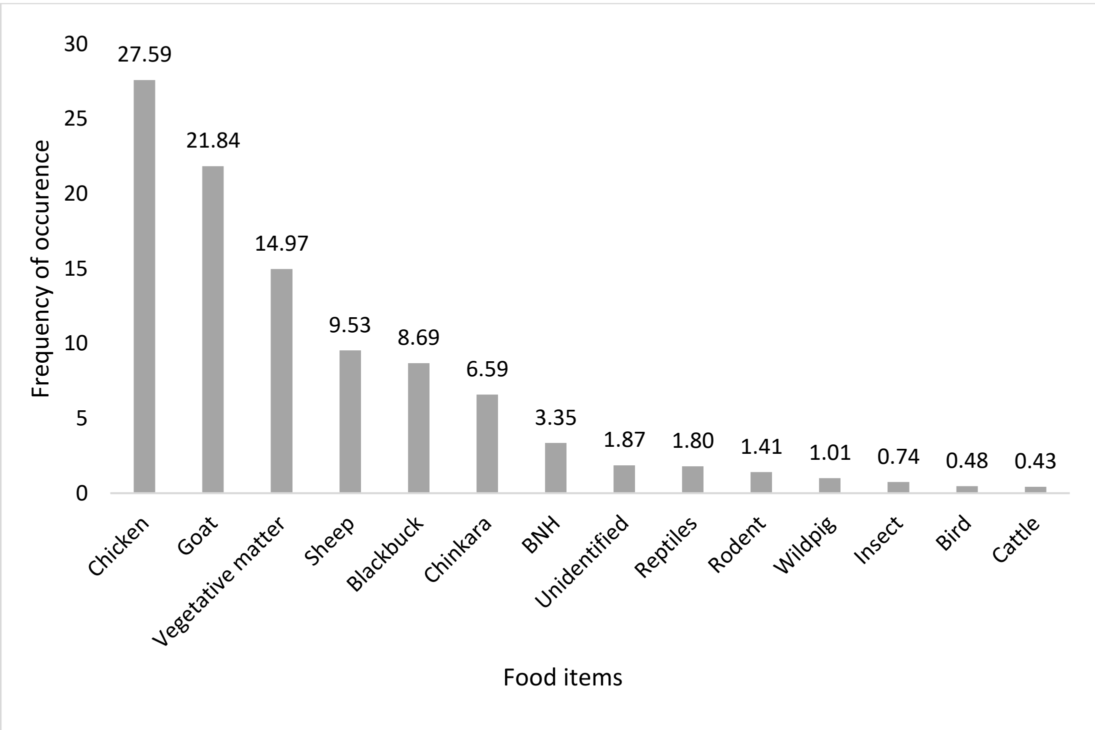


Figure 4.3: The frequency of occurrence of food items in the Indian wolf diet in the human-dominated landscape of Maharashtra, India. (N = 348)

Table 4.1: Average live weight of prey consumed (X), frequency of occurrence (A), the weight of consumed prey represented by one field-collectable scat using correction factor (Y), relative biomass consumed (D), and the relative number of prey individuals consumed (E) by wolves based on scats collected from the human-dominated landscape of Maharashtra, India (n = 348).

Items	Frequency of Occurrence (A)	Prey weight (X)	Correction Factor (Y)	Relative biomass of prey (D)	Relative number of individuals consumed (E)
Goat	21.84	11.60	0.43	31.06	26.61
Blackbuck	8.69	22.46	0.63	21.50	9.52
Sheep	9.53	19.40	0.57	20.98	10.75
Chinkara	6.59	20.00	0.58	16.60	7.17
Chicken	27.59	1.50	0.24	3.77	37.48
Wildpig	1.01	38.00	0.91	3.64	0.95
Cattle	0.43	35.00	0.85	1.48	0.42
Black Naped Hare	3.35	2.00	0.25	0.91	4.51
Rodent	1.41	0.20	0.22	0.05	1.93
Bird	0.48	0.25	0.22	0.02	0.66

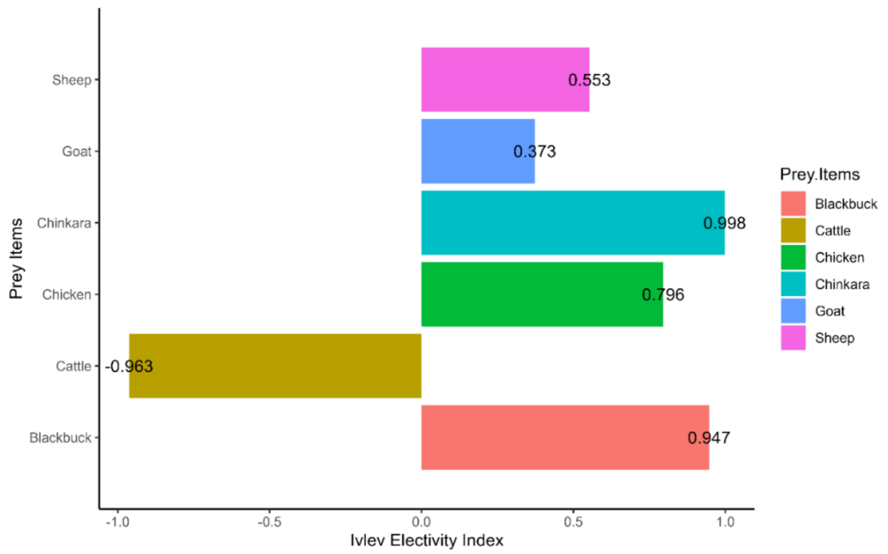


Figure 4.4: Ivlev electivity index for prey preference in wolves' diet across the human-dominated landscapes of Maharashtra. The scale ranged from − 1 to + 1, representing strong avoidance and strong preference, respectively. Chinkara and blackbuck were wolves' most preferred prey, followed by sheep, chicken and goat. Cattle (buffalo and cow) were the least preferred prey. The density of cattle, goats, sheep, and chicken was acquired from livestock census data in 2019, and the density of chinkara and black buck was obtained from Habib et al. (2018).

Food habits of different collared wolf packs

The details of the food habits of seven collared wolf packs studied across the human-dominated landscape of Maharashtra are given below:

Gangewadi 1 Pack: The relative frequency of occurrence of different prey items in the wolf scats of Gangewadi 1 Pack (n=25) suggested that the pack is mainly dependent on wild prey, which constituted 38.0% of its diet, whereas only 30% of its diet was represented by the domestic prey. The proportion of vegetative matter was also represented in a significant amount, i.e., 30% in the diet of the pack, with a major contribution of Ziziphus. Among domestic prey, sheep constituted a major portion (16.0%) of the diet of the Gangewadi 1 Pack, followed by goats (12.0%), whereas, among wild prey, blackbuck comprised 30.0% and black-naped hare 6% of its diet (Figure 4.5). Out of the total scats collected from the pack's home range, 60% of scats had one prey item, and 40% had two prey items.

Gangewadi 2 Pack: The relative frequency of occurrence of different prey items in the wolf scats of Gangewadi 2 Pack (n=70) suggested that the pack is mainly dependent on domestic prey, which constituted 64.28% of its diet, whereas only 20.24% of its diet was represented by the wild prey. The proportion of vegetative matter was 14.05% in the diet of the pack. Among domestic prey, goats constituted a significant portion (44.76%) of the diet of the Gangewadi 2 Pack, followed by sheep (9.29%) and chicken (8.81%), whereas, among wild prey, blackbuck comprised 12.86% and black-naped hare 3.81% of its diet (Figure 4.5). Out of the total scats collected from the pack's home range, 60% of scats had one prey item, 31.43% had two prey items, and 8.57% had three prey items.

Nannaj Pack: The relative frequency of occurrence of different prey items in the wolf scats of the Nannaj Pack (n=23) suggested that the pack is largely dependent on domestic prey, which constituted 39.19% of its diet and 34.05% of vegetative matter, whereas only 26.80% of its diet was represented by the wild prey. Among domestic prey, goats constituted a significant portion (28.98%) of the diet of the Nannaj Pack, followed by sheep (7.97%) and chicken (2.17%), whereas, among wild prey, blackbuck comprised 13.77% and black-naped hare 2.90% of its diet. The Nannaj pack constituted the highest proportion of reptiles (4.35%) among all the packs (Figure 4.5). Out of the total scats collected from the pack's home range, 65.22% of scats had one prey item, 17.39% had two prey items, and 17.39% had three prey items.

Chapalgaon Pack: The relative frequency of occurrence of different prey items in the wolf scats of the Chapalgaon Pack (n=23) suggested that the pack is largely dependent on domestic prey, which constituted 51.81% of its diet, whereas only 23.91% of its diet was represented by the wild prey. The proportion of vegetative matter was 24.27% in the diet of the pack. Among domestic prey, goats constituted a major portion (44.93%) of the diet of the Chapalgaon Pack, followed by sheep (2.17%) and chicken (4.71%), whereas, among wild prey, blackbuck comprised 18.48%, followed by rodents (3.26%) and black-naped hare 2.17% of its diet (Figure 4.5). Out of the total scats collected from the pack's home range, 52.17% of scats had one prey item, 39.13% had two prey items, and 4.34% had three and four prey items, respectively.

Ahmednagar Pack: The relative frequency of occurrence of different prey items in the wolf scats of the Ahmednagar Pack (n=56) suggested that the pack is largely dependent on domestic prey, which constituted 55.50% of its diet, whereas only 22.77% of its diet was represented by the wild prey. The proportion of vegetative matter was 16.37% in the diet of the pack. Among domestic prey, chicken constituted a major portion (27.23%) of the diet of the Ahmednagar Pack, followed by goats (17.86%) and sheep (10.42%), whereas, among wild prey, blackbuck comprised 8.63%, chinkara (5.80%) and black-naped hare 3.57% of its diet (Figure 4.5). Out of the total scats collected from the pack's home range, 64.29% of scats had one prey item, 29.79% had two prey items, 5.36% had three, and 3.57% had four prey items.

Morgaon Pack: The relative frequency of occurrence of different prey items in the wolf scats of Morgaon Pack (n=56) suggested that the pack is mainly dependent on domestic prey, which constituted 66.50% of its diet, whereas only 22.27% of its diet was represented by the wild prey. The proportion of vegetative matter was 10.26% in the diet of the pack. Among domestic prey, chicken constituted a major portion (51.92%) of the diet of the Morgaon Pack, followed by goats (7.37%) and sheep (6.73%), whereas, among wild prey, chinkara comprised 16.03%, followed by black-naped hare 1.76% of its diet (Figure 4.5). Out of the total scats collected from the pack's home range, 70.12% had one prey item, 25.96% had two prey items, and 3.84% had three prey items.

Saswad Pack: The relative frequency of occurrence of different prey items in the wolf scats of Morgaon Pack (n=56) suggested that the pack is mainly dependent on domestic prey, which constituted 71.88% of its diet, whereas only 23.44% of its diet was represented by the wild prey. The proportion of vegetative matter was 1.56% in the diet of the pack. Among domestic prey, chicken constituted a major portion (45.31%) of the diet of the Morgaon Pack, followed by sheep (17.19%) and goat (9.38%), whereas, among wild prey, chinkara comprised 17.19%, followed by black-naped hare 4.69% of its diet (Figure 4.5). Out of the total scats collected from the pack's home range, 78.12% of scats had one prey item, and 21.87% had two prey items.

Dietary overlap between different packs

The dietary overlap between the seven collared packs was observed. The results showed that the highest overlap was between Chapalgaon and Gangewadi 2 pack (0.96), followed by Morgaon and Saswad Pack (0.95) and Chapalgaon and Nannaj Pack (0.91) (Figure 4.6). The overlaps were found high within the packs of Solapur District and within the packs of Pune and Ahmednagar Districts.

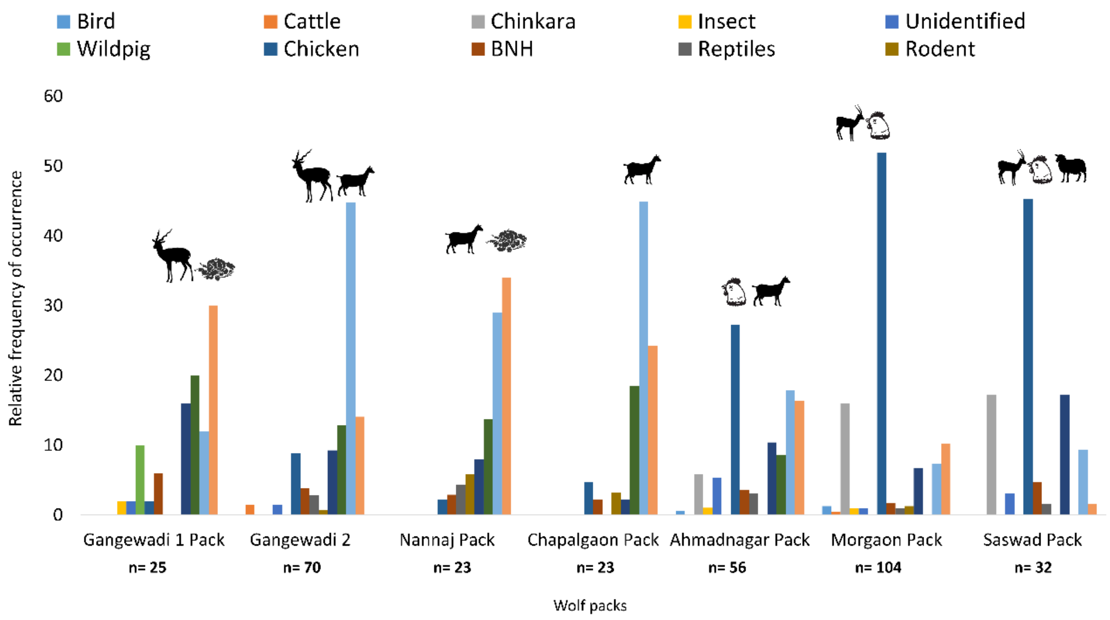


Figure 4.5: The frequency of occurrence of food items in the seven collared wolf packs studied across the human-dominated landscape of Maharashtra. The pack-wise scats were identified based on the 95% contour BBMM home range of the respective pack.

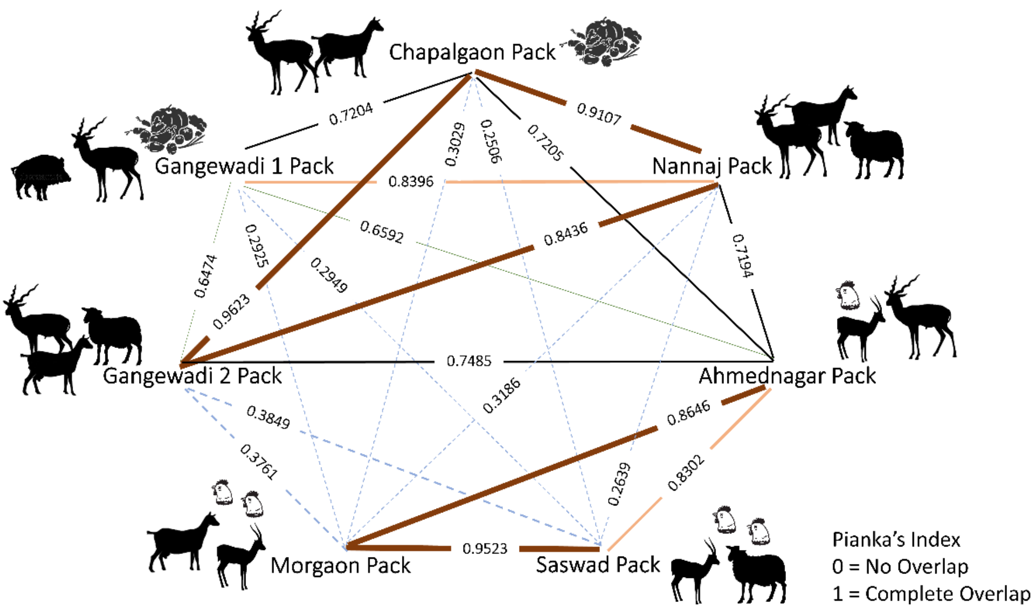


Figure 4.6: Dietary overlaps between the seven-collared packs of wolves in the human-dominated landscape of Maharashtra, India.

Change in wolf food habits in the last 15 years

The study conducted in the same landscape by Habib in 2007 reported the frequency of different food items by analysing 3947 scats, and the scats were collected from the core areas of wolves between 2002-2005. I compared this study's results with the previously reported frequency of occurrence and found that the consumption of wild prey significantly decreased from 38.01% (Habib, 2007) to 23.77% (P <0.001), and the consumption of domestic prey increased from 47.16% (Habib, 2007) to 59.38% in the last 15 years. However, there was no change in the consumption of vegetative matter in the landscape in the last 15 years (Figure 4.7). The study found that chicken consumption increased 27 times more than previously reported, results were significant (P <0.001), and blackbuck consumption decreased significantly from 27.5% (Habib, 2007) to 8.40%; P <0.001 in these years (Figure 4.8).

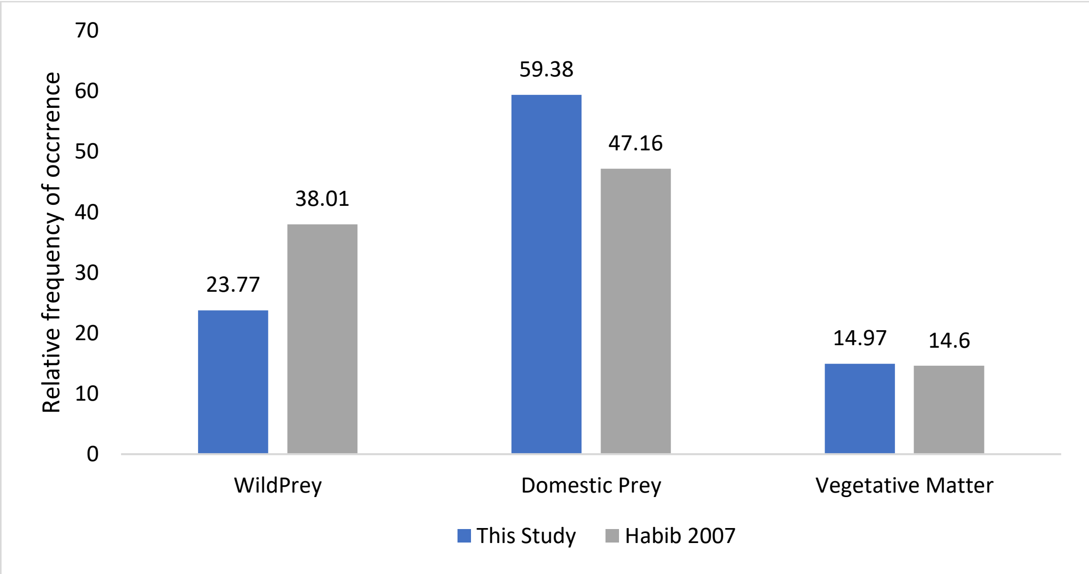


Figure 4.7: The comparison of the frequency of occurrence of wild, domestic prey and vegetative matter in the diet of Indian wolves, where the blue bar denotes the FO of this study and the grey bar denotes the frequency of occurrence reported in Habib's (2007) study.

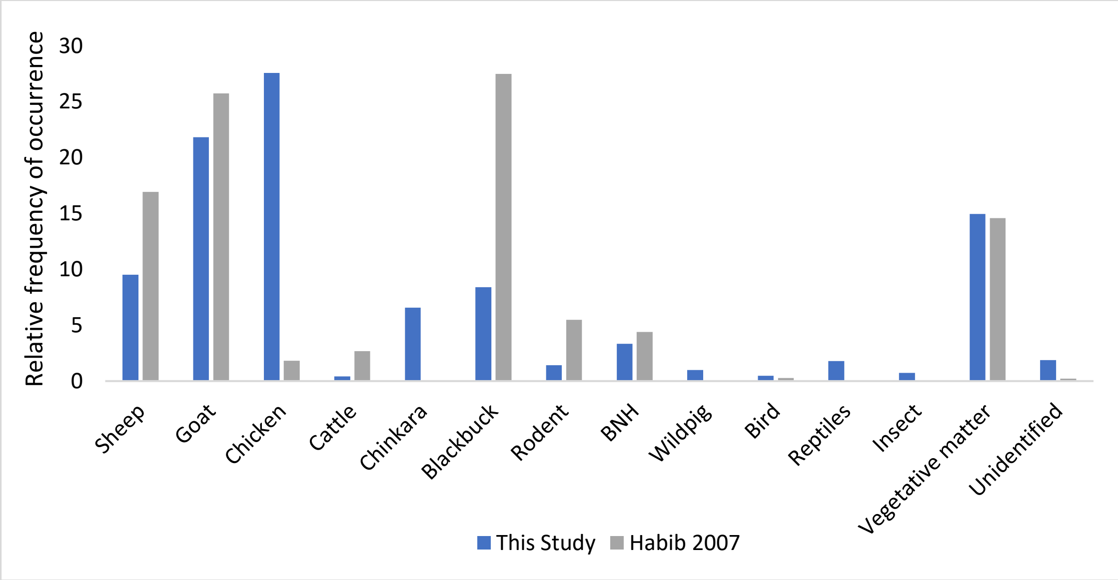


Figure 4.8: The comparison of the frequency of occurrence of different food items in the diet of the Indian wolf, where the blue bar denotes the FO of this study and the grey bar denotes the FO reported in Habib's (2007) study.

4.4 Discussion

The study provides insights into the food habits of the Indian wolf in the human-dominated landscape of Maharashtra by combining conventional non-invasive scat analysis with molecular methods for validating scat identification. Regarding food habit analysis, this work differs from earlier Indian wolf diet studies in that I decided to investigate exponential biomass models over linear models and did not depend exclusively on the frequency of occurrence of prey. A total of 348 scats out of 430 scats were identified as Indian wolf scats.

The results from scat analysis established that domestic prey such as goats and sheep contributed 52.04% of the biomass consumed and 37.36% of the relative numbers of individuals harvested. The wild prey, such as blackbuck and chinkara, contributed 38.10% of the biomass consumed and 16.69% of the relative numbers of individuals harvested. I also found most scats with vegetative matter, mostly ziziphus, grapes and grasses. Vegetation matter has been recorded previously in the wolf diet (Khan et al., 2022) and may probably aid in the digestion or excretion of indigestible food items.

The diet of Indian wolves varies in different areas based on their availability (Khan et al., 2022). The wolf has been reported to eat almost every animal that shares their range with them (Mech, 1970). Several studies conclude that wolves feed on various prey species, from large mammals to insects to vegetative matter. The present study showed that chicken, goat, vegetative matter, sheep and blackbuck constitute the majority (82.62%) of food items of the Indian wolf. Previous studies conducted on the diet of Indian wolves in India reported different items and proportions. Wild pigs were the most consumed prey (43.1%), followed by goats (30%) in the diet of wolves in Bihar, India (Shahi, 1982). Another study conducted in Velvadar National Park with 690 wolf scats reported that wolves preyed primarily on blackbuck and comprised a significant portion (62.8%) of the diet (Jhala, 1991). The study conducted in Nannaj Bustard Sanctuary, Solapur, reported that 85% of wolf kills were goats (43.8%) and blackbuck (42%) (Kumar, 1998; Kumar and Rahmani, 2000). In Lokhapat, Kutch, Gujarat, the most dominant food item in the diet of Indian wolves were black-naped hare (35.5%) followed by sheep (32.5%), rodents (14.4%) and goats (9.6%) (Jethva et al., 1997) whereas, in Abdasa, Kutch on 550 wolf scats, the most dominant food item was goat (51%), followed by sheep (22%), black-naped hare (8.3%) and cattle (7.1%) (Jhala, 2001). In a review paper, Khan et al. (2022) combined all these studies to understand the Indian wolf diet across India and reported that the wild prey comprised 49.32% of the diet, whereas domestic prey comprised 40.34% of the diet.

The previous studies reported the frequency of occurrence of birds in the wolf diet, which was reported to be only 1.31% of the total diet (Jhala 1991; Jethva and Jhala 2004b). Also, Habib, 2007 reported the chicken's frequency of occurrence in the wolf diet as 1.81%. However, this study found chicken that the frequency of occurrence of chicken (27.39%) was highest in wolf scat, with 3.77% of biomass consumed and 37.48% of the relative number of individuals consumed. Most of these chickens consumed by the wolf in the landscape were poultry waste. In the landscape, numerous small poultry farms are distributed across the area. These poultry farms usually do not decompose these wastes and throw the dead chicken illegally into the open areas consumed by carnivores.

Throwing poultry waste can have several negative effects on the ecosystem and native wildlife (Gerber et al., 2007). The high consumption of these wastes is an example of a disruptive natural balance in the area and can have many serious consequences. Poultry waste, which also includes manure and bedding materials, can contain high levels of nutrients and pathogens that can disrupt the natural balance of the environment (Gerber et al., 2007; Gržinić et al., 2023). When poultry waste is thrown onto the ground, the excess nutrients can seep into the soil. This can lead to soil contamination and nutrient imbalances. High nutrient levels in the soil can alter the composition of plant species, favouring invasive species and disrupting the natural vegetation. Poultry waste can contain harmful bacteria, viruses, and parasites. When these pathogens come into contact with native wildlife, they can cause diseases that spread rapidly and devastate local populations. This can have cascading effects on the food chain and ecosystem dynamics.

Moreover, introducing poultry waste to an ecosystem can alter the availability of food sources for native wildlife. It also attracts scavengers and predators that would not naturally be present, leading to increased competition for resources and potential impacts on local species. Native wildlife might be attracted to poultry waste for feeding or other reasons. While this might seem positive, it can lead to negative interactions between wildlife and poultry. Predators attracted to the waste might also target poultry flocks, leading to conflicts between wildlife and human interests (Chakraborty, 2020; Reshamwala, 2020).

Addressing these issues as soon as possible is crucial to avoid such changes. It is important to manage poultry waste properly to mitigate these effects. This includes implementing responsible waste disposal practices, composting, and utilising waste as fertiliser appropriately to minimise negative environmental impacts. Also, practising good biosecurity measures on poultry farms can help reduce the risk of pathogens spreading to native wildlife.

Regarding relative biomass consumption, goats and blackbuck contributed a major proportion of the wolf diet, followed by sheep, chinkara and chicken. Based on the Ivlev electivity index, I found that chinkara and blackbuck were the most preferred food items of Indian wolves, followed by chicken, sheep, and goat, whereas cattle were the least preferred. As per the Forest Department's Waterhole census data, the density of blackbuck and chinkara in the landscape decreased in the last few decades. Habib, 2007 reported that the blackbuck density in the wolf areas was as high as 4300 individuals per 100 km^2, which decreased by 40 times and was reported 74 individuals per 100 km^2 in the study conducted in GIB-bearing areas of Maharashtra (Habib et al., 2018). The chinkara density was reported as two individuals per 100 km^2. Considering such low densities of wild prey, the relative frequency of occurrence was 15.28%, with 38.10%

of relative biomass consumed in the area. Hence, they strongly preferred wild prey as per the availability. Increasing the wild population in the wolf-bearing areas will decrease the consumption of goats and sheep, decreasing the human-wolf conflict in the area.

Out of the total of seven collared wolf packs surveyed across Pune, Ahmednagar, and Solapur Districts, three packs were identified in Pune (Morgaon pack; Saswad pack) and Ahmednagar District (Ahmednagar pack), while the remaining four packs were located in Solapur District (Gangewadi 1 and 2 pack; Nannaj and Chapalgaon pack). The assessment of dietary overlap indicated that the highest overlap was observed between Pune and Ahmednagar Districts, while the lowest overlap occurred with the Solapur pack. This disparity in dietary overlap primarily stemmed from variations in food resource availability.

Notably, Pune and Ahmednagar Districts supported a population of chinkara, whereas blackbuck inhabited the Solapur district. Specifically, the Solapur district pack displayed a dietary composition consisting of 16.27% blackbuck, 32.67% goat, and a mere 4.42% chicken consumption. In contrast, the combined dietary preferences of the packs from Pune and Ahmednagar districts encompassed 2.88% blackbuck, 13.01% chinkara, 11.53% goat, and a substantial 41.49% chicken consumption. Consequently, chicken emerged as the dominant food source in the diets of wolf packs in the Pune and Ahmednagar districts.

The outcomes of this study, conducted within the same landscape as the previous research by Habib 2007, exhibit substantial alterations in the dietary patterns of wolf populations. Habib's 2007 study, which conducted a thorough analysis of 3947 scat samples collected from core wolf habitats between 2002 and 2005, did not genetically identify the wolf scats. Nevertheless, it serves as the baseline against which the findings of the current investigation are compared.

Firstly, a significant transformation in the dietary composition is evident. The consumption of wild prey, as evidenced by Habib's 2007 data, has significantly reduced from 38.01% to 23.77% in the current study. This shift suggests a potential change in predator-prey dynamics within the ecosystem. Such a decline in wild prey consumption could be attributed to various factors, including changes in prey availability as it decreased drastically over the years, wolf population change, availability of poultry waste, or an increase in anthropogenic activity in the landscape. The availability of poultry waste may lead to a decrease in wolf consumption of wild prey. Access to human-generated food sources like poultry waste can alter the wolves' dietary preferences, creating a shift away from natural prey as they exploit alternative and more easily accessible food resources in their environment.

On the contrary, the consumption of domestic prey has increased from 47.16% (Habib, 2007) to 59.38% in the last 15 years. This change may reflect the decreased wild prey population and increased proximity of wolves to human settlements and livestock-rearing areas, leading to more frequent encounters with domestic animals. Additionally, changes in land use patterns, habitat fragmentation, and human activities could contribute to this trend. Consuming domestic prey might provide wolves with a relatively easily accessible and abundant food source. Vegetative matter consumption has exhibited no change over the 15 years. This stability could be attributed to the consistent availability of plant-based food sources in the landscape. Wolves might consume vegetation opportunistically, either as supplementary nutrition or to aid digestion. While examining coyote behaviour, Tremblay et al. (1998) and Samson and Crete (1997) conducted investigations within the forested regions of northeastern Canada. Their findings suggested an elevated consumption of wild berries, which appeared to be influenced by their seasonal availability. While fruits and wild berries can contribute to the energetic demands of carnivores, their dietary value may not align with that of mammalian prey. The specific dietary preferences of carnivores are notably influenced by a convergence of factors, including seasonal dynamics and energy requirements.

Furthermore, the significant increase in chicken consumption, increasing 27 times more than previously reported, underlines a potential shift in food preferences. This may be linked to the widespread availability of poultry due to human agricultural practices. The shift towards consuming more chicken could also be influenced by factors like ease of access, reduced risk from hunting wild prey, and potentially higher caloric content from domestic sources.

The substantial decline in blackbuck consumption from 27.5% to 8.40% is noteworthy. This could indicate changes in the distribution and availability of blackbuck in the landscape, along with shifts in wolf hunting strategies or predation pressures. The changes in landuse patterns, increasing anthropogenic factors affecting blackbuck habitats and interactions with other species could contribute to this decline. The observed changes in wolf dietary preferences underscore the intricate interplay between ecological factors, human activities, and predator-prey dynamics. These findings emphasise the need for ongoing monitoring and conservation efforts to maintain balanced and sustainable ecosystems, considering the potential cascading effects of such dietary shifts on predator and prey populations.

The food habits of wolves hold significant scientific importance due to their multifaceted implications for ecological understanding, conservation management, and ecosystem health. Knowledge of wolf food habits enables assessment of their impact on prey species. This is crucial for managing prey populations. Insights into wolf dietary preferences aid in developing effective conservation strategies. Understanding what wolves consume helps anticipate potential human-wildlife conflicts. Information on wolf food habits aids in adaptive management. Conservationists and policymakers can continuously monitor diet preferences and adjust management strategies in response to changing ecological conditions.

In conclusion, the scientific investigation of wolf food habits provides a holistic understanding of ecosystem intricacies, enabling informed conservation decisions and sustainable management strategies. By unravelling the dietary preferences of wolves, researchers contribute to the broader field of ecology, ultimately fostering the coexistence of wildlife, humans, and healthy ecosystems.

Chapter 5

Chapter 5

5.1 Conclusion

Grey wolves are widely distributed across North America, Europe, and Asia, occupying diverse habitats. They feed on various prey, with diet variations among subspecies and regions. Wolves are vital to ecosystems, yet their survival hinges on human coexistence and conservation efforts.

In India, two major wolf populations, the Himalayan/Woolly wolf (*Canis lupus chanco*) and Indian wolf (*Canis lupus pallipes*), have distinct lineages. While the woolly wolf adapted to cold desert regions in India, the Indian wolves adapted to arid conditions and are vital for open plains ecosystems. Their distribution spans 13 Indian states, primarily in semi-arid zones. Despite legal protection, human-dominated landscapes and conflicts threaten their existence. Indian wolves rely on domestic livestock due to low natural prey availability.

The thesis emphasizes the need for focused conservation in rapidly changing habitats. Understanding wolf movement, denning ecology, and food habits is essential for effective mitigation strategies. With increasing human populations and habitat alterations, studying how wolves adapt and cope is crucial for devising species-specific conservation plans. Overall, this thesis underscores the urgent need for conserving wolves to maintain ecological balance and biodiversity.

This thesis investigated the movement patterns and behaviour of Indian wolves in the context of their ecology in the human-dominated landscape. The research focused on aspects such as daily movement, seasonal variation, sex-based differences, home ranges and habitat preferences to gain insights into the adaptation of wolves in a changing environment.

The study reported that Indian wolves exhibit a wide range of daily movement, with an average of 10,357 meters per day and a significant variation between individuals, attributed to factors like age and sex. Other studies reported that, depending on prey availability, wolves can travel up to 80,000 meters per day. Various ecological conditions also influence movement patterns. In North America, wolves in areas with high ungulate density cover distances between 1,600 and 9,000 meters per day, while in regions with rich ungulate populations, as in Poland's temperate lowland forest, they cover about 4,400 meters per day.

Sex-based differences in movement are evident, with males showing 19.17% higher movement than females. This difference is associated with males' and females' distinct roles in the pack, with males being more active hunters. Adult wolves generally exhibit greater movement than subadults, possibly due to the involvement of subadults in nurturing the pups. During the denning and breeding seasons, females' movement decreases significantly, aligning with their responsibility for pup care and den maintenance. The study underscores the nuanced relationship between movement and reproductive activities, revealing a 36.94% reduction in female movement during the breeding season.

Seasonal variation is prominent, with wolves moving more during the summer and pre-monsoon periods, attributed to food scarcity. During winter, when the denning and breeding season occurs, movement decreases, and the presence of a nomadic community provides food resources in the form of sheeps and goats in the landscape.

Habitat preferences indicate that Indian wolves predominantly utilize grasslands and open areas, demonstrating a preference for grassland patches despite their availability. Water bodies are generally avoided, possibly due to the association with human presence in the landscape. Human-influenced areas like agriculture and built-up regions are strongly avoided.

This study examined the den and rendezvous site selection patterns of Indian wolves in a human-dominated landscape. By examining factors such as proximity to water, vegetation cover, and human influence, the research provides insights into the ecological choices made by these wolves in a changing environment.

The study revealed that the presence of grasslands, plantations, and scrub forests significantly influences den and rendezvous site selection. Vegetation cover and proximity to water emerge as crucial factors for den site selection, while proximity to escape cover and negative association with vegetation cover are associated with rendezvous sites. The investigation aligns with previous findings suggesting wolves prefer grassland areas for den sites and rendezvous sites near open areas bordered by tree cover or thickets.

Notably, the study reported that a significant portion of dens are constructed on bunds, which are soil and stone structures lining agricultural fields. This unique den site choice is likely linked to water confinement, aiding soil fertility and moisture retention. Furthermore, dens are strategically situated away from human settlements, with proximity to essential water sources. Water proximity reduces the need for adults to venture far from the den, ensuring their presence for pup care.

The study underscores the importance of den sites for pup protection and early development. Den temperature and humidity provide optimal conditions for pup survival, and dens continue to serve as central hubs as pups transition to consuming regurgitated food. Rendezvous sites serve as resting and play areas where pups are left under subadult supervision while adults go out to hunt.

While similar studies have been conducted in North America and Europe, this research pioneers the investigation of den and rendezvous site selection in the Indian context. The findings contribute baseline information for Indian wolf conservation in a landscape characterised by habitat degradation, human expansion, and declining prey abundance. By identifying key characteristics of den and rendezvous sites, this study lays the foundation for informed conservation strategies to safeguard the unique ecological role of Indian wolves in the face of growing anthropogenic pressures.

This thesis also investigated the food habits of Indian wolves within the human-dominated landscape of Maharashtra. The study employed a combination of conventional non-invasive scat analysis and molecular techniques to validate scat identification, providing novel insights into the wolves' diet composition and changes over time. Notably, the study goes beyond traditional linear models, utilising exponential biomass models to understand the relative contribution of different prey items.

Out of 430 collected scats, 348 were identified as Indian wolf scats. The analysis revealed that domestic prey, such as goats and sheep, constituted a significant portion (52.04%) of the biomass consumed, while wild prey, including blackbuck and chinkara, contributed 38.10%. Vegetative matter, such as ziziphus, grapes, and grasses, was also present in most scats, potentially aiding digestion.

A notable difference was observed by comparing this study’s findings with previous studies on Indian wolf diets. Domestic prey consumption has increased, while the consumption of wild prey has declined. The significant increase in chicken consumption is likely attributed to the widespread availability of poultry waste in the landscape. The decline in blackbuck consumption and stability in vegetative matter consumption also shed light on changing ecological dynamics.

The study also assesses dietary overlap among Pune, Ahmednagar, and Solapur Districts wolf packs. Notably, variations in food resource availability lead to differing dietary preferences. Chinkara and blackbuck emerge as the most preferred food items, while chicken is a dominant choice in Pune and Ahmednagar districts due to its availability from local poultry waste.

The study contributes novel insights into Indian wolf ecology, shedding light on their movement patterns and adaptation strategies in a human-dominated environment. The findings underscore the complex interplay between ecological factors, human activities, and predator-prey dynamics. The shifts in wolf dietary preferences highlight the need for ongoing monitoring and conservation efforts to maintain balanced ecosystems. Understanding these dietary patterns aids in assessing the impact of wolves on prey species, developing conservation strategies, predicting human-wildlife conflicts, and guiding adaptive management approaches. This comprehensive investigation into the food habits of Indian wolves enhances our ecological understanding and contributes to effective conservation and management strategies. By unravelling the complexities of wolf diets, the research supports harmonious coexistence between wildlife, humans, and the environment.

In conclusion, the findings enhance our understanding of how wolves move, select den and rendezvous sites, and their food habits in the landscape. This research provides valuable information for conservation and management efforts to conserve the unique ecological role of Indian wolves in shared landscapes.

5.2 Management Implication

The Indian wolf is vital to India's biodiversity and crucial to maintaining ecosystem health and balance. However, this study has indicated significant shifts in the wolf's diet, habitat preferences and changes in movement patterns. A comprehensive scientific management strategy is proposed to ensure the conservation of this species.

The primary objectives are to conserve and sustainably manage the Indian wolf population while mitigating conflicts with humans and promoting coexistence. The strategies aim to address changes in diet, movement patterns, habitat selection, and anthropogenic influences.

Habitat Protection and Restoration: Collaborate with local communities, NGOs, and government agencies to establish and manage protected areas encompassing critical wolf habitats, including grasslands, scrub forests, and plantations. Over the years, the plantation that plays a crucial role in the denning ecology of these wolves has not changed area-wise, but the anthropogenic disturbances around these areas and expansion of village boundaries toward these areas have increased significantly. These plantations should be well monitored, and fewer activities should be allowed, especially during the breeding season of Indian wolves.

Seasonal Movement Monitoring: Continuously track wolf movements and analyze data to understand seasonal variations, helping identify critical corridors and potential barriers for movement.

Habitat Connectivity: Collaborate with infrastructure development projects to incorporate wildlife corridors and underpasses in critical areas to ensure safe movement and gene flow between populations.

Monitoring Diet Composition: Continue regular scat analysis to assess changes in diet composition and evaluate the impact of shifting preferences on prey populations. Implement measures to enhance the availability of natural prey species through habitat management and restoration.

Human-Wildlife Conflict Mitigation: Develop and implement measures to minimize conflicts with humans, such as providing incentives for adopting livestock protection practices, improving waste management in human settlements to reduce attractants, and promoting community-based initiatives for coexistence.

Habitat Conservation at Den Sites: Strengthen the protection of den sites by establishing buffer zones and restricted access areas, limiting human disturbance during the breeding season.

Poultry Waste Management: The significant increase in poultry waste consumption by wolves in Landscape is a matter of concern, and dumping this waste should be stopped immediately. Consuming poultry waste poses several risks and potential harm to Indian wolves. Poultry waste, which includes discarded parts of chickens, can negatively impact wolves' health and behaviour due to disease transmission, chemical contaminants, altered nutritional balance, dependence on human proximity, and disruption of natural behaviour. In the context of the proposed management plan, understanding the risks associated with consuming poultry waste will be crucial for devising effective strategies to discourage wolves from accessing such waste and promoting their reliance on natural prey sources.

Awareness and Education: Conduct outreach programs to educate local communities about the importance of den and rendezvous site protection and involve them in monitoring efforts.

Continuous Monitoring: Maintain a long-term monitoring program using advanced technology to gather data on movement patterns, diet composition, and habitat preferences, with regular updates on population dynamics.

Local Community Participation: Engage local communities as key stakeholders in conservation efforts, involving them in decision-making processes and providing economic incentives for conservation-friendly practices.

By implementing this comprehensive scientific management strategy, we can ensure the conservation of the Indian wolf population while addressing the challenges posed by changing diet patterns, habitat fragmentation, and human-wildlife conflicts. Collaborative efforts between communities, researchers, NGOs, and government agencies will play a pivotal role in securing the future of this important apex predator's future and maintaining its habitat's ecological balance.

5.3 Limitations of the Study and Proposed Future Research Plan

It is essential to acknowledge several shortcomings and limitations of the current study that may influence the effectiveness of the proposed measures.

Limited Socioeconomic Context: The study primarily focuses on ecological and biological aspects of Indian wolf conservation. It does not extensively consider the socioeconomic context of local communities living near wolf habitats. Economic, cultural, and social factors play a significant role in shaping human-wildlife interactions. Future research should include in-depth socio-economic studies to understand better local communities' motivations, attitudes, and perceptions toward wolves and the proposed mitigation measures.

Prey Dynamics: Although the study briefly discusses changes in the wolf's diet composition and shifts towards domestic prey, it does not delve deeply into the dynamics of prey populations. Detailed studies on the population trends of key prey species and their interactions with predators and habitat changes are necessary to understand the implications of altered diet preferences on predator and prey populations.

Radio-collaring of more individuals: Radio collars more individuals to understand wolf movement in different habitats, especially the wolves that use forested areas.

Interaction between sympatric carnivores: I evaluated the diet using 348 wolf scats in this study. A thorough study should be done by analysing Golden jackals, Indian foxes and feral dogs to understand the dietary overlap in the landscape.

Long-Term Monitoring: Extend the duration of data collection to capture long-term trends in wolf movement patterns, habitat preferences, and diet composition. This will provide a more accurate assessment of the effects of changing environmental conditions on the species.

Prey-Predator Dynamics: Conduct detailed studies on the dynamics of wild and domestic prey populations. Assess the impacts of changes in wolf diet preferences on prey populations and examine how prey availability influences wolf movement patterns and behaviour.

Enhanced Community Engagement: Develop and implement innovative community engagement strategies, including participatory workshops, citizen science initiatives, and cultural exchange programs. Collaborate closely with local communities to co-design and adapt conflict mitigation measures that align with their needs and values.

Landscape-Level Analysis: Conduct landscape-level analyses to assess connectivity between different habitats and identify potential corridors for wolf movement. This will inform infrastructure development plans that promote safe wildlife movement.

In conclusion, while the scientific management plan offers a strong foundation for Indian wolf conservation and conflict mitigation, recognising the study's limitations and directing future research efforts toward addressing these gaps will enhance the plan's applicability, effectiveness, and long-term success in promoting harmonious coexistence between humans and this important species.

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

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Abstract

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

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

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

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

KEYWORDS

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

1 | INTRODUCTION

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

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

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

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

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

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

2 | MATERIALS AND METHODS

2.1 | Study area

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

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

2.2 | Study species

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

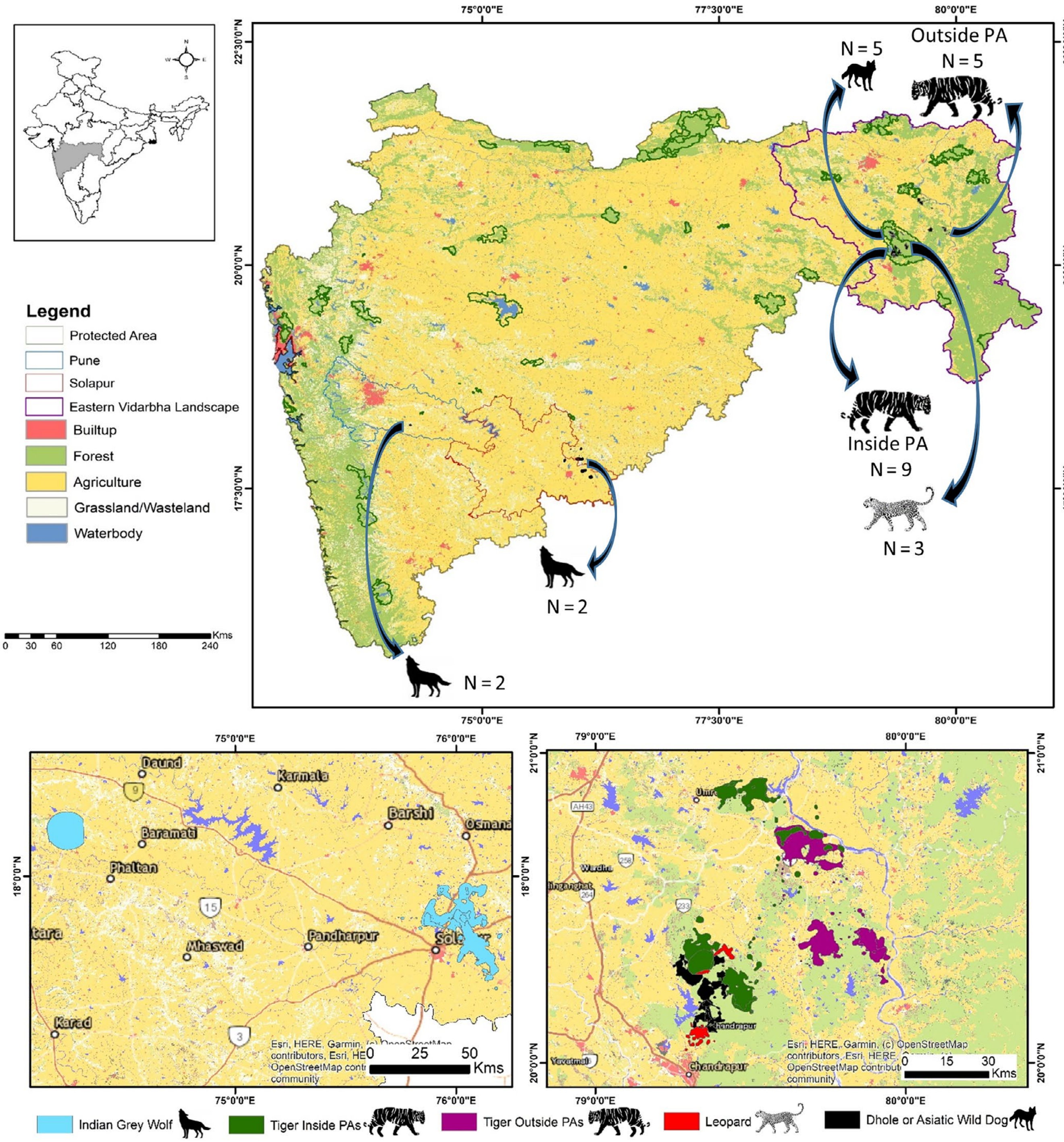

FIGURE 1 Map of study sites (top) with landuse and protected areas, (below left) home ranges of wolves and (below right) home ranges of tigers inside and outside PA, leopard, and dhole in Maharashtra, India

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

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

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

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

2.3 | Capture and radio-collaring

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

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

2.4 | Understanding movement parameters

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

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

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

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

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

2.5 | Understanding effect of anthropogenic factors on movement

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

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

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

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

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

2.6 | Core area of large carnivores in heterogeneous landscape

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

3 | RESULTS

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

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

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

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

3.1 | Movement parameters of large carnivores

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

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

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

3.2 | Effect of anthropogenic factors on movement of large carnivores

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

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

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

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

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

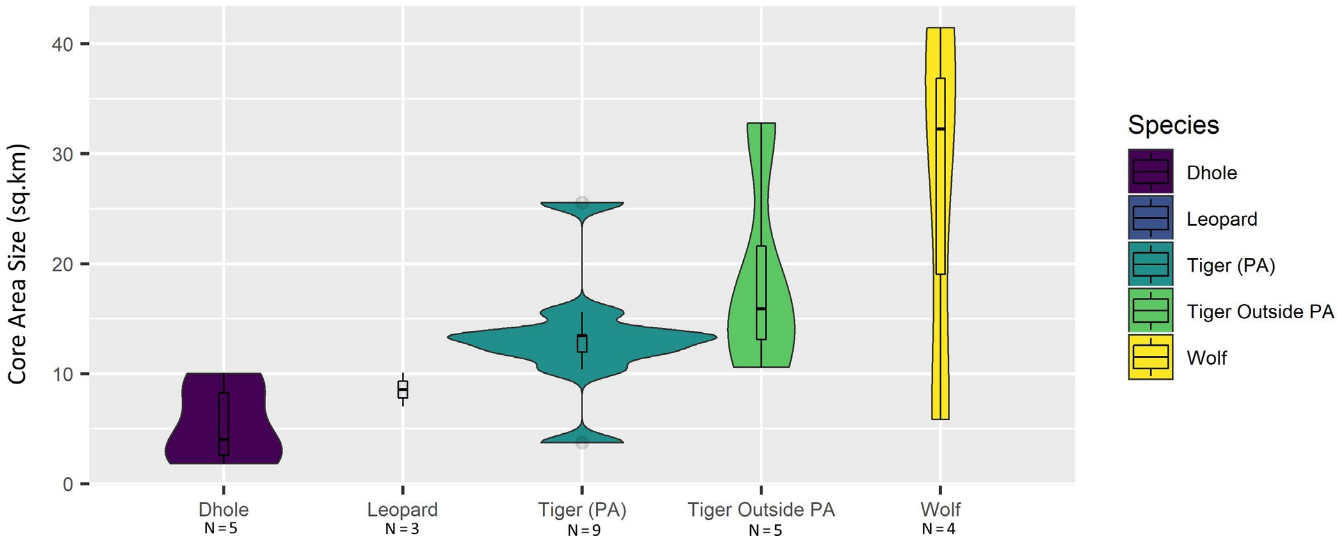

FIGURE 2 Violin plot indicating the distribution of the range of the core area size, median (black center line), and spread of the data (black rectangle) for four large carnivores in India

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

3.3 | Core area of large carnivores in heterogeneous landscape

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

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

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

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

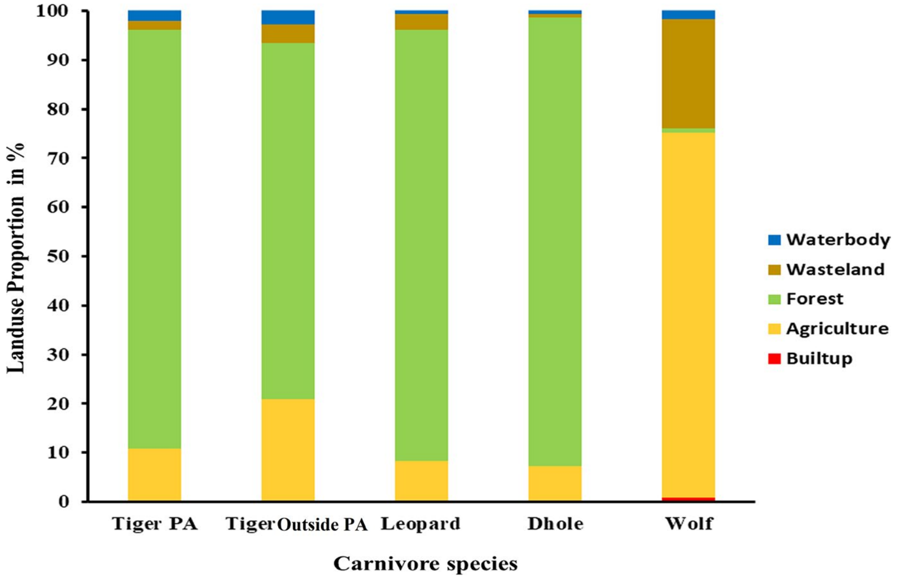

FIGURE 3 Landuse proportion within the home range of four large carnivores in India. Data from Bhuvan's LULC (http://bhuvan.nrsc.gov.in/) was used to classify home ranges

4 | DISCUSSION

4.1 | Movement of large carnivores across human-dominated landscapes

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

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

4.2 | Effects of human footprint on movement of large carnivores

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

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

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

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

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

4.3 | Core area of large carnivores in heterogeneous landscape

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

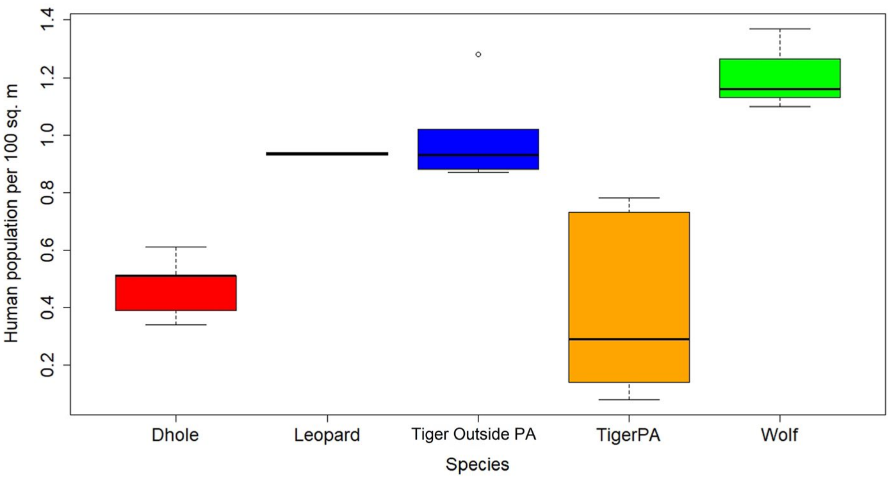

FIGURE 4 Human population density within the home range of four large carnivores in India

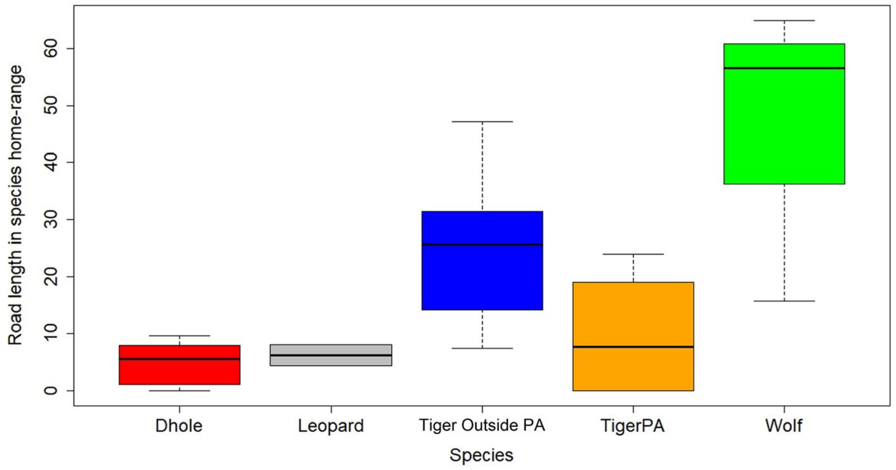

FIGURE 5 Road length (km) within the home range of four large carnivores in India

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

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

5 | CONSERVATION IMPLICATIONS

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

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

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTION

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

ETHICAL APPROVAL

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

DATA AVAILABILITY STATEMENT

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

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Comparative Ecological Perspectives of Two Ancient Lineages of Gray Wolves: Woolly Wolf (*Canis lupus chanco*) and Indian Wolf (*Canis lupus pallipes*)

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Geographical isolation can often lead to speciation, and two disconnected populations of the same species living in drastically different bioclimatic regions provide an opportunity to understand the process of speciation. The Woolly wolf is found in the cold-arid, *Trans*-Himalayan landscape, while the Indian wolf inhabits the semi-arid grasslands of Central India. Both the lineages of wolves from India have generated scientific debate on their taxonomic status in recent years. In this study, we collected data and reviewed published literature to document the ecological and behavioral differences between the Woolly wolf and the Indian wolf. Most studies have used genetic data; hence we discuss variation in spatial ecology, habitat preferences, vocalization, diet diversity and cranial measurements of these two subspecies. The spatial ecology of two lineages was compared from the data on three Woolly and ten Indian wolves tagged with GPS collars. The telemetry data shows that there has been no difference in the day-night movement of Woolly wolves, whereas Indian wolves show significant high displacement during the night. The BBMM method indicated that Woolly wolf home ranges were three times larger than the Indian wolf. The Woolly wolf diet is comprised of 20 different types of food items, whereas the Indian wolf diet consists of 17 types. The Woolly and Indian wolf largely depend upon domestic prey base, i.e., 48.44 and 40.34%, respectively. We found no differences in the howling parameters of these subspecies. Moreover, the Woolly wolf skull was significantly longer and broader than the Indian wolf. Wolves of India are ancient and diverged from the main clade about 200,000–1,000,000 years ago. Their genetic and ecological evolution in different bioclimatic zones has resulted in considerable differences as distinct subspecies. The present study is a step in understanding ecological differences between two important, genetically unique subspecies of wolves.

Keywords: howling, peninsular India, spatial ecology, *Trans*-Himalayas, conservation, food habit, movement ecology

INTRODUCTION

Divergent selection can occur among populations with varying environmental conditions, habitats, climates, resource types and phylogeographic patterns (Schluter, 2000; Dieckmann et al., 2004). The phylogeographic patterns isolate populations that inhabit same geographic range but are unable to interact due to the presence of natural barriers, unsuitable habitat or a combination of these factors that could hinder movement (Avise et al., 1987). The long isolation of closely related populations could eventually lead to speciation by accumulating genetic changes over time. Studying and tracking the differences in species ecology, climatic conditions, and reproductive isolation between populations is essential to understand the formation of incipient species and plan appropriate conservation strategies (Moritz, 1994; Rundell and Price, 2009; Sobel et al., 2010). The mechanism of geographic isolation bringing about divergent evolution is well known in the birds, e.g., Darwin's finches in the subfamily Geospizinae (Sulloway, 1982) and five sub-species of the masked yellowthroat (*Geothlypis aequinoctialis*) in Central and South America (Curson et al., 1994). Among mammals too, four subspecies of Cheetah (*Acinonyx jubatus*) (Kitchener et al., 2017) and three subspecies of snow leopard (*Panthera uncia*) (Janecka et al., 2018) have evolved in different geographical areas. While speciation is an outcome of long isolation, shorter time-scale could set the populations of the same species on different evolutionary paths. The wolves in British Columbia showed strong genetic differentiation between adjacent populations, explained by habitat discontinuity between the coastal and inland regions (Muñoz-Fuentes et al., 2009).

The gray wolf (*Canis lupus*), one of the most widely distributed mammals and most studied species across the world (Mech and Boitoni, 2003), has had several populations worldwide that evolved in isolation. The wolves are considered one of the most resilient carnivores that have adapted and succeeded in a wide range of habitats from tundra to the deserts (Mech and Boitoni, 2003). Currently, at least forty-four wolf subspecies are described based on the variations in morphological features, behavioral aspects, and geographical distribution (Wozencraft, 2005). However, the status of many of these subspecies is uncertain and contested among scientists (Busch, 2018), making gray wolf taxonomy highly debatable (Shrotriya et al., 2012; Pilot et al., 2014; Ersmark et al., 2016). Several taxonomic resolutions are pending validation and revision at the species as well as subspecies level. Amid a muddled account of the number of species and sub-species, studies suggested that wolves from the Indian regions could form the oldest lineages (Aggarwal et al., 2003, 2007; Sharma et al., 2004; Shrotriya et al., 2012; Werhahn et al., 2017, 2018; Hennelly et al., 2021).

There are two major wolf populations in India, i.e., Woolly wolf (*C. l. chanco*) (also known as Tibetan or Himalayan wolf) and Indian wolf (*C. l. pallipes*). These wolves are supposed to have diverged from the main clade about 800,000 and 400,000 years ago, respectively (Sharma et al., 2004; Aggarwal et al., 2007; Shrotriya et al., 2012; Werhahn et al., 2017; Joshi et al., 2020). However, a recent study suggested a contradicting possibility that the Indian wolf could be basal to the Woolly wolf (Hennelly et al., 2021). The study stated that Indian and Woolly/Tibetan wolves shared the most common ancestors with Holarctic wolves 200,000 and 500,000 years, respectively (Hennelly et al., 2021). These differences in the year of divergence are mainly due to the selection of genes and the method used for the analysis. Isolated evolution of the Woolly wolf corresponds with rapid uplift of the Tibetan plateau and associated habitat modifications (Sun and Liu, 2000), which may have endowed them with the genetic adaptation for the cold and arid landscape of the *Trans*-Himalayas (Werhahn et al., 2018). The Indian wolf is believed to have evolved during the drier period of the Pleistocene and adapted to survive in the arid zones (Sharma et al., 2004; Singh and Kumara, 2006). After the extinction of Cheetah from India, it became the top carnivore species of the Indian open plains (e.g., semi-arid grasslands, scrublands, and grazing lands). Some of the studies proposed that the wolves of India were not subspecies but qualified as separate species viz. *Canis himalayensis* and *Canis indica* (Aggarwal et al., 2007). The debate regarding their taxonomic status is unsettled yet (Alvares et al., 2019). Nonetheless, both wolves could be presumed two distinct lineages (Pocock, 1941) and are geographically isolated, having allopatric distribution in India (Aggarwal et al., 2003). The Woolly wolf is found in the cold-arid zone of the upper *Trans*-Himalayas of India, covering the state of Himachal Pradesh and in two union territories, Ladakh and Jammu and Kashmir, with sightings recorded from Uttarakhand and Sikkim (Bhattacharya and Sathyakumar, 2010; Habib et al., 2013; Choudhury, 2015). The population estimates for both the lineages are not very accurate. As per the last available estimate, only 350 individuals of the Woolly wolf were found (Fox and Chundawat, 1995) which is a rough estimate for the Woolly wolf as it was assessed for the Ladakh and Spiti regions of India covering an area of 60,000 km^2. The Indian wolf is distributed across 13 states of India, primarily in the semi-arid zone with the latest population estimate of 1200–1800 packs (Jhala et al., 2013). Both the wolves inhabit open and grassland habitats and survive primarily outside protected areas. However, the Woolly wolf is functioning in far less anthropogenic pressure compared to the Indian wolf. Wolves in India are majorly found in non-protected areas with low natural prey populations (Habib, 2007; Maurya et al., 2011; Shrotriya et al., 2015; Habib et al., 2021b). Therefore, in most of their range in India, wolves primarily subsist on domestic livestock (Shahi, 1982; Mishra, 1997; Jethva and Jhala, 2004; Habib, 2007; Werhahn et al., 2019; Lyngdoh et al., 2020; Habib et al., 2021b) and are severely persecuted as a consequence. Although both these wolves are protected as Schedule I species under the Indian Wildlife (Protection) Act 1972. In spite of protection, conserving a species that resides in a human-dominated landscape and comes in direct conflict is a challenge.

The two lineages of wolves from India are unique and require focused conservation measures. Since both the lineages have remained isolated for a long period and functioning in two different bioclimatic zones, biological, ecological, and behavioral differences are expected to arise in these two populations. Understanding the differences is important because both subspecies are subject to management actions as they survive in a human-dominated landscape in India. In this study, we provide a comparative ecological perspective on spatial ecology, vocalization, food habits and cranial morphometry of these two lineages. The current study will help plan and implement better conservation and management actions. Moreover, information incorporating genetic analyses, morphology, and behavior using a comparative approach will help understanding key differences between the two lineages.

MATERIALS AND METHODS

We used primary as well as secondary data to elucidate differences in movement, space use, habitat use, howling characteristics, cranial morphology and diet.

Habitat Preferences, Movement, and Space Use Using Primary Data

A total of 14 individuals (11 Indian wolves and three Woolly wolves) were captured, radio-collared, and monitored from 2015 to 2021 to understand the movement, space use, and habitat preferences of two wolf lineages (**Table 1**). The Woolly wolves were captured in Himachal Pradesh and Indian wolves in Maharashtra, states of India. These wolves were captured using soft leg-hold traps. The traps (n = 25) were placed in a circular setup (radius = 70–80 cm), placed ∼20 cm apart from each other and tied with each other using rope (Habib, 2007). The wolf gland lure No. 100 (Stanley Hawbaker and Sons, Fort London, Pennsylvania) was used to attract the wolves toward traps. We also used fresh scats collected from different areas considering the scats were of different packs and placed around the traps to attract the wolf. The traps were connected to GSM-based device called "MinkPolice." This device operates with a magnetic switch and triggers a message on the registered email and phone numbers. Trapped wolves were held using double threaded nylon hockey net. The captured wolves were immobilized by injecting Ketamine–Xylazine (dosages based on the weight of the captured wolf) intramuscularly on their hind leg (Habib, 2007; Habib et al., 2021a). The immobilized wolves were fitted with 10 iridium, 3 Globalstar and 1 VHF collars.

Diet Diversity, Howling Parameters and Cranial Measurements Using Secondary Data

Data on the diet of both the wolf lineages were collected from published sources using specific keyword searches in Google scholar such as Tibetan wolf, Tibetan wolf diet, Himalayan wolf diet, Woolly wolf diet, *Canis lupus chanco*, Indian wolf diet, Indian gray wolf diet, *Canis lupus pallipes*. We found seven studies (two from India, three from Nepal, and two from Pakistan) to understand the Woolly wolf. For the Indian wolf diet, we found seven exclusive diet studies from Maharashtra, Gujarat, and Bihar States of India.

To understand the food habits of the Woolly and Indian wolves, we collected published data from different sources (detail provided in **Supplementary Table 1**). Different studies presented results in various forms, such as absolute frequency and relative frequency. To reduce the effect of study-specific variability, we first calculated the number of food items in the number of scats (**Supplementary Tables 2, 3**) and then calculated the relative frequency of occurrence (%RFO).

So far, there are two published studies on the howling parameter of the wolves from the Indian sub-continent (Hennelly et al., 2017; Sadhukhan et al., 2019). Hennelly et al. (2017) compared the vocalization of multiple wolf populations across the world, including the Woolly wolf and the Indian wolf and Sadhukhan et al. (2019) characterized the vocalization of the Indian wolves exclusively. Both the studies used nine parameters, such as mean frequency, maximum frequency, minimum frequency, frequency range, and end frequency, to understand the howling behavior of these two lineages. In these studies, the acoustic data were collected in the *Trans*-Himalayan region for Woolly wolf and Maharashtra for the Indian wolf.

The data on cranial morphometry of 14 Woolly and 20 Indian wolves were obtained from three studies, Allen (1938), Pocock (1941), and Srinivas and Jhala (2021). Data on total length (maximum length of skull from tip of rostrum to the nuchal crest); condyle basal length (distance from posterior projection of the occipital condyles to the anterior edge of pre-maxillary bones); zygomatic width (distance between outermost points of zygomatic arches), mandibular length (the distance from the jaw bone between the lower incisor of the anterior border of condyle); interorbital width (least distance between anterior orbits); post-orbital width (least distance between posterior orbits) and maxillary width (distance between the central fosse of the right and left first maxillary molars), PM4 (Pre-molar 4) and M1 (molar 1) were compared to understand the differences between the two subspecies (**Supplementary Figure 1**). The details of studies used for comparative ecological perspectives are provided in **Supplementary Table 1**.

Data Analyses

The movement patterns of wolves were assessed using parameters such as daily average displacement (straight-line distance between two consecutive fixes) and average displacement during day and night. The varying inter-fix intervals were made uniform by post-processing all the data into an hourly data format (Abrahms, 2015; Habib et al., 2021a). Average displacement during the day and night were calculated by classifying locations. Average displacements of both the lineages were compared using the Wilcoxon rank sum test. Home ranges were calculated using minimum convex polygon (MCP) and Brownian bridge movement model (BBMM) (Horne et al., 2007). To understand the habitat preferences of Woolly and Indian wolves the landuse data for the states of Himachal Pradesh and Maharashtra were acquired from Bhuvan's open-source website (NRSA, 2016).[1] Habitat use and preference of the Woolly and Indian wolf lineages were analyzed using Manly's resource selection function (Manly et al., 2002). The design-III study framework of habitat use, where the animals are identified individually and both the use and the availability are measured for each one, was applied (Thomas and Taylor, 1990). The data on "use" was calculated

[1] http://bhuvan.nrsc.gov.in/

TABLE 1 | Detail of each individual's characteristics and number of locations used to study the movement, space use and habitat use of wolf in India.

Species	Individual ID	Sex	Age	Area	GPS location used in the study	Monitoring days	Monitoring period
Indian Wolf	IW_F1	Female	Adult	Solapur	6748	615	25.12.17 to 01.09.19
Indian Wolf	IW_M1	Male	Adult	Solapur	2148	217	28.12.17 to 01.08.18
Indian Wolf	IW_F2	Female	Adult	Morgaon	6049	604	22.01.18 to 16.09.19
Indian Wolf	IW_M2	Male	Adult	Morgaon	*VHF Collar	604	22.01.18 to 16.09.19
Indian Wolf	IW_F3	Female	Sub-Adult	Ahmednagar	8452	416	25.06.19 to 14.08.20
Indian Wolf	IW_M3	Male	Sub-Adult	Ahmednagar	3185	141	23.06.19 to 15.11.19
Indian Wolf	IW_F4	Female	Sub-Adult	Saswad	7663	371	27.06.19 to 14.08.20
Indian Wolf	IW_M4	Male	Sub-Adult	Saswad	3111	137	27.06.19 to 11.11.20
Indian Wolf	IW_F5	Female	Adult	Solapur	2717	170	05.12.20 to 23.05.21
Indian Wolf	IW_M5	Male	Adult	Solapur	1998	141	03.01.21 to 23.05.21
Indian Wolf	IW_F6	Female	Sub-Adult	Solapur	1908	140	04.01.21 to 23.05.21
Woolly Wolf	WW_F1	Female	Adult	Spiti Valley	1049	260	06.07.15 to 21.03.16
Woolly Wolf	WW_F2	Female	Adult	Spiti Valley	729	189	03.09.16 to 10.03.17
Woolly Wolf	WW_M1	Male	Adult	Spiti Valley	1483	308	01.10.17 to 05.08.18

**IW_M2 fitted with VHF collar was not used in the analysis.*

from the number of GPS fixes and "availability" of land-use categories was calculated within the 100% MCP home range. All the measurements of movement parameters and analyses were carried out using ArcMET tool (Wall, 2014) in ArcGIS 10.6 and package "adehabitatLT," version 0.3.25 (Calenge, 2015a) and animal movement tool (amt, version 0.1.3) (Signer et al., 2017) in program R 4.0.3 (R Core Team, 2021). Habitat use analysis was performed using the package "adehabitatHS," version 0.3.15 in the program R, version 4.0.3 (Calenge, 2015b; R Core Team, 2021). For the comparison of cranial measurement of Woolly and Indian wolf we used two sampled unequal variance T-test and hedge's g test to evaluate the effect size.

We combined the food items consumed in all the studies to represent the overall diet of wolves in the landscape and calculated the relative frequency of occurrence (RO) of each food item. We tabulated the RO of each item (number of occurrences of each prey item in scats/total number of scats $\times$ 100). We categorized the food items into wild and domestic prey and also in the body-weight classes (0–10 kg small prey; 11–70 kg medium-sized prey; >70 kg large prey) to compare the food habits. The details of studies used to comprehend the feeding habits of the two subspecies is provided in **Supplementary Tables 2, 3**.

RESULTS

Spatial Ecological Perspectives Based on the Movement Characteristics and Home Ranges of Woolly and Indian Wolves

A total of 47,240 fixes across 13 individuals (five males and eight females) of the wolves were analyzed (**Table 1**) to examine daily movement, movement during day and night time, space use, and habitat use. The average hourly displacement of the Indian wolf (527.68 $\pm$ 111.52 m/hr) was significantly (W = 29, p = 0.01) higher than the Woolly wolf (338.54 $\pm$ 34.82 m/hr). The mean hourly displacement during the day for Indian wolf (393.71 $\pm$ 172.43 m/hr) and Woolly wolf (316.70 $\pm$ 18.7 m/hr) was not significantly different (W = 12; p = 0.6). However, the mean hourly displacement during nighttime was 53% higher for the Indian wolf than the Woolly wolf and the result was significantly different (W = 28, p = 0.02) (**Figure 1**).

We evaluated the home range and core area sizes of both the lineages (Woolly wolf n = 3; Indian wolf n = 10) to compare the space use (**Figure 2**). The Woolly wolf home range was significantly larger (1689.80 km^2, range 827.54–3055.45 km^2) than the Indian wolf home range (212.26 km^2, range 4.92–981.48 km^2) based on 95% MCP (W = 1; p = 0.01). The core area (50% MCP) for the Woolly wolf was also larger (352.71 km^2, range 273.18–477.51 km^2) than that of the Indian wolf (20.37 km^2, range 0.53–51.05 km^2) (**Figure 3**). The 95% BBMM of the Woolly wolf was significantly larger (374.17 km^2, range 283.93–422.17 km^2) than that of the Indian wolf (130.86 km^2, range 4.7- 399.56 km^2) (W = 3; p = 0.04). The core area (50% BBMM) for Woolly wolf was also larger (37.74 km^2, range 37.74–28.37 km^2) than the Indian wolf (13.07 km^2, range 0.63–54.43 km^2), but values were not statistically significant (W = 4; p = 0.07) (**Figure 3**).

Habitat Ecology Based on the Land Use Preferences of Woolly and Indian Wolves

Resource selection function revealed a preferential selection for landuse categories by the Woolly wolf (Khi2L = 77.26, df = 6, $p < 0.001$) and the Indian wolf lineages (Khi2L = 520.3487, df = 35, $p < 0.001$). While riversides, marshes (valley habitat) (Wi = 6.44 $\pm$ 3.86SE) and scrub forests (Wi = 2.58 $\pm$ 3.39SE) were preferred by the Woolly wolf whereas the Indian wolf preferred grassland areas (Wi = 2.86 $\pm$ 0.37SE) and plantations (Wi = 2.71 $\pm$ 1.25SE). Builtup and agriculture areas were very less used in proportion to its availability by both the wolves (**Figure 4A**). In addition, the Woolly wolf and the Indian wolf avoided snow cover and waterbodies, respectively (**Figure 4B**).

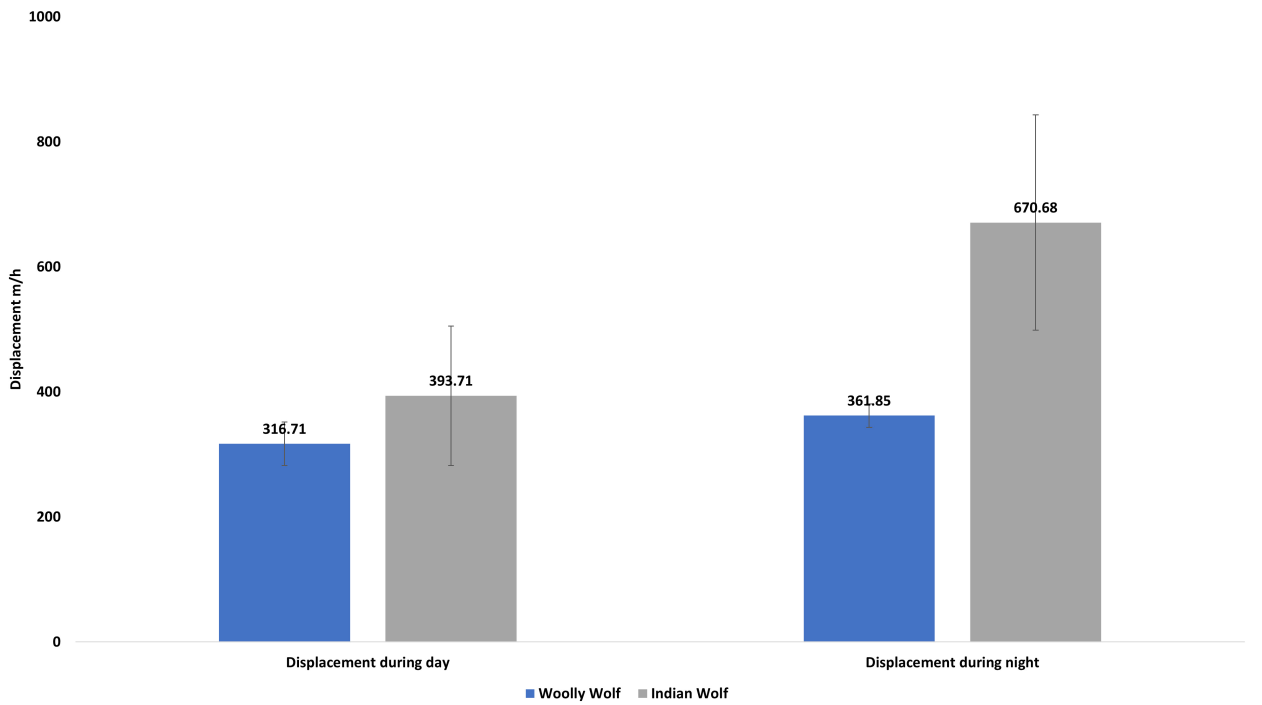

FIGURE 1 | Daily overall displacement, average daytime and nighttime displacement (meter per hour; m/h) of the Woolly and Indian wolf.

Comparison of Howling Parameters of Woolly and Indian Wolves

Hennelly et al. (2017) suggested that the Indian wolf exhibited higher mean frequencies (593.5 Hz ± 211.4SE), wider frequency ranges (197.1 Hz ± 137.4SE), and longer duration (2.71 s ± 2.11SE) based on 117 howl recordings. On the other hand, 301 howls of the Woolly wolf characteristically had a lower mean frequency (428.5 Hz ± 125.7SE), shorter duration (2.56 s ± 1.68SE), and unmodulated frequency variation (101.8 Hz ± 107.1SE) (**Table 2**). In contrast to Hennelly et al. (2017), the Indian wolf howl parameters reported by Sadhukhan et al. (2019) were broader in range and overlapped with the howling parameters of the Woolly wolf (**Table 2**). Sadhukhan et al. (2019) reported 422.2 Hz ± 126.40SE mean frequency and longer duration 5.21 s ± 2.49 for the Indian wolf howl (**Table 2**). Sadhukhan et al. (2019) collected data on 238 howling records of the Indian wolves from Maharashtra, in the same landscape where Hennelly et al. (2017) collected their samples of 117 Indian wolf howls.

Comparative Food Habits of Woolly and Indian Wolf

We found seven studies exclusive on the diet of Woolly wolf covering the Himalayan region in India, Pakistan and Nepal. There were 20 different items (**Supplementary Table 2**) reported in Woolly wolf diet from 869 scats with 124.14 (± 190.94 SD) scats per study. The relative frequency of occurrences (RO) in scats for wild prey, domestic prey and vegetative matter were 41.93, 48.44, and 6.46%, respectively. The RO in scats of Woolly wolves for large, medium and small-sized prey were 32.32, 33.87, and 24.18%, respectively (**Figure 5A**). About 70% of the Woolly diet consisted of goat, marmot, blue sheep, and pika, with a major contribution of cattle.

Another seven studies exclusively on the diet of Indian wolves from Rajasthan, Bihar and Maharashtra states of India revealed 17 different prey items from 6,877 scats with 982.42 (± 1363.67 SD) scats per study (**Supplementary Table 3**). The RO in scats for wild prey, domestic prey and vegetative matter was found 49.32, 40.34, and 9.31%, respectively. The Indian wolf diet primarily consisted of 67.95% of medium-sized prey followed by small (13.65%) and large-sized prey (7.15%) (**Figure 5B**). 75% of food items consisted of blackbuck, goat, sheep and hare in the Indian wolf diet with the major contribution of livestock.

Cranial Measurement of Woolly and Indian Wolves

We re-examined the data and compared the morphological differences between the two sub species. We found a significant difference between the two subspecies in the total length of the skull (p = 0.004; hedge's g = 2.15), condyle basal length (p = 0.003; hedge's g = 1.21), zygomatic width (p < 0.001; hedge's g = 1.31) and mandibular length (p = 0.04; hedge's g = 1.002) (**Figure 6A**), interorbital width (p < 0.001; hedge's g = 1.79), post-orbital width (p < 0.001; hedge's g = 1.12), maxillary width (p = 0.001; hedge's g = 1.29), pre-molar4 (p < 0.001; hedge's g = 1.52), and molar1 (p < 0.001; hedge's g = 1.65) (**Figure 6B**).

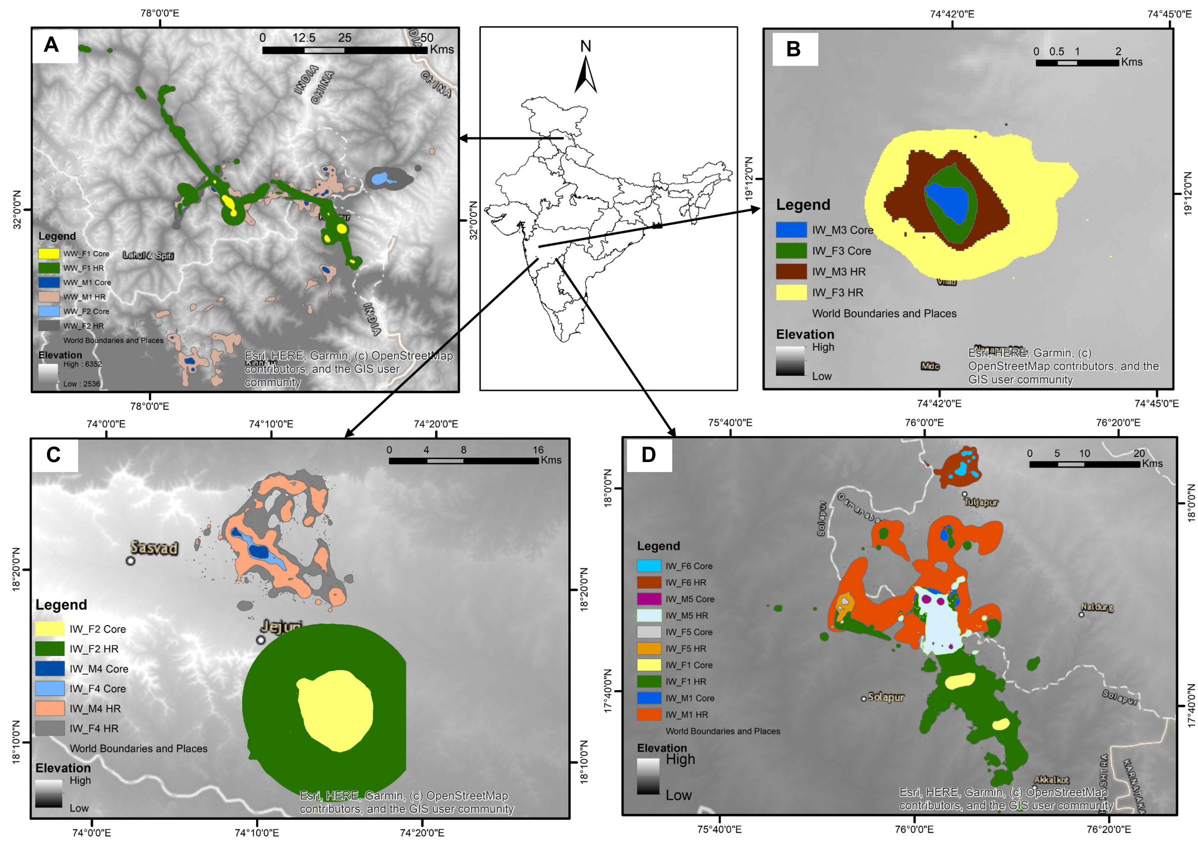

FIGURE 2 | Distribution pattern of the collared individuals [**(A)** Woolly wolf, **(B–D)** Indian Wolf] using BBMM (50% contour- core area; 95% contour- home range) from Himachal Pradesh, and Maharashtra, India, respectively (BBMM: Brownian bridge movement model).

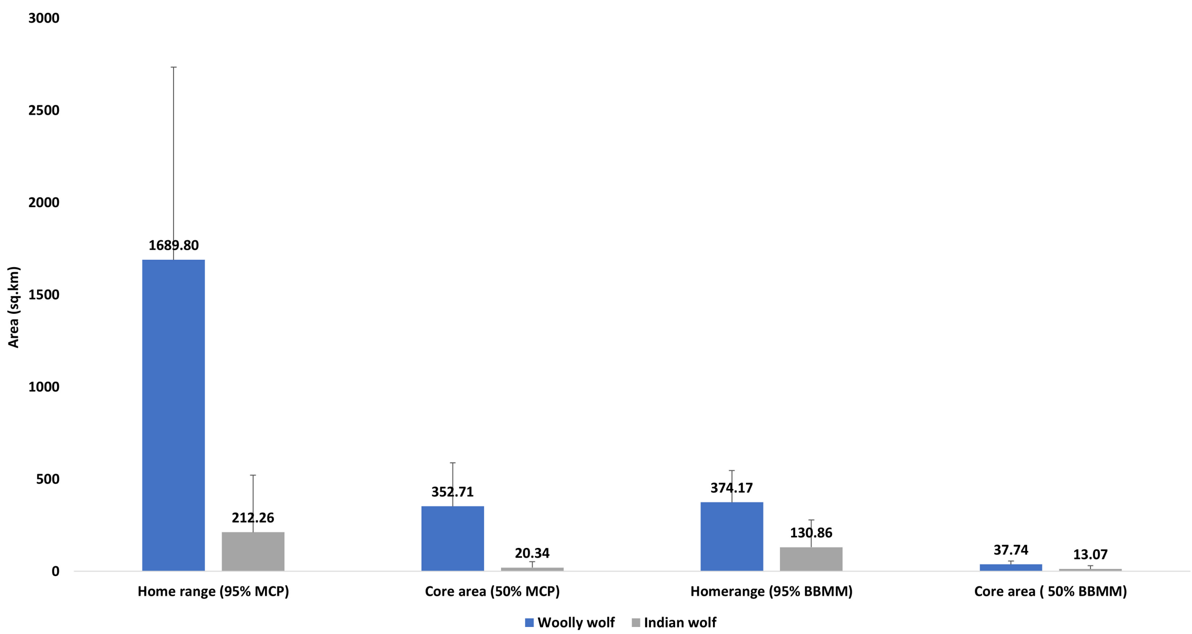

FIGURE 3 | Comparison of the home ranges (95% MCP and BBMM) and core area (50% MCP and BBMM) used by the Woolly and Indian wolf (MCP; minimum convex polygon; BBMM: brownian bridge movement model).

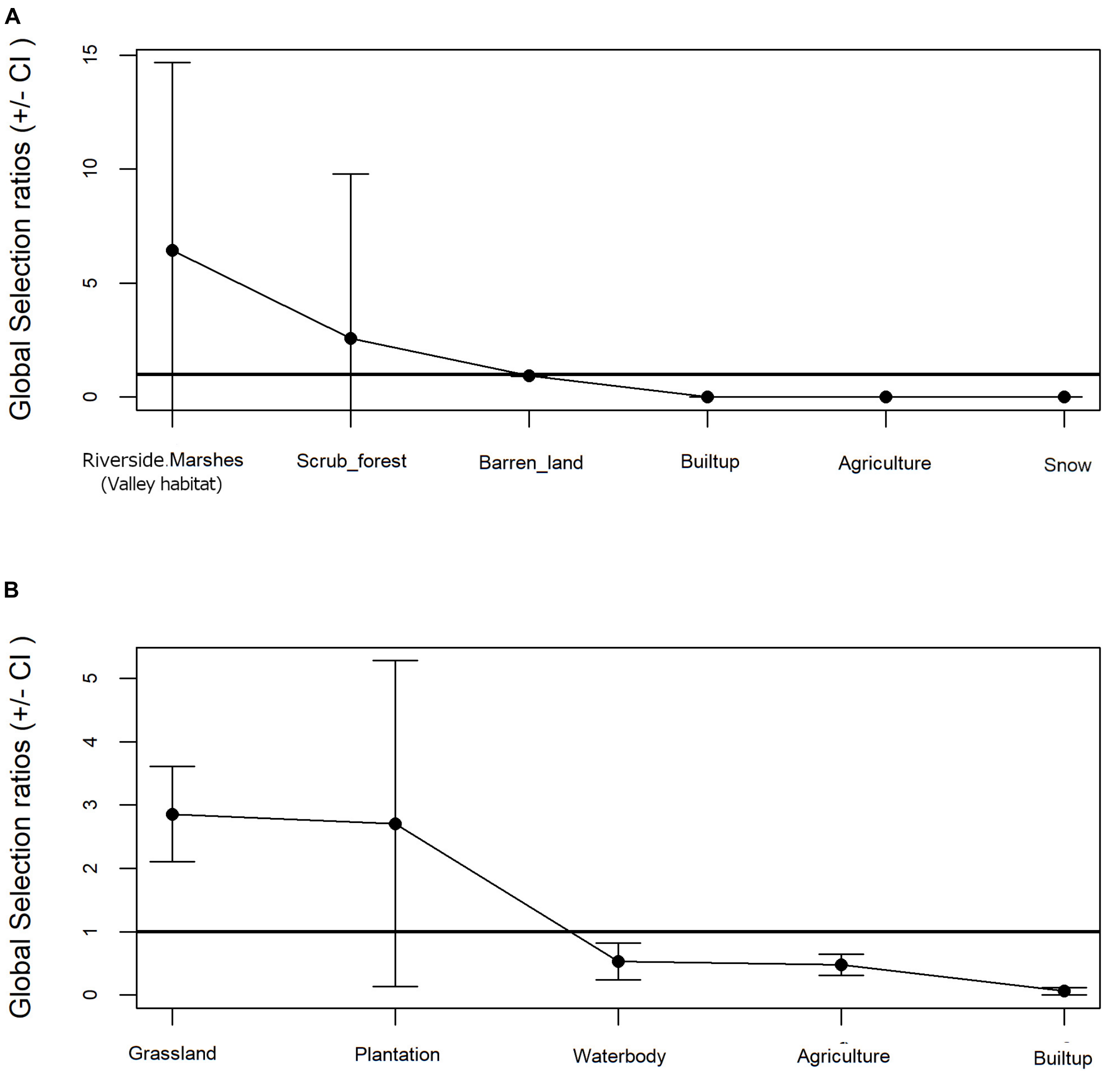

FIGURE 4 | Land use proportion in relation to availability vs. used based on Manly's test for **(A)** Woolly wolf and **(B)** Indian wolf.

TABLE 2 | Comparison of the vocalization parameters of the Woolly and Indian wolf based on the published literature.

Variable	Woolly wolf * No. of howls = 301	Indian Wolf * No. of howls = 117	Indian Wolf # No. of howls = 238
Meanf	428.5 ± 125.7	593.5 ± 211.4	422.2 ± 126.40
Maxf	465.4 ± 141.9	692 ± 243.3	469.7 ± 141.6
Minf	369.5 ± 126.3	496.9 ± 202.6	359 ± 116.8
Rangef	101.8 ± 107.1	197.1 ± 137.4	110.6 ± 65.8
Endf	404.5 ± 141.9	572.5 ± 225.8	390.4 ± 124.3
Cofv	6.22 ± 5.97	8.96 ± 4.87	7.17 ± 3.69
Posmax	0.33 ± 0.28	0.38 ± 0.33	0.41 ± 0.28
Posmin	0.53 ± 0.45	0.57 ± 0.38	0.48 ± 0.44
Duration	2.56 ± 1.68	2.71 ± 2.11	5.21 ± 2.49

*The data for the Woolly wolf were collected from Trans-Himalayas of Spiti Valley in Himachal Pradesh and the Changthang plateau of Ladakh in Jammu and Kashmir, and for Indian wolf from Maharashtra. [Meanf- Mean frequency of fundamental (f_0) at 0.1 s interval over the duration; Maxf- maximum frequency of f_0; Minf- minimum frequency of f_0; Rangef- Range of f_0 (maxf–minf); Endf- End frequency of f_0; Duration- Duration of howl measured at f_0 (t_{end}–t_{start}); Cofv- Coefficient of frequency variation of f_0; Posmax-Position in the howl at which the maximum frequency occurs; Posmin- Position in the howl at which the minimum frequency occurs]. All the frequencies given in the table were measured in Hz and duration in seconds with ± SE. (Sources: *Hennelly et al., 2017; #Sadhukhan et al., 2019).*

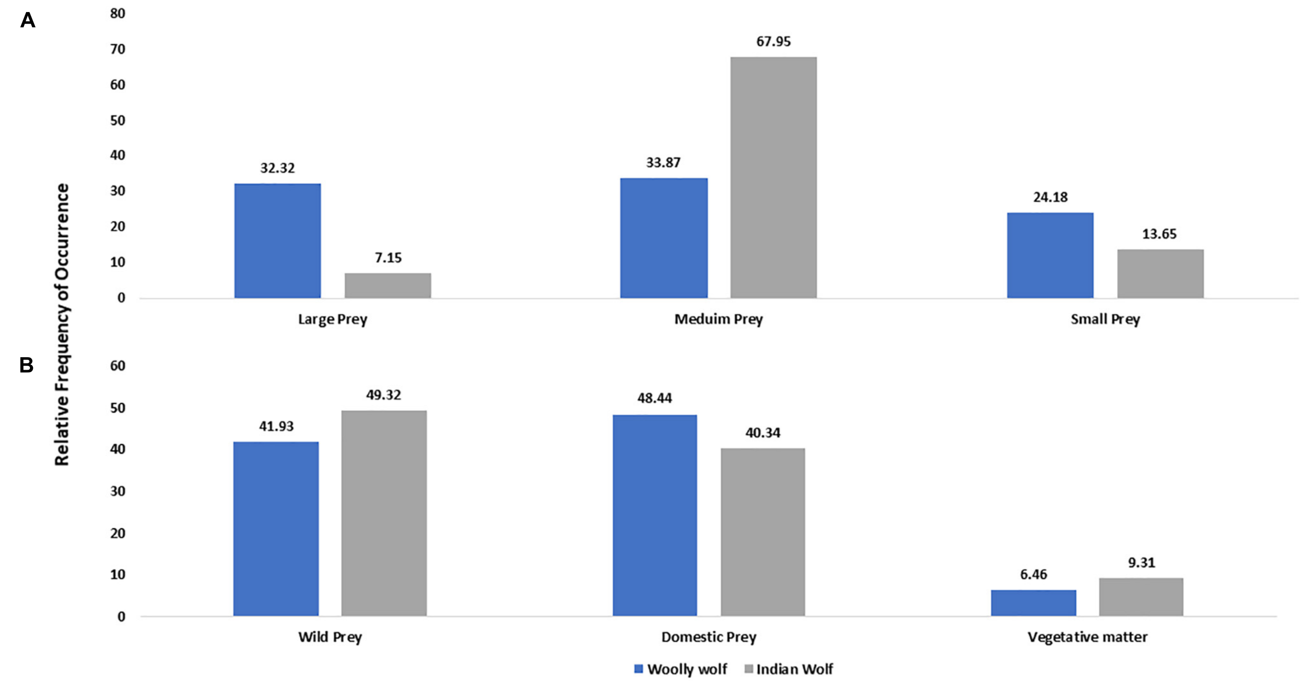

FIGURE 5 | Comparison of the relative frequency of occurrence of different food types of Woolly and Indian wolf; based on **(A)** prey size (0–10 kg small prey; 11–70 kg medium-sized prey; >70 kg large prey) and **(B)** prey types in the diet.

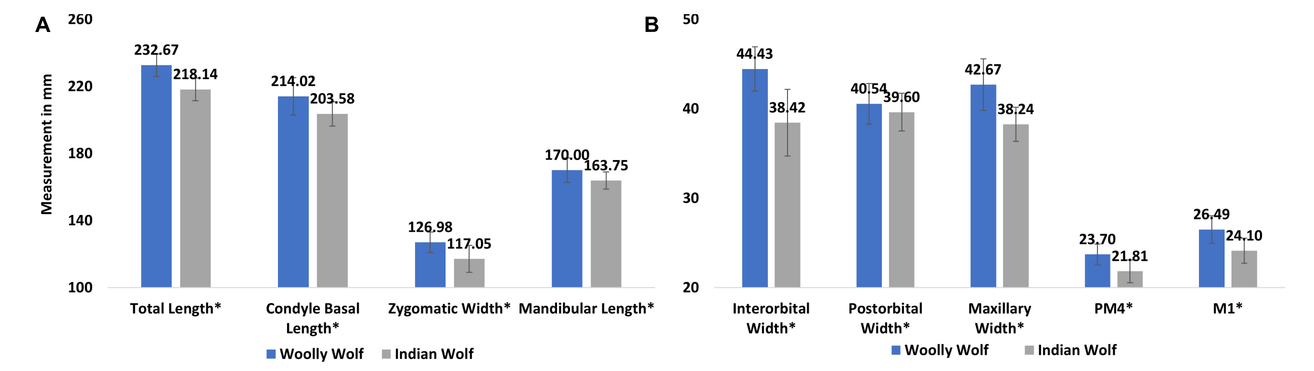

FIGURE 6 | Comparison of different cranial measurement of eight Woolly and eight Indian wolves obtained from Allen (1938), Pocock (1941), and Srinivas and Jhala (2021) **(A)** measurement of total length, condyle basal length, zygomatic width and mandibular length, **(B)** measurement of inter and post-orbital, mandibular width, length of pre-molar4 and molar 1. *The difference between the sub species of wolves were found statistically significant.

DISCUSSION

Spatial Ecological Differences Based on Home Range and Core Area Size in Woolly and Indian Wolf

The home range of Woolly wolf (95% MCP) was found eight times larger than the Indian wolf home range. Moreover, the extensive use area within the home range (50% MCP or core area) of the Woolly wolf was 17 times larger than the core area of the Indian wolf home range. The difference between the home ranges of these two lineages narrowed down in home range estimation by the advanced method of BBMM. The 95% isopleth of BBMM and 50% isopleth of BBMM of Woolly wolf were found only three times larger than those of the Indian wolf. The Woolly wolf resides in high-altitude rugged terrain areas with harsh climatic conditions. They usually used gentle slopes and valleys to move from one place to another (Lyngdoh, 2020), while MCP included cliff areas that the wolves could not use due to inaccessibility (Kenward et al., 2001; Silva et al., 2018). Different methods provided different information about home range size (Swihart and Slade, 1985; Gese et al., 1990; Silva et al., 2018). However, the MCP is widely used and can be useful to compare the home ranges of wolves from different studies. The BBMM provides reliable home range estimation, especially for central-place foragers and territorial carnivore species (Börger et al., 2008). This method is also reliable when the animals used several core areas or important travel corridors (Bullard, 1999; Horne et al., 2007; Kie et al., 2010).

Moreover, we also compared the home ranges and core areas of Indian wolf (MCP) with the previous studies and found that the home ranges in the previous studies were smaller (148.49 km^2) (Jethva et al., 1997; Habib, 2007). The increase in the Indian wolf home ranges may probably be due to increased human pressure, habitat fragmentation, and prey depletion.

Large home ranges and core areas of the Woolly wolf could result from sparsely distributed prey species (Shrotriya et al., 2015) and suitable habitat continuity (Belongie, 2008). Wolves in mountainous regions selected low elevations, moderate slope and southwest aspect, probably to avoid snow cover and prey availability (Whittington et al., 2005). The home range for Mongolian wolves, which are closely related to the Woolly wolf, were among the largest home ranges (26,619 km^2) of the wolves worldwide (Kaczensky et al., 2008). Kaczensky et al. (2008) argue that long-range seasonal shift in the used area could dramatically increase the overall home-ranges. Therefore, the reason of large home range of Woolly wolf may due to the seasonal variation of space use. In contrast, the Indian wolf is surviving in patchy, fragmented habitat within high human-dominated landscape. In such landscapes where wild prey is almost absent, factors such as the type and distribution of food resources, human interference, and topography may have played a significant role in determining home-range size. The human disturbance could also be the reason for having multiple core areas in Indian wolf, as they use small undisturbed patches for resting, mating, and rearing pups (Habib, 2007).

Spatial Ecological Differences Based on Movement Characteristics of Woolly and Indian Wolf

The mean displacement (m/h) of the Indian wolves was 35.2% higher than the Woolly wolves' daily per hour movement. The daytime and nighttime displacement of the Indian wolves was 19.5 and 46.0% higher than the displacement of the Woolly wolf, respectively. The wolf is a widely distributed carnivore and its survival tactics involve a fine-tuned adaptation to local conditions. Their movement decisions are often the best functional compromise between finding food and avoiding humans (Ciucci et al., 1997). Some studies suggested that the wolf was primarily nocturnal in some areas, which allowed it to visit and move in intensive human-use areas without confrontation (Ciucci et al., 1997; Theurkauf et al., 2007). The Woolly wolf showed no difference between the day and night movement. In contrast, the Indian wolf movement aligned with the previous studies as their nighttime movement was almost twice the daytime movement. The no difference in the day night movement pattern of the Woolly wolf agreed with the findings of Vilà et al. (1995), who found that the wolf in Spain tended toward bimodal activity where nocturnality developed to cope up with human presence. Some studies suggested that wolves were most active during the night in summer (Fancy and Ballard, 1995) and during the daytime in winter (Mech, 1970).

As discussed above, the Woolly wolf home range was much larger than that of the Indian wolf. The functioning of the Woolly wolf in large home ranges but having less daily movement might be due to their use of valleys which makes the home range more linear, less compact, and larger. The higher movement of the Indian wolf in our study is in line with Daan (1981), who suggested a temporal shift in movement due to human disturbance. The other reason might be habitat fragmentation as the Indian wolves occupied fragmented areas, and the Woolly wolf inhibited continuous habitat. The results showed that the Indian wolf holds multiple core areas (**Figure 2**). Therefore, they need to travel more to find a secure area for resting and mating, as also supported by Ciucci et al., 1997. stated that the wolf activity mostly involved daily round-trip traveling from retreat areas to the core area of home ranges for some sort of social activity, which was also observed in previous studies (Carbyn, 1974).

Habitat Use and Preferences of Woolly and Indian Wolf

Wolves are known as grassland and openland species (Pocock, 1941; Mech, 1970). While the Indian wolves clearly showed a preference toward the grasslands and used the grassland patches more than its availability, the Woolly wolves did not show much preference toward grassland and openland (included in the barren land category) and used it according to the availability. This is due to the high availability of openland in continuity in the *Trans*-Himalayan region. The Woolly wolf showed an affinity to the riverside and marshes (valley habitat), which is energetically economic travel routes along with the refuge areas. Moreover, these areas are often also more sheltered from the harsh conditions inclusing cold wind. Avoidance of waterbodies by the Indian wolf could be better explained by the association of water presence with the proximity of humans in the peninsular Indian landscape. Both the wolves showed avoidance toward human-influenced areas such as agriculture and builtup more strongly so in the case of the Indian wolf. Paquet et al. (1996) found that mountain wolves did not have many options to avoid humans due to the selection of valley habitats which is often used by humans. The Indian wolf also faces higher human pressure than the *Trans*-Himalayan population because of the higher human population density in plains than in the *Trans*-Himalayan region (Mishra et al., 2009).

Differences in Howling Parameters of Woolly and Indian Wolf

Based on published literature, we compared the magnitude and pattern of howl acoustic structure to evaluate whether the long-range vocalizations showed acoustic differences between two wolf lineages in India. It is well understood that howl characteristics vary among different wolf subspecies (Kershenbaum et al., 2016). Due to the unique features of high amplitude and low frequency, a howl can travel for six kilometers or more and can be used to identify individuals for population estimation (Sadhukhan et al., 2021). Hennelly et al. (2017), compared the differences in the howls of the Himalayan wolf (aka Woolly wolf), Indian wolf, North African wolf (now African golden jackal; Sarabia et al., 2021), and Holarctic clades. The study found that small wolf subspecies, North African, Indian, and Israeli wolf had higher mean frequencies than the large wolf subspecies. Hence the body size could affect acoustic parameters.

In contrast, the study by Sadhukhan et al. (2019) reported lower mean frequencies for the Indian wolf. The difference between the Woolly wolf and the Indian wolf howls in Hennelly et al. (2017) could be an artifact of sub-sampling bias as Hennelly et al., 2017 used 117 howl recordings. In contrast, Sadhukhan et al., 2019 used 238 howl recordings. Although both the studies sampled in the state of Maharashtra, yet their sampling years and locations varied. Both the studies sampled only a section of the Indian wolf population rendering the Indian wolf with a larger variation in mean frequencies overall.

Further, earlier studies have shown the similarities between the howls of various canid species and subspecies. *Canis rufus* showed similar howl type as coyotes *Canis latrans*, while European wolf (*C. l. lupus*) and Iberian wolf (*C. l. signatus*) howls were similar in signatures (Kershenbaum et al., 2016). The Indian wolf, Mackenzie Valley wolf (*C. l. occidentalis*) and Mexican wolf (*C. l. baileyi*) also showed similar howling signatures (Kershenbaum et al., 2016). The similarities in acoustic signatures between the two lineages may advocate the evolutionary history playing a role in howling behavior (Kershenbaum et al., 2016). We also second that canid howling is not an arbitrary signal but possesses species-specific information, reflecting that the adaptive processes of isolation or habitat features play a key role in howling behavior (Hennelly et al., 2017). Habitat and temporal variability might be the reason for different outcomes from the two studies. More studies are recommended to understand the differences in the howling parameters of these two lineages.

Differences in the Food Preferences of Woolly and Indian Wolf

Wolves are pack hunters and are known to feed on a variety of different food items. They choose their prey based on availability, abundance, pack stability, season, and habitat accessibility in the human-dominated landscapes (Imbert et al., 2016; Lyngdoh et al., 2020). Our study revealed that the diet of Woolly wolf from the Himalayan region consisted of 20 different food items from small birds, reptiles to large mammals and domestic animals such as cattle and yak. A review study on the Woolly wolf dietary spectrum across their global distribution, including Tibet and China, reported 39 different food items (Lyngdoh et al., 2020). The energy requirement of large carnivores makes them prone to conflict with humans as they need a large prey base (Carbone et al., 1999; Mech and Boitoni, 2003). The Woolly wolf also consumed a sufficient proportion of the large-sized prey (32.32%) and medium-sized prey (33.87%) with a considerable quantity of small prey (24.18%) consumption in their diet (**Figure 5**). Various studies across the wolf distribution range confirm that large prey forms the major part of the wolf diet (Imbert et al., 2016; Mengulluoglu et al., 2019; Petridou et al., 2019; Sin et al., 2019). The dependency on small prey might be because of the scarcity of the large and medium-sized animals to avoid interactions with humans or to gain and fulfill energy requirements in the harsh climatic condition. The Woolly wolf is also heavily dependent upon the domestic prey items in the Himalayan region. Livestock (Yak, Dzo cow, Goat, and Sheep) were the most consumed mammals in the Woolly wolf diet compared to sparsely distributed wild prey. Hence, it is not surprising that Woolly wolf showed a marginal preference for domestic prey than wild prey. Many studies from the *Trans*-Himalayas accounted that low abundance of wild prey and poor management of livestock resulted in depredation by snow leopard and Woolly wolf (Jackson and Ahlborn, 1984; Mishra, 1997; Namgail et al., 2007; Anwar et al., 2012; Suryawanshi et al., 2013; Chetri et al., 2017).

Despite the Woolly wolf's significant domestic animal consumption, they are being tolerated by the locals in some regions (Rangarajan, 2001; Lyngdoh et al., 2020). At the same time, they are persecuted in many areas for the same reason (Mishra, 1997). Apart from domestic animal consumption, major wild prey species were Asiatic ibex (*Capra sibirica*), Urial (*Ovis vignei*), Tibetan wild ass (*Equus kiang*), Tibetan argali (*Ovis ammon hodgsoni*) and Blue sheep (*Pseudois navaur*) (Anwar et al., 2012; Subba, 2012; Ahmed et al., 2017; Bocci et al., 2017; Chetri et al., 2017; Werhahn et al., 2019; Lyngdoh et al., 2020; Habib et al., 2021b). However, their combined contribution was as low as 16.77% of the total food items. It could be related to the small population size and sparse distribution of the ungulate species in the region (Shrotriya et al., 2015).

The Indian wolf also primarily preyed upon domestic animals, followed by wild prey items. The Indian wolf consumed a considerable amount of vegetative material (fruits and plant items, etc.), which was absent in the Woolly wolf diet. The absence of vegetative matter in the diet of the Woolly wolf may be due to the scarcity of wild fruiting plants in the *Trans*-Himalayan region or missed reporting in the studies due to difficulties in identification in the studies we reviewed in this study. The Indian wolf primarily preyed upon medium-sized mammals relating to the availability of blackbuck, chinkara, and especially livestock such as sheep and goat. The Indian wolf-bearing states (Rajasthan, Andhra Pradesh, Maharashtra, Telangana) have the highest goat and sheep population (20th Livestock Census: All India Report, 2019). The average pack size of the Indian wolf varied from 1.5 to 4.7 individuals in the breeding and non-breeding season (Kumar, 1998). The preference toward medium-sized prey could be due to the smaller pack size and body size of the Indian wolf. Small packs would require less food and find it difficult to prey upon large prey species. The studies used to understand the food habits were from different protection regimes, such as the protected area of Velvadar Blackbuck Sanctuary (Jhala, 1991) and the human-dominated landscape of Maharashtra (Habib, 2007). The diet of the wolves from Velvadar Blackbuck Sanctuary was dominantly comprised of wild prey base (91.8%), whereas Maharashtra wolves' diet was dominated by domestic prey (47.8%). This shows that the wolf may prefer wild ungulates over domestic prey, depending upon the availability. Consequences of human-wolf conflict due to low prey abundance and unavailability can hinder conservation measures. Therefore, it is essential to address prey restoration and livestock security to reduce conflict and achieve better conservation management for wolves in the Himalayas and in the plains of India.

Cranial Morphometric Differences Between Woolly and Indian Wolf

The Woolly wolf exists at 3,900–5,600 m elevation across the low-oxygen region of the Himalayas (Habib et al., 2013; Werhahn et al., 2018). Survival in such a landscape requires the Woolly wolf to face metabolic challenges such as severe oxidative stress and increased metabolic rates (Beall, 2007; Hassanin et al., 2009). Several studies have conducted a genetic analysis of the Woolly wolf, identified the genes facilitating their adaptation to cope with hypoxia (Zhang et al., 2014; Werhahn et al., 2018; Wang et al., 2020). However, their morphological adaptations against hypoxic conditions have not been paid much attention yet. Butaric and Klocke (2018) studied the adaptation of upper respiratory structures to hypoxic and cold dry air in humans occupying high and low altitudes. These adaptations in skull structures help in increased uptake and air conditioning processes. The Woolly wolf exhibited longer (total length) and broader (post and inter-orbital width) skulls than the Indian wolf. Hence, their skull size and structure could be an adaptation to meet respiratory demand of more oxygen (Butaric and Klocke, 2018). However, the wolves are known to conform Bergmann's rule, that is the wolves in the northern latitude are generally larger in body size (Meiri et al., 2007).

Taxonomic Dilemma

The systematics of wolves from the Indian subcontinent is less studied, remains controversial and confusing regarding their taxonomic status as sub-species and species. Indian wolves gathered the interest of the scientific community for their unique evolutionary history and uncertain taxonomic status. Although the Indian wolf was first described by Hodgson (1847), a consensus on its nomenclature is yet to be reached after 175 years with several attempts made to clear their taxonomy (Aggarwal et al., 2003; Sharma et al., 2004; Werhahn et al., 2017; Alvares et al., 2019; Joshi et al., 2020; Wang et al., 2020, 2021). Hodgson (1847) described the Himalayan wolf as separate species, *C. laniger*, noting its appearances. Later, Blanford (1888) rejected Hodgson's proposal and combined *C. laniger* with *C. lupus*, and elevated the Indian wolf to *C. pallipes*. However, after 50 years, Pocock (1941) described both the taxa as subspecies of *C. lupus*. In Pocock's scheme, *C. pallipes* became *C. l. pallipes*, and *C. laniger* merged with *C. l. chanco*. Later on, more studies suggested the uniqueness of these two taxa and identified them as the oldest lineage of wolves but did not reach any conclusion (Sharma et al., 2004; Aggarwal et al., 2007; Werhahn et al., 2017). A recently conducted study of the Woolly wolf by Joshi et al., 2020 found no evidence for *C. l. chanco* to be distinct species. They suggested the acceptance of Woolly wolf as *C. l. chanco* and not as *C. langier* or *C. himalayensis*. Their findings were additionally supported by Wang et al. (2020), who found that wolves across the Himalayas and Tibetan plateau are closely related. The Woolly wolf adapted to survive in a low oxygen environment and the Indian wolf represents two of the most endangered wolf populations (Joshi et al., 2020; Hennelly et al., 2021; Wang et al., 2021). Therefore, the wolves from India have been identified as unique and qualified as an important population and proposed as Evolutionary Significant Units (ESUs) due to their distinct evolution and adaptation (Hennelly et al., 2021).

CONCLUSION

Identifying the ecological and behavioral differences in closely related species provides understanding in the evolutionary process of speciation and helps identify a species or subspecies (Arnegard et al., 2010; Ramasindrazana et al., 2011). The literature clearly highlights the uniqueness of these two wolves from India (Sharma et al., 2004; Aggarwal et al., 2007; Shrotriya et al., 2012; Joshi et al., 2020). The genetic study strongly suggested that both the subspecies were distinct and the most ancient lineages. These lineages did not show any genetic admixture or geographic overlap with other wolves from rest of the world (Aggarwal et al., 2003, 2007; Sharma et al., 2004). Geographical isolation and differential habitat selection of closely related adjacent wolf populations is the leading mechanism of the evolution of genetically and ecologically different subspecies (Leonard, 2014), for example, Mexican wolf, North American wolf, Italian, Iberian and Scandinavian wolf (Wayne et al., 1991; Vilà et al., 1999, 2003; Lucchini et al., 2004). The two geographically non-overlapping wolf subspecies from India also showed genetic as well as ecological differences exhibiting their evolutionary divergence. In this study, we found a clear difference in the spatial ecology of both the wolves.

Wolves are considered a typical grassland species in Asia and Europe (Mech, 1970). Both the lineages in India primarily choose grassland or openlands. The Woolly wolf lives in a landscape with vast openlands, hence the habitat type did not show up in preferential analysis. Plantations by the Indian wolf and marshes/riversides and shrubs by the Woolly wolf were preferred as potential refuge. The wolves are known to live in variety of habitats and are considered ecological tolerant animals (Jedrzejewski et al., 2004). The habitat use by wolves can be influenced by many factors, e.g., habitat type, prey availability and anthropogenic pressure (Meriggi et al., 1996; Ciucci and Boitoni, 1998; Mech and Boitoni, 2003). We postulate that the ecological differences between Woolly wolf and Indian wolf could be mainly due to their functioning in entirely different habitats. The home range of the Woolly wolf was significantly larger than that of the Indian wolf. The differences in home range sizes and movement patterns could be because of the *Trans*-Himalayan region having low prey base, less anthropogenic pressure and connected suitable patches compared to the Peninsular India having disturbed landscape with patchily distributed suitable habitats. However, to understand the ranging pattern and habitat use of Woolly wolf, we used only three individual data collared from Spiti region of *trans*-Himalayas. More data from different regions could help us better understanding of wolf ecology as the space use may vary with different regions based on prey base and habitat/landscape characteristics. There was no significant difference in the daytime and nighttime movement of the Woolly wolf, whereas the Indian wolf traversed more during the nighttime. Variation in the level of human disturbance could be the reason for Indian wolf being more nocturnal than Woolly wolf.

Both the lineages had significant differences in their cranial measurement, and we found that the Woolly wolf has longer and broader skulls than the Indian wolf. Moreover, the data presented in two studies on the vocalization characteristics were conflicting and did not show a clear picture of the difference. The canid howling may vary species-wise or depend upon the environment, still it possesses species-specific information which may reflect adaptive and or neutral processes of isolation (Kershenbaum et al., 2016). The studies used in this review showed contrasting results. Hennelly et al. (2017) suggested a clear difference but the results of Sadhukhan et al., 2019 suggested that howling parameters of both the lineages overlapped. The differences in their feeding ecology occurred primarily due to the availability of landscape-specific prey species. Both the wolves of India depended on the livestock for more than 50% of their diet. The wolves across the world have been reported to feed on a wide variety of food items from animal matter to vegetative matter. Their main prey in most of the areas are large and medium-sized prey depending upon the availability (Jhala, 1991; Meriggi et al., 1996; Jethva and Jhala, 2004; Chavez and Gese, 2005; Stahler and Smith, 2006; Habib, 2007; Hosseini-Zavarei et al., 2013; Newsome et al., 2016). Nevertheless, since these populations are geographically isolated, genetic, morphological data and ecological requirements suggest apparent distinctiveness. The Indian and Woolly/Tibetan wolves shared the most common ancestors with Holarctic wolves 0.2 mya (0.17–0.3 mya) and 0.5 mya (0.38–0.64 mya), respectively (Hennelly et al., 2021). These two lineages diverged and become incipient species with genetic distinctiveness a long time ago. Their geographic isolation is persistent and would facilitate the behavioral and ecological changes to intensify over time. The wolves of Asia are paid less academic attention compared to their counterparts in Europe and America. This study sheds light on the ecological and behavioral differences of the two oldest wolf lineages of the world found in India. We further suggest detailed morphological analysis and further studies should be conducted to understand the in-depth differences in ecological requirements of the subspecies.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the Wildlife Institute of India, Animal Ethics Committee.

AUTHOR CONTRIBUTIONS

SK collected data, performed analysis, reviewed all the potential manuscript and reports that were included in the meta-analysis, and drafted the manuscript. SL and SoS collected data. ShS guided in analysis. BH, ShS, SG, and SL reviewed the manuscript. BH conceptualized and acquired funding of the study. All authors contributed to the article and approved the final version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.775612/full#supplementary-material

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SHORT COMMUNICATION

First photographic record of Spotted Deer *Axis axis* (Erxleben, 1777) (Artiodactyla: Cervidae) in Great Indian Bustard Sanctuary, Maharashtra, India

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Abstract: *Axis axis* also known as Chital, Spotted Deer or Axis Deer, is native to Asia. The Chital ranges over 8–30 °N in India and through Nepal, Bhutan, Bangladesh, and Sri Lanka. Chital is listed as Least Concern in the IUCN Red List of Threatened Species because it possesses a very wide range, however, the population is declining outside protected areas. Although widely distributed, there is no record of Chital from the Great Indian Bustard (GIB) Sanctuary, Maharashtra. Here we report the first photographic record of Chital from the sanctuary, in the Gangewadi region of Solapur District. During a field work exercise for radio collaring of Indian Grey Wolves to monitor movement in the human-dominated landscape of Maharashtra, camera traps were placed in the Gangewadi area of the GIB sanctuary. Over the survey period, the species that were photo-captured included the Indian Grey Wolves, Indian Fox, Jungle Cat, Black Buck, Wild Boar, porcupine, and Black-naped Hare on multiple occasions. The male Spotted Deer was captured at one event in a single camera trap (17.8324°N, 76.0043°E) on 30 December 2020 at 0517 h. This is the first record of Spotted Deer in the grassland ecosystem of Solapur region in Maharashtra.

Keywords: Camera trap, Chital, Gangewadi region, GIB sanctuary, grassland ecosystem, semi-arid landscape, Solapur region, ungulates.

The Chital *Axis axis* was first described by the German naturalist Johann Christian Polycarp Erxleben in 1777. The species is crepuscular, inhabiting a variety of habitats mostly on the periphery of dense forests (Nowak 1991). It is a medium-sized herbivore, with males attaining a height of 80–100 cm at the shoulder and a length of 119–185 cm; females are slightly smaller, 67–87 cm in height and 114–147 cm in length with no antlers (Long 2003). Adults have a reddish-brown coat with white spots (Schaller 1967). The antlers, three-pronged, are nearly 1 m long. The usual life span of Chital in the wild is 10–15 years (Walker et al. 1964) and in captivity up to 20 years (Crandall 1964).

The Chital ranges over 8–30°N in India and through Nepal, Bhutan, Bangladesh, and Sri Lanka (Anderson 1999; Grubb 2005). The western limit of its range is eastern Rajasthan and Gujarat whereas the northern limit is along the foothills of the Himalaya and

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विज्ञान एवं प्रौद्योगिकी मंत्रालय MINISTRY OF SCIENCE AND TECHNOLOGY

भारतीय वन्यजीव संस्थान Wildlife Institute of India from Uttar Pradesh and Uttarakhand through to Nepal, northern West Bengal and Sikkim and then to western Assam and the forested valleys of Bhutan, which are below 1,100 m (Duckworth et al. 2015). The eastern limit of its range is through western Assam (Sankar & Acharya 2004) to the Sunderbans of West Bengal (India) and Bangladesh (Duckworth et al. 2015) and Sri Lanka is the southern limit (Schaller 1967). Chital occurs sporadically in the forested areas throughout the rest of the Indian peninsula (Sankar & Acharya 2004). Within Bangladesh, it currently exists only in the Sundarbans and some ecoparks situated around the Bay of Bengal, as it became extinct in the central and northeastern parts of the country (Duckworth et al. 2015). Introduced populations also occur within Andaman & Nicobar Islands. Chital is listed as 'Least Concern' on the IUCN RedList of Threatened Species because they possess a very wide range. The population is declining outside protected areas. Although they are widely distributed across India, there are no record of Chital from the Great Indian Bustard (GIB) Sanctuary, Maharashtra.

Study Area

The study area lies in the Deccan landscape which is a large plateau in western and southern India. The landscape is semi-arid region of India and receives very less rainfall which makes it suitable for GIB. The summer season, lasting from mid-February to mid-June (Habib 2007), is very dry and extremely hot, with temperatures regularly exceeding 48°C. The Great Indian Bustard Sanctuary, established in 1979, is a wildlife sanctuary for the Great Indian Bustard *Ardeotis nigriceps* at Solapur Maharashtra, India. The sanctuary is spread over seven talukas: Mohol, Mhada, northern Solapur, Karmala, Nevasa, Karjat, and Shrigonda. The original spread of the GIB Sanctuary was 8,469 km^2, which has been reduced to 1,222.61 km^2, including reserved forest, Gairan lands, and private lands (including grasslands) in 2011. This vast grassland is home for many resident wildlife species and a variety of migratory species, along with the GIB. The major floral species are *Azadirachta indica, Acacia nilotica, Ziziphus* spp., *Glericidia sepium, Hardwickia binata*, & *Albizzia lebbeck* and the prominent grasses are *Aristida funiculate, Aristida stocksii, Chrysopogon fulvus, Heteropogon contortus, Lodhopogon tridentatus,* & *Melanocenchris jacquemontii* (Habib 2007). Also, the sanctuary has a good population of Blackbuck, Indian Wolf, Indian Fox, Golden Jackal, and Jungle Cat. There has been no previous record of the Spotted Deer from any part of the sanctuary.

Materials and Methods

During the field work exercise for radio collaring of Indian Grey Wolves to monitor movement in the human-dominated landscape of Maharashtra, camera traps have been placed in the Gangewadi area of the GIB sanctuary. The trails and junctions of the area were targeted and Cuddeback Ambush/C1 camera traps (http://cuddeback.com/cameras) were placed. Cameras were tied up on tree trunks at the height of 25–35 cm from the ground at the animal trails. The camera delay was set at multi-shot mode with a delay of 5 seconds and were active for 24 hours.

Results

Over the survey period, species photo-captured included the Indian Grey Wolf, Indian Fox, Jungle Cat, Black Buck, Wild Boar, porcupine, and Black-Naped Hare. A male Spotted Deer was captured by a single camera trap (17.83240°N, 76.00439°E) on 30 December 2020 at 0517 h (Image 1). This is the first record of Spotted Deer in the grassland ecosystem of Solapur region of Maharashtra (Image 1).

Discussion

The Spotted Deer is endemic to southern Asia (Schaller 1967) and found in dry deciduous, moist deciduous, thorn forest, and mangroves. As per the IUCN RedList, the distribution data show that Spotted Deer are present in the entire state of Maharashtra. They are found almost exclusively in dry and mixed deciduous forest habitat intermixed with grasslands. They are most commonly associated with a mixture of forest and more open grass-shrub, but they occupy a wide range of habitats throughout their native range, often avoiding rugged terrain (Anderson 1999). It is one of the most common prey species for carnivores in the forest ecosystem. Carnivores that may prey upon Chital in the GIB Sanctuary include Indian Wolf *Canis lupus pallipes*. The sanctuary is dominated by a matrix of grasslands, barren lands and agricultural land, with small patches of *Azadirachta* sp. and *Gliricidia* sp. plantation. The sanctuary has long record of research activities on various flora and fauna (Kumar 1988; Rahmani 1988; Habib 2007; Habib & Kumar 2007; Kumar & Rahmani 2008; Vanak & Gompper 2010; Janakiraman & Jalal 2015; Varghese et al. 2016; Khan et al. 2019) but there is no earlier record of the Spotted Deer. The present work is the first record of Spotted Deer from this region. In the surrounding of the sanctuary various other wildlife sanctuaries are present. The closest sanctuary which has Spotted Deer population is Nayangaon Mayur Wildlife

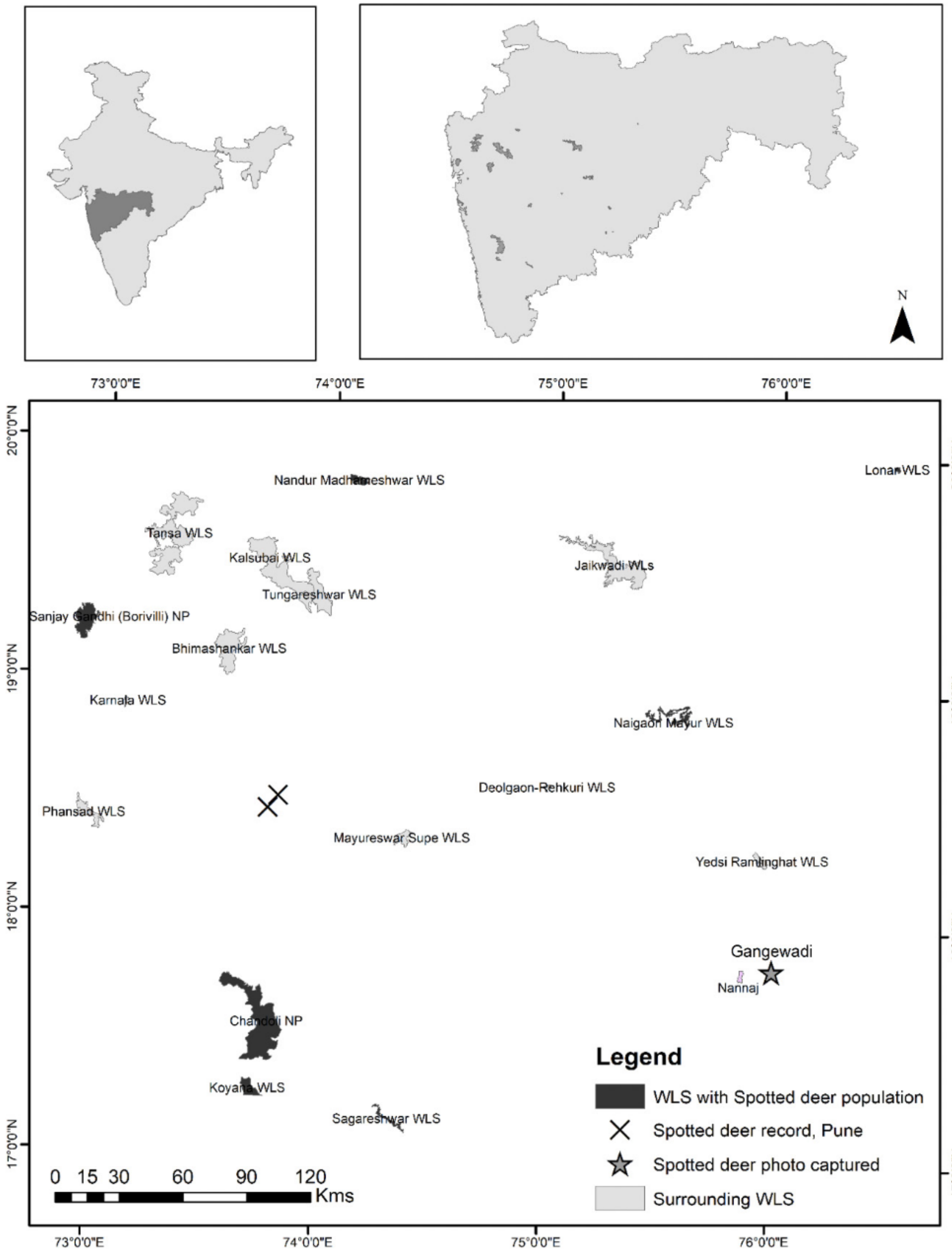

Figure 1. The location of the first photographic evidence of Spotted Deer *Axis axis* from Great Indian Bustard Sanctuary (marked with star symbol) along with the record of dead Spotted Deer from Pune (marked with cross in 2016 and 2017). The solid black colour polygons are the PAs where Spotted Deer population is present and the light grey polygons show surrounding PAs. Topleft: map of India showing the state of Maharashtra (topright), showing the PAs of Maharashtra around Great Indian Bustard Sanctuary. Bottom figure shows protected areas and Spotted Deer presence around the sanctuary along with the photographed location of Spotted Deer in Gangewadi area of the sanctuary.

Image 1. First photographic record of Spotted Deer *Axis axis* from Great Indian Bustard Sanctuary, Maharashtra.

Sanctuary (WS) (Show as symbol and name in legend in bottom map of Figure 1) which is about 124 km away from the photo-captured point. The other close by sanctuaries are Sagareshwar WS (190 km), Lonar WS (240 km), Nandur WS (305 km), and SGNP (356 km), where Spotted Deer population is present (Figure 1). There have been a few earlier records of Spotted Deer from Pune district (250 km away from Nannaj Bustard Sanctuary). In 2016, a dead male Spotted Deer was found at dumping site in Warje, Pune (The Golden Sparrow 2016) and in 2017 a male was killed by dogs in Khadakwasla area of Pune (Phadnis 2017). These two areas are close to each other and surrounded by forested area. Each year Pune division of the state forest department conducts waterhole census in four wildlife sanctuaries: Nannaj Bustard Sanctuary (10 km; part of GIB Sanctuary as Gangewadi area), Bhimashankar (292 km), Rehekhuri (145 km) and Mayureshwar (178 km). In the census during year 2021 no Spotted Deer was recorded from the above given wildlife sanctuaries, and the species was never recorded from Solapur district. This is the first wild record of Spotted Deer here. The other ungulates recorded from the Solapur region, including the GIB Sanctuary are Black Buck *Antilope cervicapra*, Chinkara *Gazella bennettii*, and Wild Boar *Sus scrofa*.

Systematic studies are necessary to assess whether populations of *A. axis* have started colonising the area or are using the area as a corridor. This data may support actions for conservation of regional biodiversity.

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Silencing the call of the wild – howling behaviour and responses of the wolf to Anthropocene in India

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Keywords
behavioural shift; cumulative impact; vocal species; anthropogenic pressure; ecosystem services; wolf howling behaviour; anthropogenic disturbance.

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Abstract

Wolves use howls to maintain large territories, intra-pack communication and social bonding. Besides their physical presence, howls are also instrumental in creating fear and impacting foraging behaviour among the lower cascade. Anthropocene-led behavioural alteration in vocalization has been observed in a wide range of species, but the effect on wolf howl is unknown. In this context, we have studied the howling behaviour of the Indian wolf through playback surveys ($n = 264$) across the anthropogenic gradient. We found a disparity in their howl response – based on the distance to villages. In the low disturbed East-Maharashtra (EM), wolves mostly avoided responding to howling surveys (HS) if done within 1200 m of villages [response rate (RR) = 0.03 ± 0.021], but they did respond once it was done far from villages (>1200 m) (RR = 0.226 ± 0.075). In high human-density West-Maharashtra (WM), wolves showed high RR within 1200 m from the villages (RR = 0.148 ± 0.031). But the RR within 500 m from villages was less as howling near villages might lead to easy detection. The collared wolf data showed significantly high RR (0.635 ± 0.067) in their home-range core, but low RR if the core area was close to a village. Therefore, howling too close to a village is disadvantageous, although their tolerance for responding to HS has increased in the human-dominated landscape. The extent of the village may increase further with development, which will leave fewer areas for the wolf to defend territory with a long-range howl. The wolves might behaviourally adapt to a human-modified landscape by reducing their howling intensity. Adaptation to a fragmented habitat may save the wolves from extinction, but the repercussions of the fundamental behavioural alteration might adversely impact wolf behaviour and the ecological cascade. Whereas ecologists are mainly concerned with the extinction of species, this study highlights the vulnerability of fundamental behaviour of a keystone species attributed to human-induced contemporary evolution.

Introduction

Howls are a long-distance vocalization of the grey wolf (*Canis lupus*) (Joslin, 1966; Sadhukhan, Hennelly, & Habib, 2019). These signatory calls are used to defend their territories (Harrington & Mech, 1978, 1982) and maintain social cohesion and bonding within the pack (Mazzini *et al*., 2013; Watson, Townsend, & Range, 2018). Additionally, the wolf howl significantly impacts associated predator and prey species, which subsequent influence their foraging behaviour (Cooke *et al*., 2013; Suraci *et al*., 2016; Janczarek *et al*., 2021). Therefore, apart from the wolf's presence as an 'apex predator' and direct killing of prey, the howl has a substantial ecological role in influencing the lower cascade (Suraci *et al*., 2016). Changes in their howling behaviour could potentially impact the entire ecosystem. Such behavioural alteration in the Anthropocene has been highlighted recently in a wide range of vocal species, from invertebrates like crickets to amphibians like frogs to large mammals like whales (Wale, Simpson, & Radford, 2013; Nedelec *et al*., 2017; Tennessen *et al*., 2018; Halliday *et al*., 2019). The impingement of spatial disturbance and noise is dire on the vocally active animals, often disrupting their parental, territorial and breeding behaviours (Injaian, Taff, & Patricelli, 2018; Berger-Tal *et al*., 2019; Cañadas Santiago *et al*., 2020). Since a large portion of wolf habitats falls within the human-modified landscape (Mech, 2017) and anthropogenic factors may influence their fundamental howling behaviour (Viola et al., 2021).

Wolves are highly adaptive and occupy a wide range of habitats worldwide (Boitani, Phillips, & Jhala, 2018).

Besides their wide distribution throughout the northern hemisphere, wolves face extinction threats at local and subspecies levels due to escalating anthropogenic pressures and increasing human–wildlife conflicts (Berger, 1999; Gómez-Sánchez *et al*., 2018). In most parts of the USA and across the northern hemisphere, wolves were extirpated during the European colonization and remained in conflict with humans across their habitats (Berger *et al*., 2001; McNay, 2002; Rich *et al*., 2012; Mech, 2017). Human-induced population decline and genetic bottleneck are causing significant genetic diversity loss worldwide, and the damage is irreversible (Dufresnes *et al*., 2018). Fragmentation of wolf habitat due to village and agricultural expansion drives wolves to adapt to the human-modified landscape through behavioural alteration (Mancinelli *et al*., 2019; Rio-Maior *et al*., 2019; Habib *et al*., 2021). Adapting to human-modified land may save the population from extinction but may lead to radical behavioural alteration with unknown outcomes (Ordiz, Bischof, & Swenson, 2013; Ciucci *et al*., 2020).

The Indian grey wolf (*Canis lupus pallipes*) is the oldest lineage of modern wolves, hence considered an evolutionary significant unit (ESU) (D. K. Sharma *et al*., 2004; Aggarwal *et al*., 2007; Hennelly *et al*., 2021). They depend on smaller to medium-size wild prey such as blackbuck (*Antilope cervicapra*), chinkara (*Gazella bennettii*), wild pig (*Sus scrofa cristatus*) and a few others (Kumar & Rahmani, 2000; Jethva & Jhala, 2004a; Habib, 2007; Kumar & Rahmani, 2008). They primarily inhabit village outskirts and frequently contact humans (Jhala & Giles, 1991; Habib & Kumar, 2007; Sharma *et al*., 2019). Adapting to human-modified landscapes, wolves have shifted their food preferences towards domestic livestock acquired via hunting and scavenging (Jhala & Giles, 1991; Kumar & Rahmani, 2000; Habib, 2007; Khan *et al*., 2022). Indian wolves have modified their ranging pattern (average home range size $\sim 210\,\text{km}^2$) and use multiple core areas (2.33 ± 1.52) to cope with the human-altered landscape, and the core areas mostly connect through villages and agricultural patches (Habib *et al*., 2021; Khan *et al*., 2022). As a result, wolves face several conservation challenges, such as hybridization risk with village dogs, den destruction and revenge killing due to livestock depredation (Linnell *et al*., 2002; Agarwala *et al*., 2010; Hindrikson *et al*., 2012; Pacheco *et al*., 2017; Kusak *et al*., 2018). Although studies have highlighted various aspects of Anthropocene-linked wolf conservation challenges, alteration in their vocal behaviour in human-altered landscape remains unexplored.

Long-range howls are the territorial calls of wolves, making them respond to the howl playbacks (Harrington & Mech, 1978; Font *et al*., 2015). Consequently, the howling survey is an effective non-invasive tool for studying this cryptic and wide-ranging species (Harrington & Mech, 1982; Suter *et al*., 2016). A howl contains the identity of an individual wolf (Root-Gutteridge *et al*., 2014; Hull, McCombe, & Dassow, 2020; Sadhukhan, Root-Gutteridge, & Habib, 2021). Additionally, studying howling behaviour can reveal various pieces of information such as social behaviour (Joslin, 1966; Biben, 1983; Faragó, Townsend, & Range, 2014), ecology (McIntyre *et al*., 2017), breeding success through the detection of pups (Palacios *et al*., 2016) and even evolutionary history (Kershenbaum *et al*., 2016; Hennelly *et al*., 2017; Chen & Wiens, 2020). To explore how howling behaviour is affected by the different factors, we conducted howl surveys on collared and non-collared wolves. We hypothesize that anthropogenic factors such as village distance and human density influence the howl responses. Furthermore, we examine the cumulative impact of factors such as home range, breeding season, time of the day and howl type (chorus, solo or duet howls) on the wolf responses. The study highlights the influence of human-modified landscape on the howling responses and how it may adversely impact the whole ecosystem. Additionally, we standardized an efficient howling survey method from our current study's findings, which will significantly aid global wolf conservation.

Materials and methods

Study site

The study was conducted in the eastern and western parts of Maharashtra, India (Figure 1). Eastern Maharashtra (EM), also known as Vidarbha, is in the central Deccan Plateau with Tropical dry deciduous broadleaf forests with generally flat terrains (Rodgers & Panwar, 1988; Reddy *et al*., 2015). Vegetation is dense in most of the areas due to moderate and high rainfall. The Vidarbha region is a tiger hotspot and comprises many national parks and sanctuaries (Habib *et al*., 2018). During our study, wolves were found mainly in the buffer of the national parks and sanctuaries. This landscape has a less built-up area and human density than West Maharashtra (WM).

WM falls under the semi-arid drought-prone areas of the Deccan peninsula Biogeographic Zone (Zone 6) (Rodgers & Panwar, 1988). Deccan thorn scrub forests are the dominant habitat type in the sampling areas (Reddy *et al*., 2015). The main characteristics of the Deccan peninsula are mild undulating slopes and flat-topped hillocks with intermittent shallow valleys. Wolves were primarily found in grassland and thorn scrub forests highly fragmented by agricultural lands and small villages.

The built-up density for EM and WM was found to be different in the sampling area. The settlement area in EM and WM is $0.22\,/100\,\text{km}^2$ (3855 villages) and $0.28\,/100\,\text{km}^2$ (7484 villages) respectively (27% higher in WM). The population density (human) of the surveying districts of WM ($1170.1/\text{km}^2$) is almost double that of EM ($604.13/\text{km}^2$) (CensusInfo India 2.0, 2011).

Data collection

The data were collected in two phases – collared wolf and non-collared wolf. Though the data on collared wolves allow us to include many more vital factors such as animals' home range and distance along with the certainty about their presence, wolf collaring is profoundly high resource-dependent.

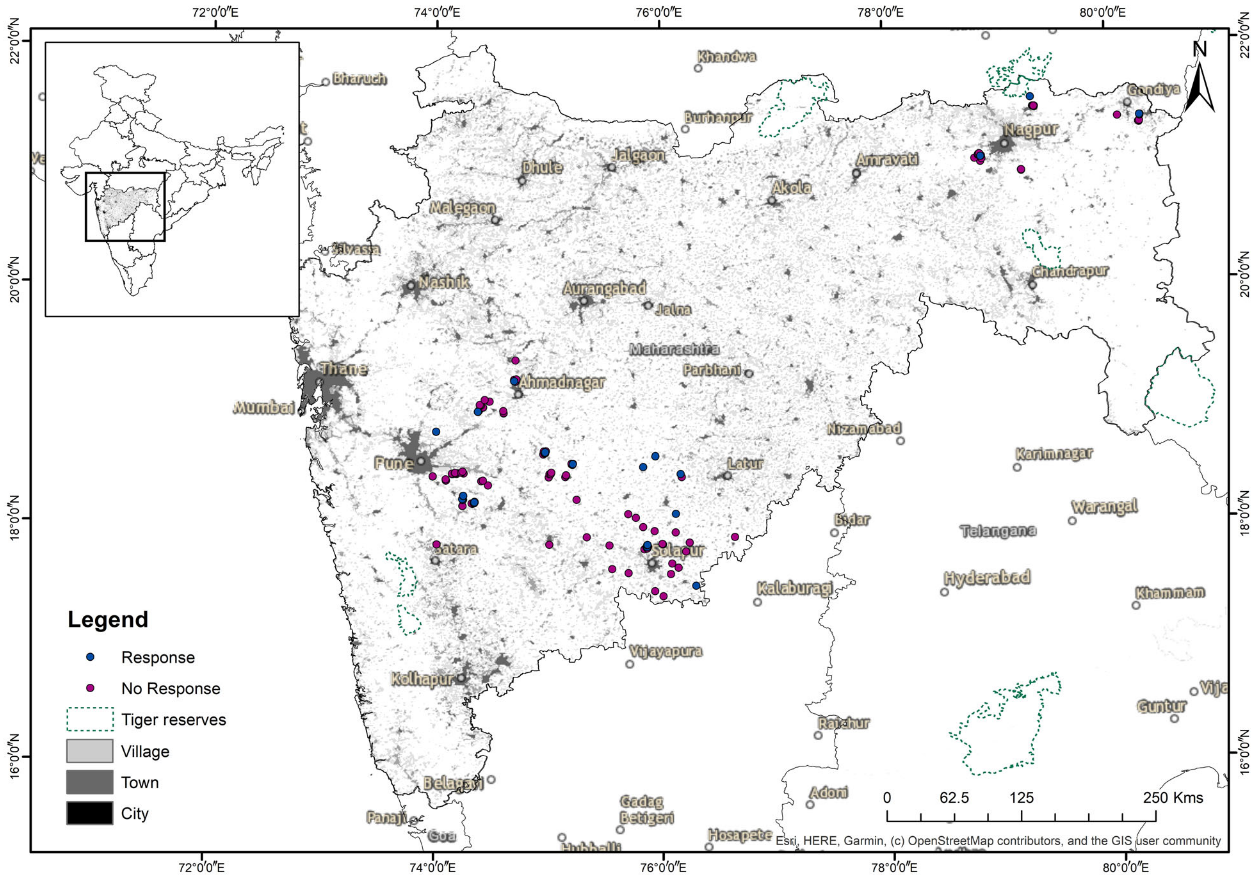

Figure 1 The map represents the howling survey locations of non-collared wolves in East and West Maharashtra. Blue represents the location where we got responses, and pink represents where we did not get any responses. The three shades of black represent cities, towns and villages, respectively, and the Green dotted boundary symbolized tiger reserves. The built-up density in Eastern Maharashtra is lower than in Western Maharashtra, which is visible on the map. Wolves utilize high human-dominated landscapes in West Maharashtra compared to wolves in East Maharashtra, mostly using the forest buffer.

Therefore, we studied the howling response pattern in collared and non-collared wolves.

In the first phase, the howling survey was conducted on the free-ranging non-collared wolves from December 2015 to December 2019 in the Deccan Peninsula and Vidarbha Landscapes (Figure 1). Surveys were conducted in the potential wolf sites during the early morning (an hour before the sunrise to an hour after the sunrise) and early evening hours (an hour before the sunset to an hour after sunset), considering the peak activity hours (Harrington & Mech, 1982; Eggermann *et al*., 2009; Šprem *et al*., 2015). About 10–15 free-ranging packs were surveyed. Every howling survey session consisted of five trials and a 3-min interval between the consecutive trials as standardized by Harrington & Mech (1982). A trial consisted of a 50-s-long pre-recorded playback *solo*, *chorus* or *mixed* (howl sequence altering solo and chorus howl) of both howls. Pre-recorded howls from the Jaipur Zoo were played using a 40 W single speaker set-up in the order of increasing amplitude in every consecutive trial [See (Sadhukhan, Hennelly, & Habib, 2019, sec. Data Collection; Sadhukhan, Root-Gutteridge, & Habib, 2021, sec. Data Collection)]. A series of solo howls (from a captive individual) and a single series of chorus howls were played during the entire sampling to maintain uniformity. The time of each playback was documented during the survey, along with GPS locations and other ecological parameters.

In the second phase, the data were collected from January 2018 to July 2019 in the Deccan Peninsula or WM (Figure 2). Seven wolves (five packs) were captured using soft-catch leghold traps and were fitted with satellite radio collars (See Habib *et al*., 2021). The packs were tracked using a VHF receiver, and howling surveys were conducted once their presence was confirmed within the proximity (<1500 m). The procedure for playback was the same as in the first phase of data collection, and other information was logged as mentioned in the first phase. Additionally, the animal locations were logged based on Satellite location, and the animal distances were calculated based on the *Pythagoras theorem*.

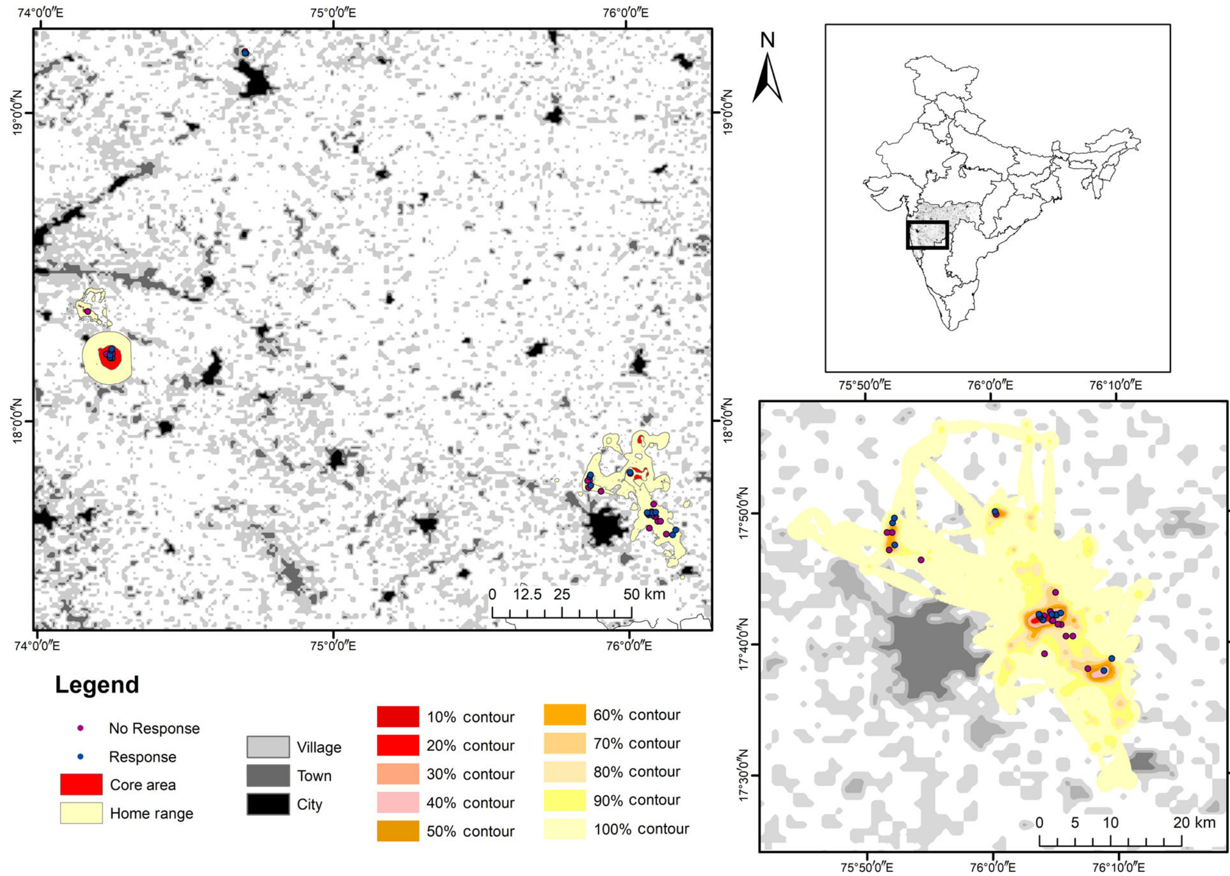

Figure 2 The map represents the home ranges of collared wolves and their response to howl playback. Howling survey locations are denoted by blue (response) and pink (no-response). Light grey, dark grey and black represent villages, towns and cities, respectively. a) Home ranges of seven collared wolf and their response to howl playback. [a few individuals own smaller, overlapping home ranges, which may not be visible at low image resoluton]. Red illustrates core areas (50% utilisation distribution), whereas yellow explains the home range (95% utilisation distribution). b) The map shows the home range and core areas of a collared wolf [Merry (F/A)], where different utilisation zones (0.1-1) are classified into ten categories and described by different colours. Fragmentation in the home range is visible, which forces the animal to use multiple core areas.

Data preparation

The human settlement data of 1 km resolution were acquired from the JRC open data portal (Martino & Sergio, 2016). The human settlement data layer has three classes (rural cells or base, urban clusters or low-density clusters, urban centres or high-density clusters). We converted the human settlement data raster image into a vector file (polygon), and the distances from the edge of the closest rural or urban areas from each howling survey location were calculated in ArcGIS (v10.6) using the nearest feature tool. The human-settlement or built-up area density was calculated separately for the sampling area of EM and WM. The Human population density of EM and WM were also evaluated by *Census Info India*, Govt. of India (CensusInfo India 2.0, 2011). Howling survey data were categorized into different seasons, October–December (pre-denning), January–March (denning) and April–July (post-denning). The radio-collared individuals were programmed to collect the GPS fix at hour intervals. The home range of seven wolves (three adults and four sub-adults of five packs) was calculated using the Brownian Bridge Movement Model (BBMM) (Bullard, 1999; Kranstauber *et al.*, 2012). Unlike traditional movement models, BBMM explores movement paths and performs temporal autocorrelation, giving a precise idea about periodic movement patterns and quantifying accurate utilization distribution (Kranstauber *et al.*, 2012). Utilization distance (UD) is the probability of finding the collared or tagged animal in a specific space over a period of time (Van Winkle, 1975). The home ranges were calculated at different percentile contours (10–100%) of the UD. Utilization hotspot spaces of resident animals are known as 'Core areas' of their home range (Samuel, Pierce, & Garton, 1985). The howling surveys of collared wolves were conducted in each UD zones (10–100%) (Figure 2) to examine the effect of home range on howling responses. Up to 30–50% of UD zones are known as ‘core areas and up to 90–95% of UD zones are known as home ranges depending on the study species and methodology (Vander Wal & Rodgers, 2012).

Data analysis

Non-collared wolf

Generalized Additive Model (GAM) analysis was performed with the package ‘*gam*’ in R (v 4.0.2) to see the cumulative effect of various factors on howling responses (Hastie & Tibshirani, 1990; Chambers & Hastie, 1992). GAM is a generalized linear model where the model relates a univariate response variable (Y = Howl response; binomial variable) with multiple predictor variables (X) (Hastie & Tibshirani, 1990). Seasons (based on the breeding behaviour), distance from the nearest settlement (rural and urban) and sunset or sunrise were the predictor variables used in the analysis.

Since EM and WM comprise different habitat types (vegetation type and human pressure differ), the response pattern might vary between these landscapes. The response rate regarding village distance was plotted in ‘*ggplot*’ in R (v 4.0.2) to understand the response variation between these two landscapes. To test whether EM and WM have different response patterns relating to village distance, we classified data into two groups – i. howling survey conducted within 1200 m from villages and ii. howl surveys were conducted more than 1200 m away from villages. The error and 95% confidence intervals were calculated and provided in Table 3.

Collared wolf

To investigate the cumulative effect of different factors (predictor variable) on howling response (response variable, binomial), ‘*gam*’ analysis was executed in the R (v 4.0.2) platform. The predictor variables were home range, animal distance to observer, seasonality, distance from the nearest settlement, playback type (solo, chorus or mixed), time of the day and maximum playback amplitude.

Results

Factors affecting the howling responses of non-collared wolves

We conducted 264 howl surveys for non-collared wolves in the identified wolf sites in EM and WM. Of the total playback events, 30 howling responses were recorded (Figure 1). The overall response rate (RR) obtained was 9.4%.

The influence of different predictor variables on howling responses was assessed through ‘*gam*’ and found that breeding season ($F_{2,254}$ = 3.09, P = 0.046) and village distance ($F_{1,254}$ = 4.79, P = 0.029) have significant effects on the howl responses of Indian wolf in Maharashtra (Table 1). The howling response was higher in the pre-denning season than in the denning and post-denning seasons (Figure 3a). The effect of village distance over howling response was significantly non-linear ($\chi^2_{3,254}$ = 12.668, P = 0.005) (Table 2). In multifactor ‘gam’ analysis, wolf responses are consistent up to 1000 m from villages, but a certain dip was observed after that (Figure 3c). However, the response rate increased after 2000 m from the village (Figure 3c). The results also show that chorus howls elicit higher response rates than solos or mixed (Figure 3d). However, this is not conclusive due to a significant overlap in the interquartile range of different howl playbacks ($F_{2,254}$ = 1.32, P = 0.21) (Figure 3d). The result showed no significant difference in response rate during sunrise or sunset ($F_{1,254}$ = 0.63, P = 0.43) (Figure 3b).

EM and WM have varied human density; therefore, we plotted the zone-wise (east zone and west zone) response rates to village distance (Figure 4). In WM, the maximum response rate was obtained when surveys were conducted within 1200 m from the villages (0.148 ± 0.031, n = 128), which is significantly higher than EM (0.03 ± 0.021, n = 66) (Table 3; Figure 4b). More importantly, wolves in WM showed a peak response rate in the HS 500–1000 m from the nearest villages (RR = 0.17; n = 40) (Figure 4a). In comparison, only four responses were recorded in 57 howl surveys conducted at 1000–2500 m from the nearest villages in the same landscape (RR = 0.07). In EM, wolves showed a high response rate in the howling survey 1200 m away from villages (0.226 ± 0.075, n = 31) (Table 3; Figure 4b).

Factors affecting the howling responses of collared wolves

Due to anthropogenic land accusation pressure, most of the wolf packs were using fragmented home ranges with multiple core areas connected through villages or agricultural lands (Figure 2b) (Habib *et al*., 2021). The average core area of three adult wolves was found to be 35.0 ± 17.94 km^2 (N = 8, range (R): 0.68–29.32 km^2), whereas, for four subadults, the average core area was 3.1 ± 2.81 km^2 (N = 6, R: 0.46–2.44 km^2) (Table 4). We also calculated the distance from the edge of each core area to the nearest village or town. It was found that the boundary of the core areas from the closest village boundary was 0–2500 m.

We conducted 70 howl surveys from five packs across WM (Figure 2). Wolf responded 39 times out of the total howling playbacks (n = 70). As the presence of the collared wolf was confirmed using a VHF signal, the response rate was 56%. Like non-collared wolves, collared wolves also showed the peak response rate when the howling survey was conducted at 500–1000 m from villages (RR = 0.73, n = 23). Through ‘*gam*’ analysis, we have found that animal’s home range ($F_{1,42}$ = 3.09, P < 0.001), maximum sound amplitude ($F_{2,42}$ = 7.43, P = 0.001), breeding season ($F_{2,42}$ = 4.73, P = 0.014) and animal distance ($F_{1,42}$ = 5.03, P = 0.03) are the significant factors influencing the howling response of Indian wolf (Table 5). The wolves frequently responded when howl surveys were conducted within the core of their home range (50% home-range contour), and the

Table 1 ANOVA table for parametric effects of probable influential factors on howl responses of Indian wolf (non-collared)

	d.f.	Sum Sq	Mean Sq	*F* value	Pr (>*F*)	Significance level
Season	2	5.28	2.6401	3.0956	0.04696	$F_{0.05}$
s (village distance)	1	4.085	4.0853	4.7901	0.02953	$F_{0.05}$
Playback type	2	2.64	1.3202	1.548	0.21468	–
Sunset/sunrise	1	0.538	0.538	0.6309	0.42778	–
Residuals	254	216.627	0.8529			

Village distance and *season* are the significant, influential factors of howl responses as they have a cumulative probability value of less than 0.05.

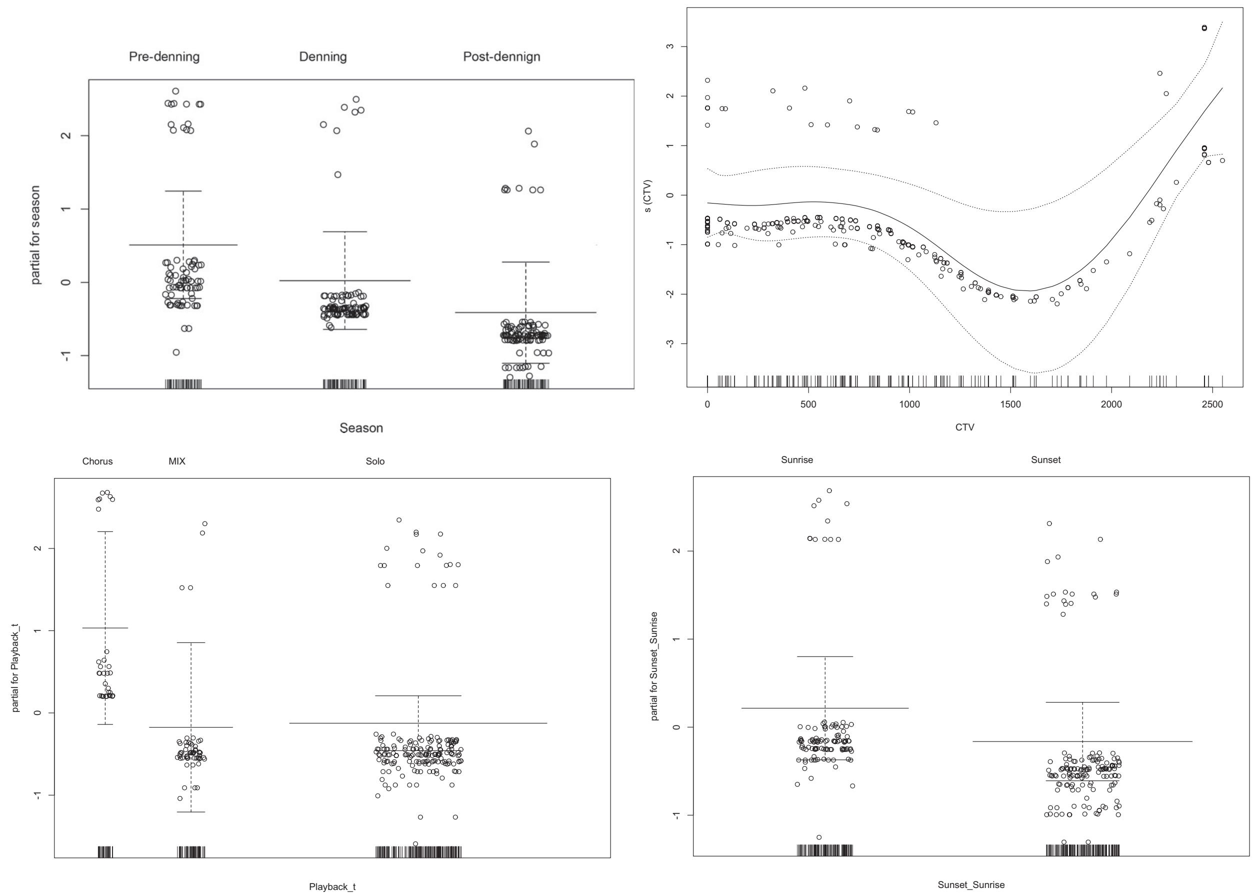

Figure 3 Graph showing how different factors influence howling responses in Indian wolf (non-collared) (a) Wolves respond more during the pre-denning season compared to denning and pre-denning season, (b) Wolf respond consistently from 0 to 1000 m from villages and response rate increases after 2000 m. (c) Wolf responds more frequently to chorus playback. (d) No significant difference in the howl response rate of the surveys conducted during sunset or sunrise.

response rate dropped gradually away from the core area (Figure 5a). Most of the time, the wolf responded in the second trial, which contains a playback with 75% sound amplitude of a 40 W speaker (Figure 5c). If they did not respond in the second trial, it was improbable to get a response from them at 100% amplitude of 40 W Speaker (Figure 5c). The breeding season also strongly impacted the howling responses of Indian wolves. Higher response rates were obtained during the pre-denning season compared to the denning and post-denning seasons (Figure 5b). The ANOVA for smooth [s()] terms indicated significant non-linear relation between observer and respondent distance ($\chi^2_{3,42} = 7.68$, $P = 0.05$) (Table 6). Wolves frequently respond up to 1200 m from the observer, but the response rate sharply drops after that (Figure 5b). Although village distance shows a weak influence on the howling response ($F_{1,42} = 1.85$, $P = 0.18$) (Table 5), this is because of the correlation between factors as home-range cores are influenced by

Table 2 ANOVA table for non-parametric ffects of the probable influential factor on howl responses of Indian wolf (non-collared)

Component	d.f.	χ^2	$P(\chi)$	Significance level
s (village distance)	3	12.668	0.005414	$F_{0.001}$

This table represents the significance level of smooth function, that is, non-linear relation. Here, the smoothening function of village distance represents a cumulative probability value of less than 0.01. That means village distance is non-linearly correlated with howling response.

village distance (Figure 5d). The response was maximum when the howl was played from 700 to 1100 m from villages (Figure 5d). However, our analysis did not incorporate anthropogenic disturbances in the surroundings during the survey.

Similar to the non-collared wolves, the collared wolf data showed no significant effect of sunset or sunrise ($F_{1,42} = 0.40$, $P = 0.529$) on howling response (Table 5).

Discussion

The indirect evidence of top predators through scent marks or vocalization shapes domestic and wild prey's behaviour and active foraging time (Cooke *et al.*, 2013; Janczarek *et al.*, 2021). Therefore, the presence of wolves in an ecosystem has both direct and indirect impacts on the tropical cascade. Our study was focused on the long-distance vocalization of Indian wolves in two habitats with varied human disturbance through the howling survey. We obtained dissimilar response rates depending upon the core-home range and village density. In the low disturbed EM, wolves mostly avoid responding to howl surveys if done within 1500 m from villages. In high human dense WM, they showed the highest response rate in 500–1000 m from the villages. Although the study on collared wolves revealed that their home-range cores areas govern their response rate, they are less likely to respond in the core areas adjacent to the village boundary. The wolf might avoid howling in those landscapes to prevent ease of detection by barring from howl response. Therefore, to survive in high human-altered habitat, wolves might need to sacrifice their fundamental territorial vocalization behaviour. Although conservationists are primarily concerned about the extinction of species, this study highlights the vulnerability of fundamental behaviour of a keystone species attributed to human-induced contemporary evolution. Howling is a critical behaviour of this pack living species, which determines their reproductive success, social cohesion and pack bonding. Therefore, this fundamental behavioural change can alter the biology of the keystone species to impact the ecological cascade.

Home range and anthropogenic factors influencing the howling response of Indian wolves

Scientists have previously emphasized how factors such as pack dynamics, home range, time of the day and seasonality

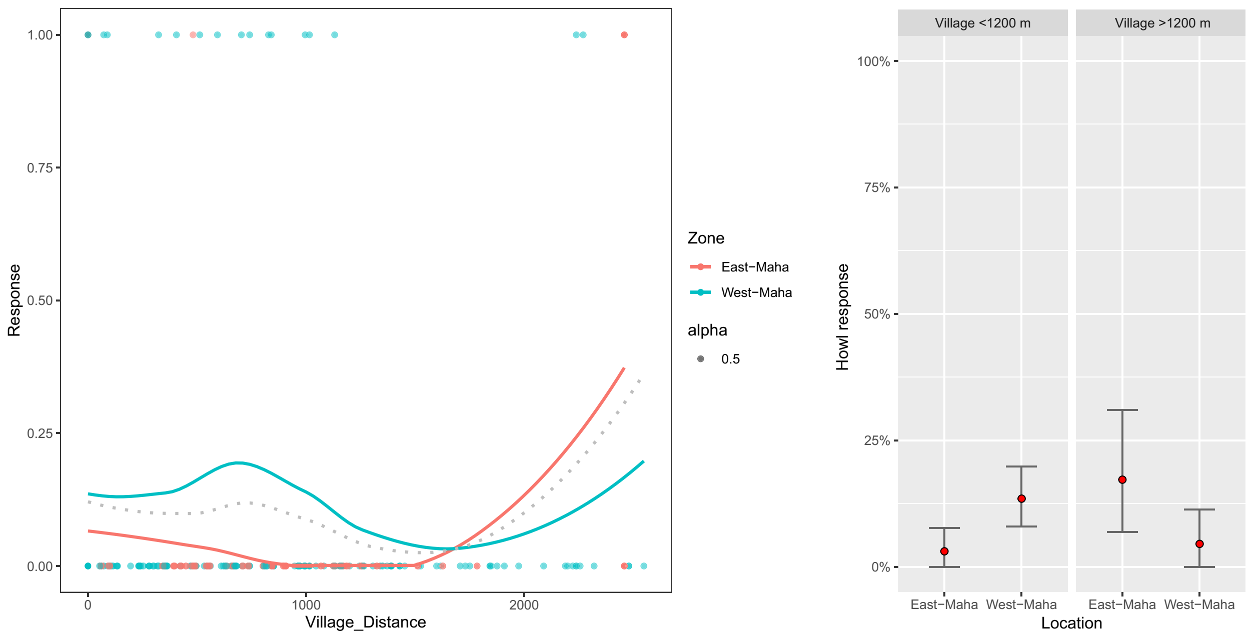

Figure 4 The graph shows how wolves from East (low human dense landscape) and West (high human dense landscape) Maharashtra have different tolerance levels towards village presence for howl response. (a) *Y*-axis represents response probability, while the *X*-axis represents village distance from the survey location. Howl response pattern with respect to village distance in EM and WM is depicted through red and blue respectively. (b) Wolf response rate is significantly higher in WM (0.148 ± 0.031, $n = 128$) than EM (0.03 ± 0.021, $n = 66$) when howling surveys were done within 1200 m from the nearest villages. While the howling survey 1200 m away from the villages resulted in more response rate in EM (0.226 ± 0.075, $n = 31$) than in WM (0.044 ± 0.03, $n = 31$).

Table 3 The table shows how EM and WM have differential response patterns based on distance from villages

Distance from village	Zone	No. of HS	No. of response	*P*-value	SE	95% CI
<1200 m	EM	66	2	0.030	0.021	0.041
	WM	128	19	0.148	0.031	0.062
>1200 m	EM	31	7	0.226	0.075	0.147
	WM	45	2	0.044	0.031	0.060

Table 4 The home ranges and core areas of seven GPS collared wolves in Maharashtra

Individual wolf	Area	95% BBMM (km^2) or home range	50% BBMM (km^2) or core area
Breeze (M/A)	Gangewadi, Solapur	399.56	31.56
Merry (F/A)	Sangdari, Solapur	325.92	19.03
Firky (F/A)	Morgaon, Baramati	284.11	54.43
Finn (M/SA)	Ahmednagar	4.7	0.63
Rain (F/SA)	Ahmednagar	13.96	1.69
Rolfe (F/SA)	Saswad (Pune)	96.39	7.07
Rolf (M/SA)	Saswad (Pune)	54.35	3.11

The average home range of the Indian wolf is 168 km^2, whereas the average core area is 117 km^2. M, male; F, female; A, adult; SA, subadult.

influence howl responses, keeping anthropogenic factors unnoticed. This study measures the impact of village distance on howl response with the combinations of earlier established factors to avoid any possible biases. The howling survey was conducted on both the non-collared and collared wolves. We found that the wolf's home range primarily governs the howl response rate followed by village distance. The response rate is almost double in the respective core areas ($P_{0.63}$; 33 responses on 52 occasions) than in the buffer ($P_{0.33}$). The pattern is similar to what Harrington and Mech (Harrington & Mech, 1978) reported in their study ($P_{0.29}$ in the non-rendezvous site and $P_{0.78}$ in rendezvous sites). Collared wolf data also reveal that home-range cores are restricted mostly by village and agricultural patches. In '*gam*' analysis, we observed wolves were more responsive at 700–1100 m from nearest villages, and RR further increased from 2000 m from villages after a certain dip at 1500 m (Figure 3b). To understand the reason behind the drop, we plotted EM and WM's howling response rates distinctly; it showed a clear distinction in the howling response pattern between the two zones (Figure 4).

In the EM region exhibiting less village density, wolf responded in a few occasions to howl playback up to 1200 m from villages but the response rate increases after that (Figure 4). Whereas in human-dominated WM, wolves exhibit greater tolerance towards villages. They showed a high response rate to howling playback 700 m from villages because wolves in a human-dominated landscape are highly adapted to use village resources (Jethva & Jhala, 2004; Singh & Kumara, 2006; Habib, 2007). A drop in the howling response rate of WM was observed with the howling surveys that were done 1200 m away from villages. As WM is densely packed with villages, once wolves move away from one village, the chances are higher that they find another nearby village. In WM, due to high village density, the wolf has less free habitat to move, whereas in EM, with less density of village wolves have more habitat space to move, showing no inclining after the response rate peak (Figure 4). Although the datasets are independent, the howling survey on collared wolves (WM) showed a similar pattern (Figure 5d). Even if some of their home-range cores were situated adjacent to the villages, they rarely responded to a howl playback once the howling survey was conducted closer than 700 m from a village. Since howling very close to villages might increase their detection and vulnerability towards humans, they restrict themselves from responding to howling playback in those areas. In the course of development, the villages may expand further, which might leave far less habitat for wolves to defend by their long-ranging howl. Therefore, wolves might need to conceal their presence by avoiding the howl to survive in the human-dominated landscape soon. Howl is also a mode of territorial advertisement to avoid inter-pack antagonism (Harrington & Mech, 1978). Without howl and high resource competition in a human-modified landscape, the wolves may face a high degree of

Table 5 ANOVA table for parametric effects of probable influential factors on howl responses of Indian wolf (Collared)

	d.f.	Sum Sq	Mean Sq	*F* value	Pr (>*F*)	Significance level
Season	2	5.4698	2.7349	4.733	0.014006	$F_{0.05}$
s (Animal_Distance)	1	2.9071	2.9071	5.0311	0.030231	$F_{0.05}$
s (Home_range)	1	7.7593	7.7593	13.4281	0.00069	$F_{0.001}$
s (Village_dist)	1	1.0703	1.0703	1.8523	0.180772	–
s (Sunset)	1	0.2329	0.2329	0.403	0.52897	–
Max_amp	2	8.5816	4.2908	7.4256	0.001733	$F_{0.01}$
Residuals	42	24.2694	0.5778			

The *home range* is the most important factor that determines howl response (F value < 0.001), followed by the *Maximum amplitude* used in the playback survey (F value < 0.01). Other significant factors are *Seasonality* (based on breeding behaviour) and Animal Distance (F value < 0.05).

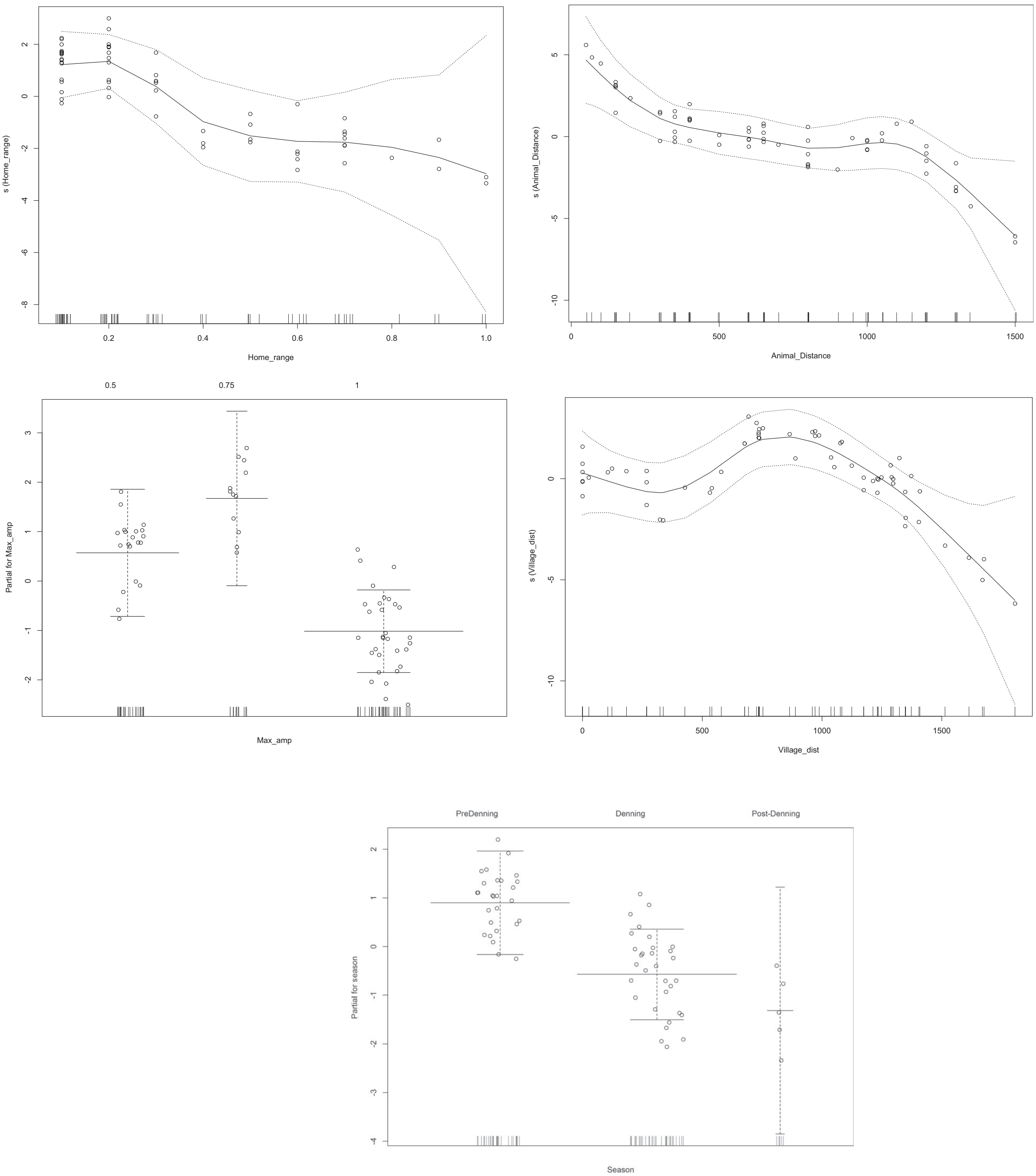

Figure 5 Graph showing how different factors cumulatively influence howling responses in Indian wolves (Collared). *Y*-axis represents the howl response rate, and *X*-axis represents the corresponding factors. (a) *X*-axis represents utilization distribution distance of respective wolf pack (0.1–0.5 is core; 0.5–.95 is a home range). The response rate was higher in the core areas and decreased as the howling survey were conducted away from the core. (b) Response rate gradually dropped as howling surveys were conducted away from the collared animals. Animal distance might affect the observer's detection of response due to high anthropogenic noise in the human-dominated landscape. (c) Graph represents wolves mostly respond on the second trial, which uses 30 W playback sound (0.75 sound amplitude of 40 W speaker). It is unlikely to get a response in the playback that contains full volume of 40 W speaker. (d) Figure illustrating how distance from the nearest village influences howl response. Wolf responded more frequently during the howling survey conducted 700–1100 m from the villages. (e) Ggraph showing howl seasonality (based on breeding behaviour) affected the howl response rate. Wolf responded more during the pre-denning season, and the response rate dropped during the denning and post-denning seasons.

Table 6 ANOVA table for non-parametric effects of the probable influential factor on howl responses of Indian wolf (Collared)

	d.f.	χ^2	$P(\chi)$	Significance
s (Animal_Distance)	3	7.6885	0.052907	$F_{0.1}$
s (Home_range)	3	1.881	0.597414	–
s (Village_dist)	3	13.0046	0.004626	$F_{0.01}$
s (Sunset)	3	5.3356	0.148822	–

This table represents the significance level of smooth function, that is, non-linear relation. The influence of *animal distance* and *village distance* is significantly non-linear with howl responses (F value < 0.1).

physical conflict with neighbouring packs. The possibility of wolves losing a 'Landscape of fear' cannot be ignored as wolf howl has a significant impact on prey, co-predator and domestic animals' fear and their foraging behaviour (Cooke *et al*., 2013; Suraci *et al*., 2016; Janczarek *et al*., 2021).

Standardizing protocols for howling survey in a human-dominated landscape

For the conservation of wolves, we need an efficient technique to study their population and biology. Studies suggest that the howling survey is the potential and most efficient non-invasive technique for studying the cryptic wolf (Harrington & Mech, 1982; Suter *et al*., 2016; Garland *et al*., 2020). We have found that the breeding season strongly influences the howl response rates, and wolves responded more to the howl playback during the pre-denning season than during the denning and post-denning seasons. Higher response rates support that wolves hold their territories antagonistically in the pre-denning season. The response becomes restricted from denning season onwards since howling from the den or near the early aged pups might make pups vulnerable to the invaders. A study on the Yellowstone wolf also suggested that wolves respond more frequently during their breeding season, that is, February (McIntyre *et al*., 2017), similar to the Indian wolf. However, the breeding season for Indian wolves (pre-denning season in our classification) is around early November. Therefore, the preliminary information on wolf breeding behaviour will facilitate an efficient howling survey design. In contrast, the study in North-Eastern Minnesota National Park (Harrington & Mech, 1982) and Białowieża Primaeval Forest (Nowak *et al*., 2007) revealed a second peak in the howl response rate from July to September [post-denning season]. We did not observe such a trend in Indian wolves because the post-denning season overlaps with the Indian monsoon, and no howling survey was conducted during that period. Besides those behavioural (breeding season and home range) and anthropogenic factors, the response rate also depends on a few stimuli factors such as distance, type and intensity of the playback. We found that they respond more frequently towards chorus howls. Since, many times in the field, wolves visited the sound source after hearing a solo howl instead of responding (field observation), we nullified the possibility of the animal missing the solo howl, due to a higher attenuation rate. They might prefer howling in response to the chorus for defending their territory and avoid direct visit towards the visitor pack at first to steer away from physical conflict. Whereas, for solo howl, they have less threat from individual and they prefer direct visit. Further investigation is required to understand this behaviour. The data from collared animals revealed that animal response rate drops when they are more than 1200 m away from the playback source, or it might be the chance of detecting the response decrease from the observer end due to anthropogenic noise. Collared wolves responded mostly in the second trial (if not in the first trial that uses 50% sound amplitude) with 75% sound amplitude of 40 W speakers. If they do not respond to the second trial, the chances of getting a response are unlikely in third (with 100% sound amplitude) or consecutive trials. It can be concluded that a 30 W speaker (75% amplitude of 40 W speaker) is sufficient for doing a howling survey which is loud enough so that wolf can hear it from 1200 to 1500 m in the high human disturbed landscape, but not as loud as to restrict the wolf from responding. Since we can detect a wolf through its howl from 1.2 km in either direction, the optimal grid size for doing systemic howling survey in a human-dominated landscape is $1.7 \times 1.7\ \mathrm{km}^2$ [Calculated from the formula of square inscribed in a circle, $1.2 \times \sqrt{2} = 1.69$]. The animal distance graph from the collared wolf will help in calculating the detection function for population estimation model through the howling survey.

Limitations of this study and future directions

We address many critical aspects of wolf conservation in our study. The wolf collaring programme was conducted exclusively in WM because of resource limitations. A comparative study on the collared wolf from EM would have been a more substantial way to conclude our findings. Although we have found that wolves visit survey locations more often as a response to solo howls from our field observations, the quantitative data are not available to test its significance level. The noise level would be a piece of additional information that might influence the detection of animal response. However, we were not able to include the impact of noise due to sample size restriction.

Managemental recommendation

Ecologists are often delighted to see human–animal coexistence and are more concerned about how adaptation in the human-modified environment saves them from extinction (Madden, 2004; Gross *et al*., 2021; Pooley, Bhatia, & Vasava, 2021). Human-induced adaptation habitually alters the fundamental behaviour of many species. A few studies explored the aftermath of this behavioural alteration that shifts the top predator's ecological role. The crucial finding from our research shows the potential adaptation in the fundamental howling behaviour of the Indian wolf in response to the high human-dominated landscape, which may critically impact the whole ecosystem. Therefore, surviving in mosaic patches of the human-modified landscape may save the wolf from local extirpation, but the impact on their long-range signatory call might have a severe outcome for the species and the landscape. Ecologists often solely consider the physical space in their conservation efforts, but our study highlighted that the acoustics space critically influences the fundamental behaviour of the vocal species. As the vocalization is associated with reproductive success and social cohesion of this pack living species and impacts, the foraging behaviour of the lower cascade, an urgent conservation effort is required so that 'acoustics space' is not compromised. Howling without increasing vulnerabilities is possible only in continuous large wolf habitats instead of conserving them in habitat fragments of a human-altered landscape. These required a national park-centric species conservation approach for wolves. This requires a significant policy revision in India to protect grassland habitats for conserving wolves. This national-level conservation plan might provide the necessary acoustics space for the wolves, which is the only way to save the keystone species with their fundamental behaviour and functional ecological role.

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Ethics Statement

The survey of free-ranging wolves of Maharashtra was performed with the consent of the Principal Chief Conservator of Maharashtra Forest Department [Letter no-22(8)/WL/CR-947(14–15)/1052/2015-16; Dated – 6th Aug 2015]. No animal was harmed during the study, and the standard non-invasive protocol of the howling survey was maintained (Approved by the Wildlife Institute of India animal ethics committee). Wolves were captured and followed standard and approved protocols after due permission from the Ministry of Environment, Forests and Climate Change, Govt. of India and Maharashtra Forest Department [MOEF&CC – F. No. 1-69/2017-WL/16.05.2017; MFD – SPP-15/01.06.2017].

Data Availability Statement

Compiled reports from R Scripts and all the data required to recreate the analysis can be found in the following Data S1, S2, S3, S4

Filename	Description
gam(nc).pdf	'gam' analysis of 28 howling responses from 264 howling surveys in the probable wolf sites in the different parts of Maharashtra
Zonal Effect.pdf	Plotting Howl Response from non-collared wolf from East and West Maharashtra with village distance
gam(collared).pdf	Generalized Additive Model (GAM) analysis of Howling Response from Collared Wolf
dataset.pdf	Dataset required for replicating the analysis

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Supporting information

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

Data S1. Generalized additive model (GAM) analysis of howling response from non-Collared Wolf.

Data S2. Plotting howl response from non-collared wolf from East and West Maharashtra with village distance.

Data S3. Generalized additive model (GAM) analysis of howling response from Collared Wolf.

Data S4. Dataset required for replicating the analysis.

Certificate of Participation

Shaheer Khan

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

Living in the Anthropocene: Space use and Movement of Indian Grey wolf of Maharashtra, India

DR. AFIFULLAH KHAN
Conference Director

DR. ORUS ILYAS
Conference Co-ordinator

Organized by

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

BRITISH ECOLOGICAL SOCIETY

Ecology Live Special

This certificate confirms that:

Shaheer Khan

Attended the above British Ecological Society event

On **26 November 2020**

Amy Everard

Events Manager
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BRITISH ECOLOGICAL SOCIETY

Festival of Ecology

This certificate confirms that:

Shaheer Khan

Attended the above British Ecological Society event and presented a talk entitled
Movement and space-use of Indian grey wolf (Canis lupus pallipes) in the human-dominated landscape

From **14 December 2020** to **18 December 2020**

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BES Annual Meeting:
18 - 21 December 2022, Edinburgh, UK

This certificate confirms that

SHAHEER KHAN

Attended BES2022 in Edinburgh, UK, and delivered an in-person **POSTER** presentation in the session **BEHAVIOURAL ECOLOGY** titled:

To cross or not to cross: Effect of roads on the movement behavior of Indian wolves (Canis lupus pallipes) in a human-dominated landscape, India.

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CERTIFICATE

Of Participation

Presented to

Shaheer Khan

for an Oral Presentation
on the topic

Den and rendezvous sites selection of Indian wolves Canis lupus pallipes in the human-dominated landscape of Maharashtra

at the 50 Years of Project Tiger
& First Indian Conservation Conference,
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