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

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Abstract

1.Large carnivore conservation is complex and remains a massive challenge across the world. Owing to their wide-ranging habits, large carnivores encounter various anthropogenic pressures which may potentially lead to conflict. Animal movement is linked with individual fitness as it is important for various biological processes. Therefore, studying how large carnivores adapt their movement to dynamic landscape conditions is vital for management and conservation policy. 2.We first quantified the movement parameters of four large carnivores in and outside protected-areas in India (tiger, leopard, dhole and wolf). We then tested the effects of human pressures like human density, road density and land use types on the movement of the species. Finally, we examined the configuration of core areas as a strategy to exploit human-dominated landscape. 3.Our findings suggest that the mean hourly displacement of 4 large carnivores differed across habitats. Mean displacement of large carnivores varied from 77.58m/h for leopards to 665.3m/h for wolves. Tigers outside PAs exhibited higher displacement as compared to tigers inside PAs. Displacement during day and night were significantly different for tigers inside and outside PAs (P=0.03), and wolf whereas no difference was found for leopard and dholes. The movement and ranging patterns of species outside PAs were influenced by anthropogenic factors such as human population, road network density, and landuse. All carnivores showed multiple areas of intensive use or cores in their home ranges. The range of the core area sizes was greater for species outside PAs (tiger and wolf) in human-altered landscapes. 4.Movement ecology of large carnivores has not been explored using such an exhaustive dataset in India. Our study attempts to extend theoretical concepts to applied management problems. This study can be a starting point for rigorous studies on interlinking animal movement and landscape management for large carnivore conservation and policy-making in the Anthropocene.

BACKGROUND

Across the globe, large carnivores are considered as the most charismatic yet vulnerable components of wild ecosystems (Miquelle et al., 2005). Positioned at the top of food chains, they influence all trophic levels thereby shaping entire ecosystems (Ripple et al., 2014). However, throughout their distributional range, large carnivore populations continue to decline rapidly due to anthropogenic pressures like habitat degradation and fragmentation, persecution, illicit commercial trade in body parts, depletion of wild prey and diseases (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. In order to survive, large terrestrial predators must negotiate human-modified landscapes adjoining Protected Areas (PAs) which are under various land use types. Such peculiar scenarios may lead to perceived or potential human- wildlife conflict posing a risk to their existence. Consequently, large carnivore conservation has become the prime focus of various stakeholders like biologists, politicians, activists, nature enthusiasts, funding agencies and lately with increasing awareness, the common man (Weber & Rabinowitz, 1996; Linnell, Swenson, & Anderson 2001; Treves, 2009).

India is home to the highest number of large terrestrial carnivores (average body weight >15kgs) in the world. The twelve species include Royal Bengal tiger *Panthera tigris tigris* , Asiatic lion *Panthera leo persiica* , leopard *Panthera pardus* , snow leopard *Panthera uncia* , clouded leopard*Neofelis nebulosa* , Indian wolf *Canis lupus* , Asiatic wild dog *Cuon alpinus* , striped hyena *Hyeana hyeana* , Himalayan brown bear *Ursus arctos isabellinus* , Asiatic black bear*Ursus thibetanus* , sloth bear *Melursus ursinus* and sun bear*Helarctos malayanus* . Of the total 12 species, 8 are either in the Endangered or the Vulnerable category of the IUCN Red List of Endangered Species and all are categorized under Schedule I of the Wildlife (Protection) Act, of India, 1972. India also ranks 2ndin world human population with 1.3 billion people and a density of 450 people per sq. km (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 pitching humans 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, spread over 5.6 million km, the Indian road network is the second largest in the world with the highest global density of 1.70 km roads per square kilometre of land (Basic Road Statistics of India, 2016). The aggressively developing nation aspires to achieve 8% economic growth from 2017–2022 (Niti AAYOG, 2017-2020).

In this setting, survival of large carnivores in India depends on their ability to adapt to the human-modified environment. The movement parameters of species evolve in response to the dynamic structure of a landscape (Fahrig, 2007). 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 and Reserves in India are small, isolated with compromised functional connectivity (Chundawat, Sharma, Gogate, Malik, & Vanak 2016; Mondal, Habib, Talukdar, & Nigam 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 which play a major role in determining community and population structures (Nathan et al., 2008). Such a study on large carnivores across heterogenous landscapes with fragmented metapopulations in the form of PAs interspersed within an agriculture matrix crisscrossed by linear infrastructure such as roads, railway network, canals and transmission lines is crucial for conservation planning and developing management strategies (Dickson, Jenness, & Beier 2005).

In this paper, we present the first study of movement patterns and space use of 4 large carnivores across diverse landscapes in India. We analyze movement data of tiger, leopard, dhole and wolf from the Central Indian landscape. First, we describe the attributes of movement trajectories and compare the movement pattern of these 4 large carnivores. We then examine the effect of land use, human density and road density as surrogates of human footprint on the movement of these wide-ranging, terrestrial carnivores. There have been general assumptions of space use of large predators but statistically robust data on movement of these predators both inside and outside PAs is absent. We test these assumptions and hypothesis across species and habitats with an aim to quantify a movement.

Hypothesis and Predictions

Prediction 1*: Movement of large carnivores differs across species and individuals within a species*

Tigers and leopards and dholes primarily inhabit forested areas whereas the wolf inhabits open grasslands and human dominated landscapes like agricultural lands. With vast variability in life histories and ecology of these big four carnivores of India, we hypothesized that the they would exhibit intra and inter specific variability in movement patterns.

Prediction 2*: Anthropogenic factors like human population density, road density and land use land cover types affect the movement of large carnivores*

In a country like India, humans are rapidly altering landscapes to make them conducive for development. Activities like urbanization of towns, conversion of forests to grazing land or agricultural expansion, expansion of transportation networks, etc. are rising and may affect drastically, the survival of large carnivores in small refuges like PAs. We hypothesized factors like human density, road density and land use patterns affect the movement of large carnivores. Across species and habitats, these variables would vary and pose various levels of risks and benefits (Phillips et al., 2004). We hypothesize that large carnivores will respond differently to the level of disturbance depending upon their ability to negotiate human pressures.

Prediction 3*: Core areas of large carnivores vary within and across species and habitats*

Core areas of animal home ranges have been defined as specific areas within the animal range which may be frequented by the animal for food sources or as a refuge (Kaufmann, 1962; Ewer, 1968). Within a species, although the individual home ranges may overlap, core areas within these home ranges remain exclusive (Ewer, 1968). We hypothesized that core areas would be significantly different within and across species; and the level of human disturbance may influence their configuration (number, area and perimeter).

MATERIALS AND METHODS

Study Area

The study was conducted across various PAs and non-PAs in the state of Maharashtra, India. The study sites were situated in the Eastern Vidarbha Landscape (EVL) of the Nagpur and Chandrapur Divisions and in the 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 one Forest Division (Brahmapuri Forest Division). EVL encompasses an area of about 50,000 km^2 covering six districts. It houses a human population of >10 million people, and at the same time has a forest cover of about 20,000 km^2. There are almost 8540 villages in this landscape (Habib, Nigam, Mondal, Ghaskadbi & Hussain, 2017). The landscape habitat is primarily tropical dry deciduous forest with bamboo *Dendrocalamus strictus* and teak *Tectona grandis* as the dominant flora and is home to an estimated number of 312 tigers (range 270-354) (Jhala et al, 2019). The study on wolves was conducted across the grasslands of semi-arid landscapes in two districts Pune and Solapur in Maharashtra. The area is dominated by crop fields, grazing lands, scrublands, grasslands, villages and territorial forest areas (Fig 1). The sympatric carnivores present in the area are Stripped Hyena *Hyaena hyaena,* Golden jackal *Canis aureus,* Indian fox *Vulpes bengalensis* and wide spread domestic dog *Canis familiaris* (Habib, 2007).

Study Species

Asia's largest obligate terrestrial carnivore, the tiger 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 but the size of current PAs in India are too small to maintain viable populations of this species over time. Tigers subsist in metapopulations with ongoing efforts to identify, link and conserve corridors. The leopard 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 co-exist with tigers, lions or dholes, a high degree of intraguild competition is observed (Hayward & Slotow, 2009; Wang & Mcdonald, 2009). Leopards display great behavioural plasticity by shifting feeding preferences, space use, micro-habitat use and activity pattern (Karanth & Sunquist, 2000) which enables them to survive in human-altered landscapes. The Asiatic wild dog or dhole is a shy, 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. In Asia, dholes are one of the top predators of tropical forests. Across their range in India, dholes share habitat with large carnivores like the tiger, and leopard. Previous studies on dholes have focused on intraguild competition, behavioral ecology, and genetics (Johnsingh, 1980, Acharya, 2007, Hayward, Lyngdoh, & Habib 2014, Ghaskadbi, Habib, & Qureshi 2016, Modi et al., 2018, Habib et al., 2018) but information on their movement ecology is limited. The Indian wolf is distributed across Central India, up to Rajasthan in the north and Karnataka in the south (Shahi, 1982) and is categorized as

Endangered by the IUCN Red List of Endangered Species. It is protected under Schedule I of the Wildlife (Protection) Act 1972. The 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). Evolutionarily, the Indian grey wolf is a part of an ancient clade which has not mixed with the wolf-dog clade, making them genetically ancient and unique among other wolves of the world (Sharma, Maldonado, Jhala, & Fleischer 2004; Shrotriya, Lyngdoh, & Habib 2012).

Capture and Radio-collaring

In a massive effort, 26 individuals across 4 species of large carnivores were radio collared (Fig 1) and monitored from years 2014-18. The animals were fitted with different collars and varying inter-fix 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 field daily using VHF ground tracking. For the analysis, the inter-fix interval data was homogenized to hourly inter-fix interval (Abrahms, 2007).

Table 1 Species characteristics, habitats and type of collars used to study movement of 4 large carnivores in India

Species	Habitat	Behavioural trait	Collar Type	Satellite	Int
Tiger (PA)	PA	Solitary	Vectronics GPS Plus Collars	Iridium	0.2
Tiger (NPA)	Outside PA	Solitary	Vectronics GPS Plus Collars	Iridium	0.2
Leopard	PA- Non PA interface	Solitary	Vectronics GPS Plus Collars	Globalstar	1 -
Dhole	PA	Social	Vectronics GPS Plus Collars	Ground Download	0.5
Wolf	Human Dominated Landscape	Social	Vectronics GPS Plus Collars	Iridium	1 -

We captured 14 tigers (nine from PAs; 5 outside PAs) across different age and sex classes. The tigers were monitored intensively between years 2014 to 2019 to study their movement and ranging patterns. A combination of Medetomine hydrochloride, Ketamine hydrochloride and Xylazine was used to immobilize animals in dosages based on the body weight, age, and sex. The drug mixture was remotely administered using an air-pressurized Dan-Inject projector (Model IM) and the animal was approached in a vehicle. The sedated animals were measured, weighed, radio-collared, and photographed. Furthermore, 3 leopards (two females and one male) were captured and monitored from 2014-15. Baited cages with drop-door mechanism were used to capture leopards. The animals were immobilized using a drug mixture of Ketmaine and Xylazine. We captured 5 dholes across age and sex classes including three adult males, one sub-adult male and one adult female. The dholes were intensively monitored from 2017-18 to study their ranging pattern. They were immobilized using tiletamine and zolazepam combination (Zoletil 100, Virbac) (Van Heerden, Burroughs, Dauth & Dreyer, 1991). The drug mixture was delivered from a vehicle remotely using Dan-Inject projector (Model JMSP.25) as no other method like foot traps, cages or lures proved suitable for dhole capture in a Tiger Reserve. Between 2017 and 2018, 4 wolves consisting of two males and two females were tracked intensively in the semi-arid landscape of Maharashtra. Wolves were captured using soft-catch leghold traps. 25 traps were set up in a circle 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.

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 inter-fix intervals across species were made uniform by post-processing all data into hourly data format for further analysis (Abrahms, 2007; Leblond, St-Laurent, & Cote 2016). Mean displacement during day and night was also compared across individuals. For comparison, day was defined from 0600h to 1800h and night from 1801h to 0559h.

We also calculated NSD, which is the squared distance between original location and each successive location (Papworth, Bunnefeld, Slocombe, & Millner-Gulland 2012). A graph of NSD vs. 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 time required to complete one such cycle starting at a randomly chosen original location was calculated. All movement parameters were quantified using the package 'adehabitatLT' (Calenge, 2006) in R software (R V3.5 R Core Development Team, 2018).

Understanding effect of anthropogenic factors on movement

We used the Brownian Bridge Movement Model, BBMM (Bullard, 1999) to evaluate home ranges of all species. 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 quantified BBMM at 50% and 95% contours using ArcMET extension tool (Wall, 2014) in ArcGIS 10.2. We considered 95% BBMM as the overall home range and 50% BBMM as core area of the animal home range (Fischer et al., 2013).

Anthropogenic factors such as human population density, land use land cover 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, land use land cover proportion and road network within the home range of large carnivores. We used the human population density map (100m resolution) available on the open source website (http://www.worldpop.org.uk/; Steven, Gaughan, Linard, & Tatem 2015). The land use land cover data of 1:25000 scale was acquired from Bhuvan's open source website (http://bhuvan.nrsc.gov.in/; NRSA, 2016). The LULC maps were generated using "Resourcesat AWiFS" satellite imagery, which classified Maharashtra into 13 land use classes. These original classes were re-classified into five major classes for analysis (Table 2). The road network data was obtained using Open Street Maps (Openstreetmap, 2018). We considered primary and secondary roads for our assessment because of their significant impact on the movement of animals owing to higher traffic volumes.

Table 2 Bhuvan's NRSA LULC original land use classes and reclassified classes used for evaluation of the proportion of land use within the homerange

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

The effect of human population density, different land use land cover and density of road network on the hourly displacement of species within home range was evaluated. Land use proportion of each class, average human population density and standardized road length in each animal's home-range were used as predictor variables. Coefficient of the factors was compared for same species in different landscapes (tigers inside and outside PAs), sympatric species in same landscape (tiger and leopard) and social canids with similar body size (wolf and dhole) in different landscapes using t-test. Pairwise comparison between two species was then carried out with Tukey's honest significant difference test. The statistical analyses were carried out in R 3.5 (R core development team, 2018).

Core ranges of large carnivores vary within and across species and habitats

Within home ranges, core areas are defined as exclusive areas of intensive use and likely contain features such as preferred foraging areas, dens and rest sites (Ewer, 1968) facilitating many species to co-exist. We computed the number, size and perimeter of core areas across 4 large carnivore species. All home range metrics were calculated using ArcMet tool (ArcGIS). For tigers, we compared the size and number of core areas of individuals of different sexes the same species 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 (Zar, 1984).

RESULTS

In all 32,691 fixes across 26 individuals of 4 large carnivore species were analysed. We examined the fundamental movement parameters, impact of human footprint and configuration of core areas of the animals of the 4 large carnivores across gradient of human disturbance.

Movement parameters of large carnivores

Inside PA, average hourly displacement of tiger and leopard was 161.74 ± 40.14 m/h and 77.58 ± 2.95 m/h respectively. Whereas, dhole moved of an average of 266 ± 39.63 m/h. Outside PA, the mean tiger displacement was 234.44 ± 98.79 and wolf moved an average of 665.3 ± 95.61 m/h (Table 3).

Mean hourly displacement for tigers was found to be significantly different inside (161.74 ± 40.14 m/h) and outside (234.44±98.79) PAs (P =0.04). Mean hourly displacement also varied significantly between day (157.99 ± 48.99) and night (215.32 ± 102.11) (P =0.03) with higher displacement during night across the landscape. Among sexes, mean displacement per hour of tigers varied with males having larger displacement (194.43 ± 84.49 m/h) than females (170.88 ± 32.08 m/h). Moreover, both the sexes showed longer displacement during night than day. Leopards showed least variation in mean displacement through day and night (71.06 ±8.08 and 82.22 ±0.58 respectively). One of the social canids, the dhole which inhabits forested areas showed higher displacement during daytime (521 ±202.88) as compared to night (393.6 ±277.45); whereas the wolves, social canids inhabiting human dominated landscapes showed higher mean displacement during night (877 ±129.52) as compared to day (465.3 ±190.39) and significant difference was found (P =0.03).

Based on NSD, all species across the landscape exhibited a confined movement pattern indicating territoriality. The tiger outside PA took 141.4 ± 44.77 h to complete one cycle (point of origin- maximum displacement - point of origin) whereas tiger inside PA (208.4 ± 167.7) took 32.14% higher time than outside PA. For leopards the time to complete each cycle was found to be maximum (1258.50 ± 485.59). Dholes and wolves took similar time to complete one cycle to cover their home ranges (204.915 ± 83.71 and 229.76 ± 111.6 respectively) (Table 4).

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

Species	System	Mean Displacement (m/h)	Mean displacement during day (m/h)	Mean displacement during night (m/h)
Tiger Inside PA	Dry Deciduous Forest (PA)	161.74 ± 40.14	138.90 ± 34.02	182.09 ± 52.83

Species	System	Mean Displacement (m/h)	Mean displacement during day (m/h)	Mean displacement during night (m/h)
Tiger Outside PA	Dry Deciduous Forest and Agriculture Interface	234.44±98.79	192.34 ± 56.48	275.14±146.11
Leopard	Dry Deciduous Forest (PA)	77.58 ±2.95	71.06 ±8.08	82.22 ±0.58
Dhole	Dry Deciduous Forest (PA)	266 ±39.63	521 ±202.88	393.6 ±277.45
Wolf	Human Dominated Grassland-Agriculture Mosaic	665.3 ±95.61	465.3 ±190.39	877 ±129.52

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 homer range circuit once

Species	Number of individuals (n)	Number of cycle	Range to complete one cycle (h)	Time to complete one
Tiger (PA)	9	99	15-1159	208.4 ± 167.7
Tiger (Non-PA)	5	42	21-620	141.4 ± 44.77
Leopard	3	8	216-3168	1258.50 ± 485.59
Dhole	5	28	27-708	204.915 ± 83.71
Wolf	4	17	60-480	229.76 ± 111.6

Effect of anthropogenic factors on movement of large carnivores

Mean displacement of large carnivores varied from 77.58 m/hr to 665.3 m/hr. We modelled the hourly displacement with each land use class, human density and road length in the home range of an individual. The data were analysed using two-way ANOVA to evaluate the effect of these anthropogenic factors within home ranges, between different species (Tiger inside PA, Tiger outside PA, Leopard, Dhole, Wolf) and also between different individual of the same species.

Mean displacement of tigers outside PA was 25.29% higher than inside PA and was found to be significantly different (p= 0.06). Forest area, agriculture and road length in home-range of tigers inside and outside PAs were found to be significantly different (p_{forest}=0.06, $p_{agriculture}$=0.03, p_{roads}=0.02). We compared the movement parameters of two social carnivores, the wolf and dholes. The mean displacement for wolf was 62.90% higher than dholes. All the habitat variables in the home-range were found to be significantly different between these social canids ($P_{\text{human density}}$ <0.001, P_{roads} =0.005, $P_{\text{agriculture}}$ =0.045, P_{forest} <0.001, $P_{\text{wasteland/grassland}}$ =0.008, $P_{\text{waterbody}}$ =0.005).

Core area variation within and across species and habitats

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 between species (Table 5). The range of the core area sizes was greater for species outside PAs (tiger and wolf) in human altered landscapes. The spread was lowest for species inside PAs like dholes and leopards (Fig 2).

The number of core areas of tigers inside and outside PAs was significantly different (p=0.05) whereas the difference in size of core areas was not significant (p=0.43). Although the median value of core area size was higher for tigers inside PAs (4.00) in comparison to the tigers outside PAs (1.53), the range of core area size was greater for tigers outside PAs (0.55 km^2 – 25.84 km^2) than inside (0.65 km^2-15.67 km^2) (Table 6). This signifies that tigers have a minimum size requirement of core areas across PAs and non-PAs. However, outside PAs the use of core areas may be influenced by the size of the available habitat patch and habitat matrix.

The two social canids dhole and wolf have a comparable body size, but the size of core areas was completely different. Dholes are the only social canids found in Indian forest systems and share habitat with larger co-predators like tigers and leopards whereas wolves are found in human-modified landscape in a mosaic of grasslands, and agricultural land. Number of core areas of both canids did not differ significantly (p=0.46) but core area sizes were significantly different (p=0.004). Core areas of dholes were smaller with narrow ranges (0.6 km^2-5.05 km^2), whereas wolves exhibited a wide range of core sizes (0.68 km^2 – 29.31 km^2) similar to tigers in non-PAs.

Table 5 Mean number, size and perimeter of core areas of 4 large carnivores in India.

Species	Mean No. of Core Areas	Mean Core Area Size (km^2)	Core Area Size Range (km^2)	Mean Core Area Perimeter (m)
Tiger PA	2 ±1.80	5.99 ±5.50	0.6-5.05	14.97 ±10.56
Tiger NPA	3.25 ±1.70	5.6 ±7.77	0.68-29.31	12.53 ±10.04
Dhole	2.2 ±1.7	2.21 ±1.6	1.37-7.04	8.17 ±4.48
Wolf	2.33 ±1.52	11.37 ±9.96	0.55-25.84	15.08 ±8.33
Leopard	2 ±1.41	3.85 ±2.74	0.65-15.67	11.92 ±7.23

Table 6 Number and size of the core areas of tigers across sex and between protected and non-protected area in India.

Species	Habitat	Mean No. of Core Areas	Mean Core Area Size (km^2)	Core Area Size Range (km^2)
Tiger NPA Male	Dry Deciduous Forest and Agriculture Interface	3.33 ±2.08	5.94 ±8.72	0.63-25.84
Tiger PA Male	Dry Deciduous Forest (Protected)	3.25 ±2.21	4.62 ±5.14	0.65-15.67
Tiger NPA Female	Dry Deciduous Forest and Agriculture Interface	3	4.46 ±4.16	0.55-8.84
Tiger PA Female	Dry Deciduous Forest (Protected)	1 ±0	11.23 ±5.79	4.66-15.59

DISCUSSION

Movement of large carnivores across human dominated landscapes

In our study areas, 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 disturbed habitats, wolves showed the highest movement amongst all 4 carnivores whereas the leopards in natural areas showed the least. Our findings are contrary to the findings of Tucker et al., (2018) that suggested mammalian movement in human dominated areas is only up to one half the extent of their movement in natural areas with relatively low human pressures. The major limitation of Tucker's study was that it did not include species, especially large carnivores from developing countries with high human and carnivore densities, livestock and fragmented landscapes.

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 wherein cougars and lions in human dominated landscapes exhibited higher speeds while traversing through fragmented human dominated areas to reduce time spent in multiple use areas (Kertson, Spencer, Marzluff, Hepinstall-Cymerman, & Grue 2011; Valeix, Hemson, Loveridge, Mills, & Macdonald 2012).

Across sexes, both male and female tigers traveled more at night than during the 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.

Leopards took the highest time (1258.50$\pm$485.59) to return from the point of maximum displacement to the point of origin. 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 the study area where they are faced with human pressures. Under such circumstances, leopards travel from one core area to other and spend more time in such core areas. This strategy enables them to co-exist with large carnivores and humans.

Interestingly, tigers outside PAs took comparatively lesser time (141.4 $\pm$ 44.77) to cover their home range than tigers inside PAs (208.4 $\pm$ 167.7) even though their home ranges (95% contour) outside PAs were larger in size. As discussed, tigers in human disturbed areas move faster owing to presence of habitat matrix between core areas. which enables them to cover larger areas in shorter time.

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 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. It is important to study the movement of animals through these landscapes. Land use 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 (Fig 3). Historically, wolves adapted to live in human dominated landscapes as they evolved near humans (Anderson, 2018). However, our results indicate that the wolves move faster in human dominated landscapes to negotiate human pressures within large home ranges.

Comparison of land use types within tiger home ranges suggested that proportion of forest cover was not significantly different whereas agriculture outside and inside PAs was significantly different (P_{forest}=0.06;$P_{\text{agriculture}}$=0.03 respectively). It is worth discussing that home ranges of tigers outside PAs were primarily forest areas (72.72%).

However, forest outside PAs is fragmented with high human density and road network which may explain why tigers outside PAs have larger home ranges. To negotiate this landscape, tigers outside PAs also move at higher speeds than inside PAs. We examined the proportion of human population density inside 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. In our study area, the leopard is pushed to the fringe areas of the PA due to high density of larger predator, the tiger. Tigers inside PAs (0.29 human/100 km^2) and dholes (0.51 human/100 km^2) showed the least proportion of human pressure in their home ranges signifying they occur in prime forested areas (Fig 4). Dholes in our study area show higher human population pressure than tigers in their home range as a strategy to avoid large predators. In order to avoid competition, dholes established intensive use areas near PA fringes (Ghaskadbi, P. 2017unpublished data).

Across our study sites, the home range of wolves had the maximum density of roads (56.6) followed by tigers outside PAs (25.7). The home range of dholes showed the least density of roads (5.5) (Fig 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 in our study site was a non-functioning highway with only tourist activity in limited time windows.

Large carnivore core areas across landscape

Core areas of animals have been studied to address a wide range of research queries (Hooten, Wilson, & Shivik 2008) such as social information transmission (Darden Steffensen & Dabelsteen, 2008), interspecific competition (Neale & Sacks, 2001), trophic cascades (Prange & Gehrt, 2007), habitat selection (Chamberlain, Leopald, & Conner 2003), reproductive success (Thompson, Kahlenberg, Gilby, & Wrangham 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 7). 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.

Tigers have a minimum size requirement of core areas in and outside PAs but there was high variation in core area size outside PAs which may be influenced by availability of habitat patch. There is a positive correlation (R^2=0.90) between the number and perimeter of core areas. In the fragmented landscape outside PAs, the number and therefore the perimeter of core areas is high. Large carnivores like the wolves and tigers outside PAs are likely to have a greater core area perimeter which indicates higher chances of exposure to human induced effect at interference at the perimeter of the most extensive used habitat patches (Table 8).

Table 7 Showing perimeter of core areas, an important parameter to evaluate the chance of human animal encounter for 4 large carnivores in India.

Species	Mean No. of Core areas	Mean size of core area (km^2)	Total Perimeter (km)
Dhole	2.2	2.21	18.0
Wolf	2.33	11.37	35.1
Leopard	2	3.85	23.8
Tiger NPA	3.25	5.6	40.7
Tiger PA	2	5.99	29.9

When we compared the perimeter of male and female tigers across PAs and non PAs, we found a linear relationship (Fig 6) between the number of cores and the perimeter. The female tigers in PAs had only one core area with the expected dramatic increase in number of cores and perimeter outside PAs (Table 8). This result again supports the finding that female tigers outside PAs are more prone to conflict owing to their higher energy demand and greater perimeter which means more chance of interaction with humans.

Table 8 Showing perimeter of core areas, an important parameter to evaluate the chance of human animal encounter for tigers across sex and protected and non-protected areas in India.

	Mean No. of Core areas	Mean size of core area (km^2)	Total Perimeter (km)
Tiger NPA Male	3.33	5.94	43.4
Tiger PA Male	3.25	4.62	39.2
Tiger NPA Female	3	4.46	32.8
Tiger PA Female	1	11.23	19.6

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, conservation of large carnivores is interlaced with various political, socioeconomic and emotional issues which complicate this challenge. Increasingly, wildlife is compelled to coexist with humans in highly modified landscapes highlighting the need of planned and coordinated interdisciplinary efforts. Integrating movement ecology in landscape management and policy making 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. Studies on movement ecology and conservation have primarily been conceptual. We take an applied perspective by drawing on theory to link movement ecology of an animal with conservation considerations in dynamic landscapes under anthropogenic stress. The novel findings of the large-scale study on the movement ecology of 4 large carnivores of India will have dramatic 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 a cautionary learning for countries where the densities of populations may increase in the future. If large carnivores are to co-exist 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 needs to be informed by real time knowledge of animal motion and navigation capacities if we are to safeguard the sensitive connections between the PAs. 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.

Data Accessibility Statement: The data contains locations of endangered species from areas which are prone to poaching and human prosecution. The locations of the four endangered species from India will make species prone to many risks including poaching. Under such circumstances as corresponding author, I request for exception of this clause. Since this is the first paper from India with exact GPS locations of large carnivores, our request may be considered. Some of our GPS location belong to the breeding locations, such areas are still occupied by breeding females. Making such location public will risk such individuals.

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List of Figures

Figure 1 Map of study sites (top) with land use land cover and protected areas, (below left) human population density and (below right) road density in Maharashtra, India

Figure 2 Violin plot indicating the distribution of the range of the core area size, median (white dot) and spread of the data (black line) for 4 large carnivores in India

Figure 3 Land use proportion within the home range of 4 large carnivores in India. Data from Bhuvan's LULC (http://bhuvan.nrsc.gov.in/) was used to classify home ranges

Figure 4 Human population density within the home range of 4 large carnivores in India.

Figure 5 Road density within the home range of 4 large carnivores in India

Figure 6 Relationship between number of core areas and perimeters of tiger home ranges across different sexes and habitat (protected areas and non-protected areas) in India

DECLARATIONS

Competing interest Statement: The authors declare that they have no competing interests

Authors contributions

BH and PN conceived ideas and designed methodology; SK, PG and ZH collected and analyzed the data; PG, SK, BH and ZH led the writing of the manuscript. All the authors contributed critically to the draft and gave final approval for publication.

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Ethics approval and consent to participate

All the four species where captured followed standard and approved protocols after due permission from Ministry of Environment, Forests and Climate Change, Govt. 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.

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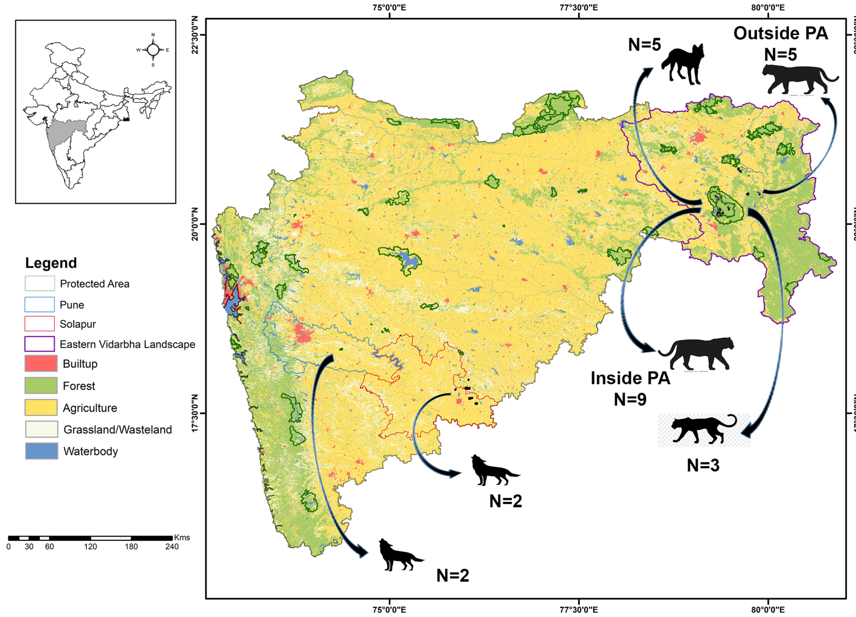
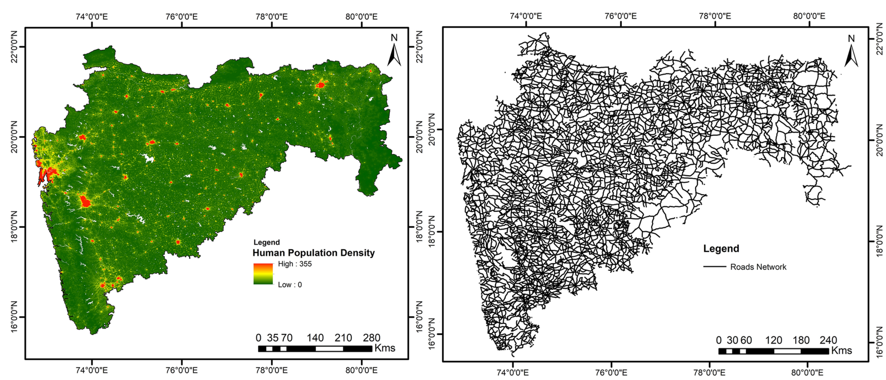
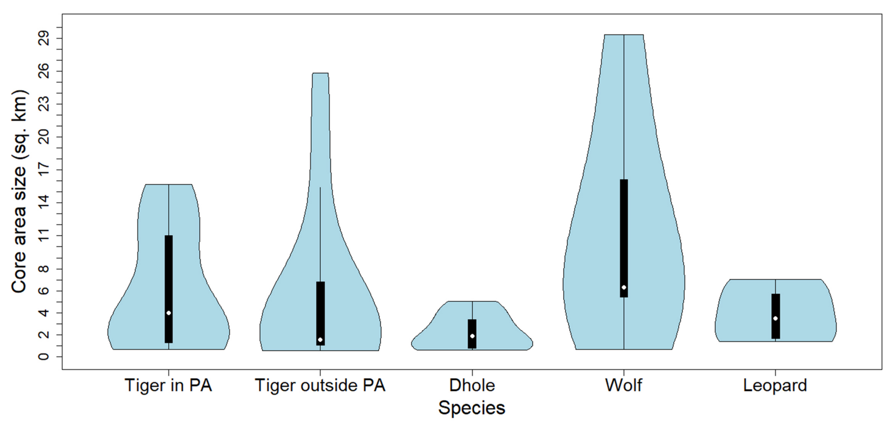
Consent for publication: Not applicable


Legend
Protected Area
Pune
Solapur
Eastern Vidarbha Landscape
Builtup
Forest
Agriculture
Grassland/Wasteland
Waterbody
Outside PA
N=5
N=5
Inside PA
N=9
N=3
N=2
N=2
Kms
0 30 60 120 180 240


Legend
Human Population Density
High : 355
Low : 0
0 35 70 140 210 280
Kms
Legend
Roads Network
0 30 60 120 180 240
Kms


Core area size (sq. km)
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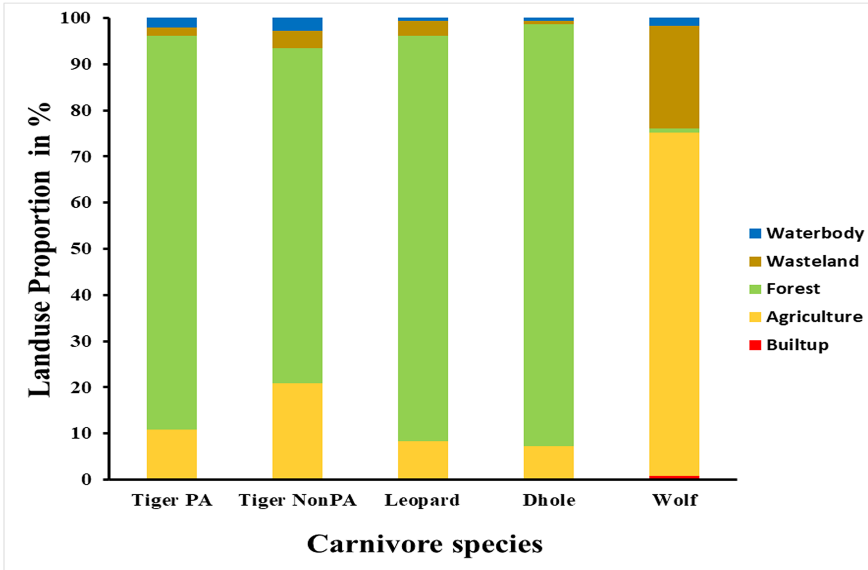
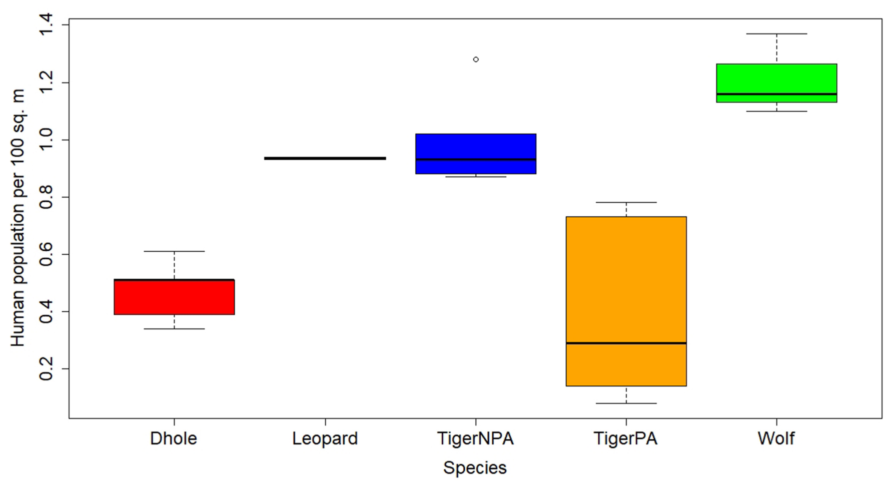
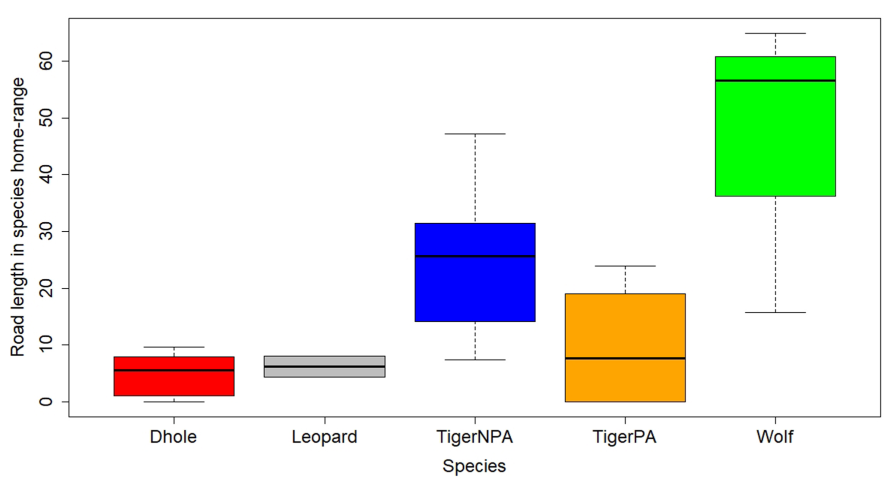
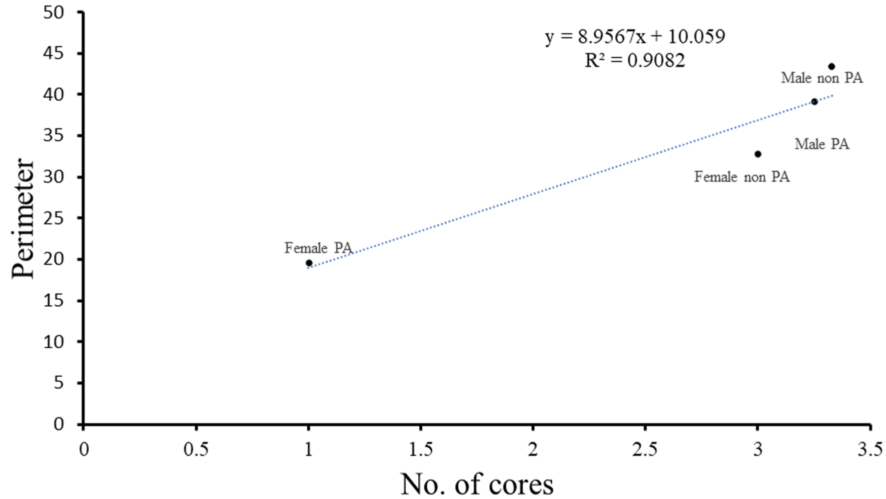
Tiger in PA
Tiger outside PA
Dhole
Wolf
Leopard
Species


100
90
80
70
60
50
40
30
20
10
0
Landuse Proportion in %
Tiger PA
Tiger NonPA
Leopard
Dhole
Wolf
Carnivore species
Waterbody
Wasteland
Forest
Agriculture
Builtup


Human population per 100 sq. m
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Dhole
Leopard
TigerNPA
TigerPA
Wolf
Species


Road length in species home-range
0
10
20
30
40
50
60
Dhole
Leopard
TigerNPA
TigerPA
Wolf
Species


y = 8.9567x + 10.059
R² = 0.9082
Male non PA
Male PA
Female non PA
Female PA
Perimeter
No. of cores
0
5
10
15
20
25
30
35
40
45
50
0
0.5
1
1.5
2
2.5
3
3.5