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Distribution, Status, and Conservation of the Indian Peninsular Wolf

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An understanding of the distribution range and status of a species is paramount for its conservation. We used photo captures from 26,838 camera traps deployed over 121,337 km^2 along with data from radio-telemetry, published, and authenticated wolf sightings to infer wolf locations. A total of 3,324 presence locations were obtained and after accounting for spatial redundancy 574 locations were used for modeling in maximum entropy framework (MaxEnt) with ecologically relevant covariates to infer potentially occupied habitats. Relationships of wolf occurrence with eco-geographical variables were interpreted based on response curves. Wolves avoided dense wet forests, human disturbances beyond a threshold, arid deserts, and areas with high top-carnivore density, but occurred in semi-arid scrub, grassland, open forests systems with moderate winter temperatures. The potential habitat that can support wolf occupancy was 364,425 km^2 with the largest wolf habitat available in western India (Saurashtra-Kachchh-Thar landscape 102,837 km^2). Wolf habitats across all landscapes were connected with no barriers to dispersal. Breeding packs likely occurred in ≈89,000 km^2. Using an average territory size of 188 (SE 23) km^2, India could potentially hold 423–540 wolf packs. With an average adult pack size of 3 (SE 0.24), and a wolf density < 1 per 100 km^2 in occupied but non-breeding habitats, a wolf population of 3,170 (SE range 2,568–3,847) adults was estimated. The states of Madhya Pradesh, Rajasthan, Gujarat, and Maharashtra were major strongholds for the species. Within forested landscapes, wolves tended to avoid top-carnivores but were more sympatric with leopards and dhole compared to tigers and lions. This ancient wolf lineage is threatened by habitat loss to development, hybridization with dogs, fast-traffic roads, diseases, and severe persecution by pastoralists. Their status is as precarious as that of the tiger, yet focused conservation efforts are lacking. Breeding habitat patches within each landscape identified in this study should be made safe from human persecution and free of feral dogs so as to permit packs to breed and successfully recruit individuals to ensure wolf persistence in the larger landscape for the long term.

Keywords: ***Canis lupus pallipes*, camera traps, radio telemetry, MaxEnt, home range, pack size, population estimate, wolf-large carnivore Interaction**

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INTRODUCTION

Reliable information on the status, that is the distribution, population size, extent, and habitat contiguity between populations, are essential for the management of any endangered species (Sousa-Silva et al., 2014). This basic information is not available for many species, and conservation management is often based on educated guesses that can have direr consequences (Blake and Hedges, 2004) and is especially relevant for threatened species that occur outside of protected areas (Maron et al., 2018; Simmonds and Watson, 2019). Carnivores, due to their wide-ranging behavior, low density, and elusive nature, are one of the most difficult taxa to study (Garshelis, 1992). The status of many carnivores was assessed from indices, such as pug-marks for tigers and lions (Wynter-Blyth and Dharmakumarsinhji, 1949; Choudhary, 1970), simulated howls for wolves (Harrington and Mech, 1982), and golden jackals (Graf and Hatlauf, 2021), questionnaire surveys, and interactions with the local community (Jhala and Giles, 1991, Karanth et al., 2009). In the absence of any better approach, the information generated by these methods was often used for policy decisions and management actions. However, now with the advent of cost-effective modern technologies, such as camera traps and radio-telemetry, and analytical approaches, i.e., species distribution models (Sousa-Silva et al., 2014), better insights on species distribution and abundance and their determining factors are possible.

Indian peninsular wolves (*Canis lupus pallipes*) are an ancient lineage of wolves endemic to the Indian sub-continent (Sharma L. K. et al., 2004; Hennelly et al., 2021). They are considered endangered and are listed on Schedule 1 of the Wildlife Protection Act (1972). Several attempts have been made to evaluate their status locally (Jhala and Giles, 1991; Kumar and Rahmani, 1997; Singh and Kumara, 2006) and at the country scale (Shahi, 1982; Jhala, 2003; Karanth et al., 2009; Srivathsa et al., 2020). Earlier range maps and population estimates were based on ground surveys, information from local pastoralists, and knowledge of wolf ecology and their habitat (Shahi, 1982; Jhala and Giles, 1991; Kumar and Rahmani, 1997; Kumar, 1998; Kumar and Rahmani, 2000; Jethva and Jhala, 2004; Singh and Kumara, 2006; Kumar and Rahmani, 2008; Agarwala et al., 2010). Karanth et al. (2009) used expert knowledge, while Srivathsa et al. (2020) used a combination of data from field surveys, citizen science, and authenticated reports, while both studies used occupancy framework with eco-geographical and human footprint covariates to model wolf distribution across India.

In this study, we used data generated from the largest camera trap survey to date covering 121,337 km^2 (Jhala et al., 2020) in combination with wolf locations obtained from radio-telemetry and authenticated records as presence data to model species distribution. We subsequently estimate population size based on territory size and pack size estimates in occupied and breeding habitats. We evaluate wolf distribution and relative abundance with respect to other large competing carnivores and identify wolf stronghold populations that should be targeted for conservation to ensure wolf persistence in the larger landscape for the long term.

MATERIALS AND METHODS

The geographical extent of our study covered the entire range of Indian wolves within India. We modeled wolf distribution using the maximum entropy approach in maximum entropy framework (MaxEnt; version 3.4.1, Phillips et al., 2006) that uses machine learning from occurrence locations of the target species and background points along with ecologically relevant spatial environmental variables to develop statistical relationships (Elith et al., 2011). These relationships are then used to predict species occurrence across modeled space (Elith et al., 2011). We used a combination of methods to infer wolf presence locations. These were (a) extensive coverage of forested habitats across 20 Indian states by camera traps carried out by State Forest Department personnel and research biologists of the Wildlife Institute of India (Jhala et al., 2020). Camera traps with heat and motion detectors were deployed at 26,838 locations in 2018–2019 to cover a forested area of 121,337 km^2 (**Figure 1**). All photo captures of wildlife were geotagged and subsequently segregated into species. Camera trap locations that recorded wolf captures were used for modeling wolf distribution. (b) Since Indian peninsular wolves were known to use agro-pastoral landscapes (outside of forest habitats; Jhala, 1993) and since these areas were not camera trapped, we obtained records of wolf presence from Shahi (1982), Jhala (1993, 2003, 2007), Jhala and Sharma (1997), Kumar and Rahmani (1997), Jethva (2003), Habib (2007), Lokhande and Bajaru (2013), Saren et al. (2019), Ghaskadbi et al. (2021), Mahajan and Khandal (2021), Maurya et al. (2021), Sadhukhan et al. (2021), Sharma (2021), and Trivedi et al. (2021), and from radio-telemetry (Jhala, 2007) and geotagged records from Jhala Y.V. et al. (2021) to augment the camera trap data.

Since many of the radio-telemetry-based locations and other locations were clumped, we picked only one location for approximately every 5 km^2. This reduced the spatial redundancy of information in location data and we were left with 571 locations that were used for model building. Based on knowledge of wolf ecology and behavior (Mech, 1970; Jhala, 1993; Mech and Boitani, 2007), we hypothesized *a priori* that Peninsular Indian wolves would occur in semi-arid grasslands, scrub, and open forests with high ambient temperatures, would avoid areas of high human density but occur in rural areas with livestock husbandry, and would avoid areas having a high density of competing carnivores. The eco-geographical variables used in MaxEnt were as follows: (a) habitat characteristics (land use land cover, Normalized Difference Vegetation Index (NDVI), elevation, and ruggedness; (b) climatic factors (temperatures of coldest and hottest months, rainfall, and aridity); (c) human footprint indices (distance to night light, distance to roads, road density, and human modification index; (d) prey indices as livestock density, goat and sheep density, and cattle density, and (e) top-carnivore density (tiger and lion density across their range of occurrence) (**Supplementary Table 1**). Linear, quadratic, and product features available in MaxEnt were used in combination with representative variables from each of the above-mentioned eco-geographical variable categories. The models were assessed based on area under the curve (AUC) of receiver operator curves (ROC), specificity and sensitivity of the models, and testing the

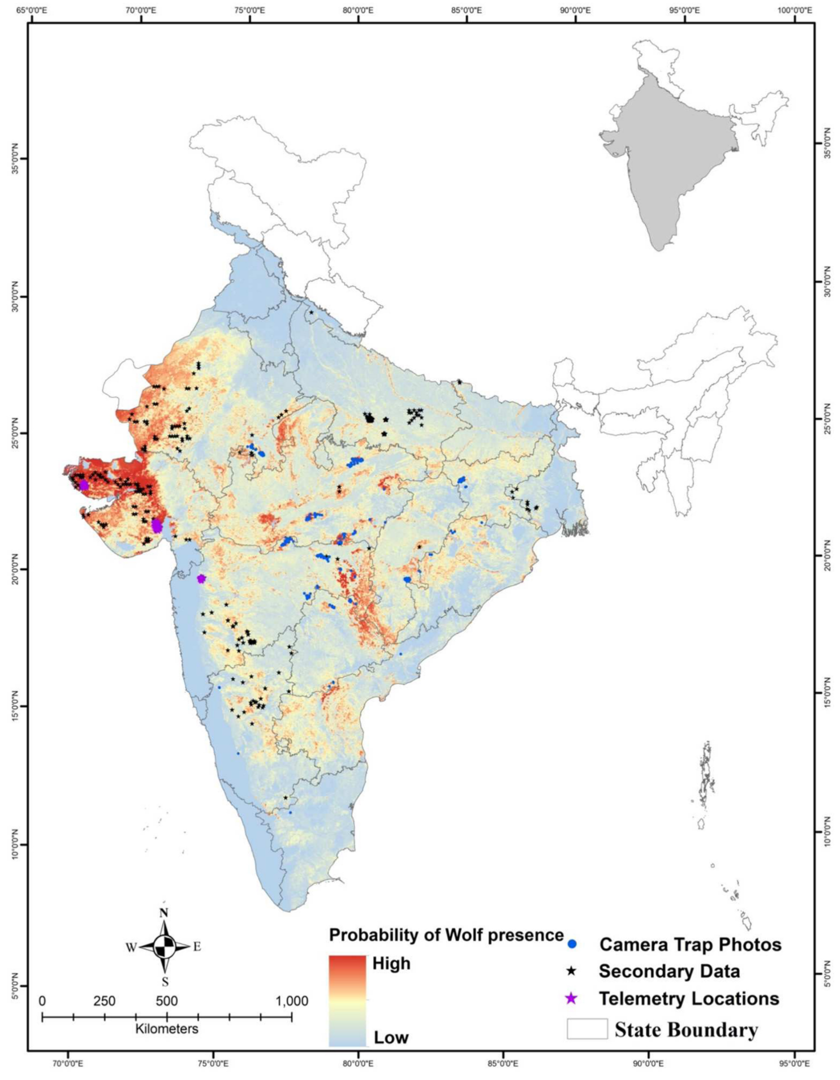

FIGURE 1 | Wolf distribution modeled in MaxEnt using presence locations with eco-geographical variables of human modification, climate, habitat, competing carnivores, and prey. Map inset shows region within India where wolf distribution was modeled.

model classification accuracy on 30% of the data that were not used for model building (Jiménez-Valverde, 2011). Best models were selected on the basis of model fit and parsimonious use of relevant ecological covariates that made ecological sense based on our *a priori* expectations (**Supplementary Table 1**). We used clog-log analysis (Phillips et al., 2017) to determine the probability value beyond which pixels had high wolf occurrence classification and below which wolves were likely absent to determine the area occupied by wolves. We also determined the pixel probabilities for 16 known breeding packs from 14 different areas spread across India and used one SD on the mean pixel values to address uncertainty in the cutoff values to determine occupied and breeding habitats.

Wolves are known to be territorial where neighboring territory areas overlap minimally (Jhala, 2003; Habib, 2007). Since 100% Minimum Convex Polygon territories of four wolf packs reported by Habib (2007) did not differ from 95% fixed kernel estimates of another eight radio-collared packs from three different sites (Jhala, 2007) (t-test, p = 0.9) we combined these estimates for our analysis to get better coverage of territory sizes from across India (**Supplementary Table 2**). We removed isolated wolf occurrence habitat patches that were <100 km^2 from further analysis as these would be too small to harbor wolves. We used data from 35 wolf packs for estimating adult pack size (**Supplementary Table 3**) to estimate the potential wolf population within areas of breeding habitat. Occupied areas outside of breeding habitats would hold dispersing individuals, old ousted pack members, and sub-adults biding their time to join packs or form their own packs (Packard and Mech, 1980). For areas that were above the MaxEnt clog-log probability value of occurrence but below the threshold of breeding packs, we used a conservative estimate of wolf density of less than one wolf per 100 km^2 (range between 0.75 and 0.5 wolves per 100 km^2).

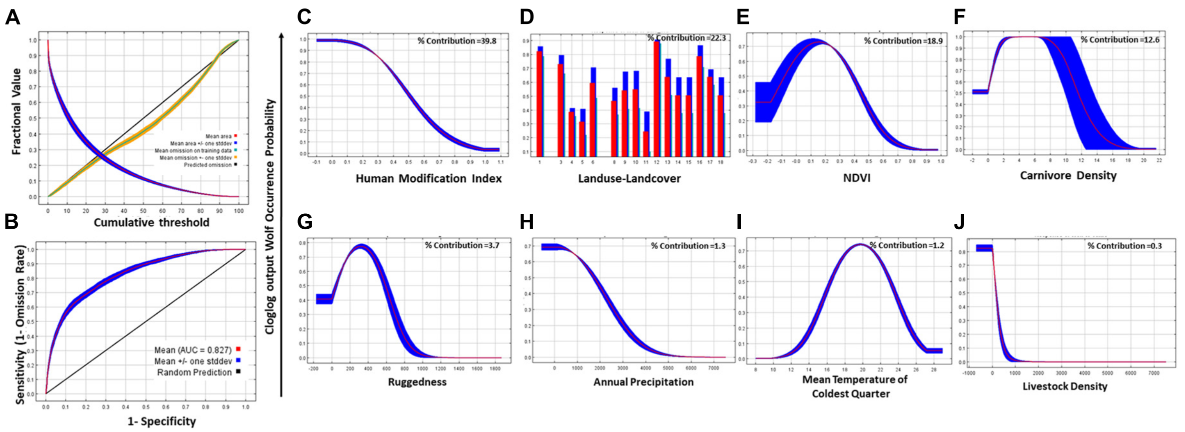

FIGURE 2 | Response curves of wolf occurrence with eco-geographical variables, their contributions, and model fit assessment obtained from 100 bootstrap runs of the best MaxEnt model. **(A)** Variation in the omission of model data and predicted area with increasing MaxEnt cumulative threshold values. **(B)** Receiver operating curve of test and training data. **(D)** Land use land cover classes were (1) arid scrub, (3) grassland, (4) agriculture, (5) settlement, (6) open, (8) water, (9) riparian, (10) evergreen open, (11) evergreen broadleaf, (12) deciduous broadleaf, (13) deciduous open, (14) mixed open, (15) evergreen broadleaf open, (16) deciduous broadleaf open, (17) scrub, and (18) coastal marsh. **(E)** Normalized Difference Vegetation Index (NDVI). **(F)** Carnivore density (density of tigers and lions) across their range in India.

To get a better understanding of species interactions within forested habitats, we computed relative abundance index (RAI, Carbone et al., 2001) as the number of photo captures per 100 trap days of wolves, dhole, leopards, and tigers and averaged these for all camera traps in 25 km^2 grids. We plotted wolf RAI against dhole RAI, leopard density, and tiger density from Jhala et al. (2020) and Jhala Y.V. et al. (2021) and inspected scatterplots, fitted models, and tested for linear correlations to better understand species interactions.

RESULTS

We obtained 34,858,623 photographs of wildlife from which 2,812 were of wolves from 313 camera locations. Published (34), other geo-tagged records (365), and radio-telemetry (2,612) contributed to a total of 3,324 wolf presence locations from across the range of the species in India (**Figure 1**). The best MaxEnt model was a good fit with an AUC of 0.83 and performed well in classifying 30% of the test data (**Figure 2**). Wolf occurrence was best explained by (1) climatic variables: (a) average rainfall, (b) average temperature of the coldest quarter; (2) habitat characteristics: (a) pre-monsoon NDVI, (c) land use and land cover; (3) Human Modification Index (maximum contribution to the model 40%); (4) prey availability in the form of livestock density; and (5) density of top-carnivores (**Figure 2**). As per our *a priori* predictions, wolves were tolerant of higher temperatures (**Figure 2** and **Supplementary Figure 1**), they preferentially occurred at semi-arid sites that had lower rainfall, higher temperatures, lower values of canopy cover (NDVI), avoided high human densities but their occurrence coincided with moderate livestock densities. As expected, the response of wolves to top-carnivore density was a right-skewed bell-shaped function, with wolves occurring in areas of low top-carnivore densities but declining at high top-carnivore densities (**Figure 2** and **Supplementary Figure 1**).

Wolf territory size was estimated at 189 (SE 23) km^2 (**Supplementary Table 2**). The total area above the threshold value obtained from clog-log analysis (p = 0.47 SE 0.0094) that could potentially be occupied by wolves after removing isolated areas that were smaller than 100 km^2 was 364,425 km^2 in India. The largest potential for wolf occupancy was in the contiguous Saurashtra-Kachchh-Thar landscape (102,837 km^2, **Figure 3**). Area suitable for breeding packs was estimated at 89,138 km^2 with the largest contiguous breeding habitats available in the Central Indian landscape (37,323 km^2, **Figure 3**). Considering an average adult pack size of 3 (SE 0.24) adult wolves (**Supplementary Table 3**) for breeding habitat and a density range from 0.75 to 0.5 wolves per 100 km^2 for occupied areas outside of the breeding habitat, the potential number of wolves in India was estimated at 3,170 (SE range 2,568–3,847). Besides the Saurashtra-Kachchh-Thar landscape, the other habitat patch that could potentially hold a population of > 150 wolves was Udanti Sitanadi-Indravati-Kawal-Tadoba (**Figure 3**). Shivpuri-Mukundara-Gandhi Sagar, Satpura-Betul-Melghat, Bandhavgarh-Sanjay, and Panna-Nauradehi were other areas that support good wolf populations. Madhya Pradesh supported the largest wolf population followed by the states of Rajasthan, Gujarat, and Maharashtra (**Table 1**).

Scatter plots of wolf RAI against dhole RAI, leopard, and tiger density categories in forested habitats (**Supplementary Figure 2**) showed that wolf relative abundance declined with an increase in competing for carnivore relative and absolute abundances. Declines in wolf photo-capture rates were sharper and statistically significant with an increase in tigers compared to that of leopard and dhole.

DISCUSSION

Assessing the status of widespread, low density, and elusive species, such as the wolf, is a difficult task (Kunkel et al., 2005).

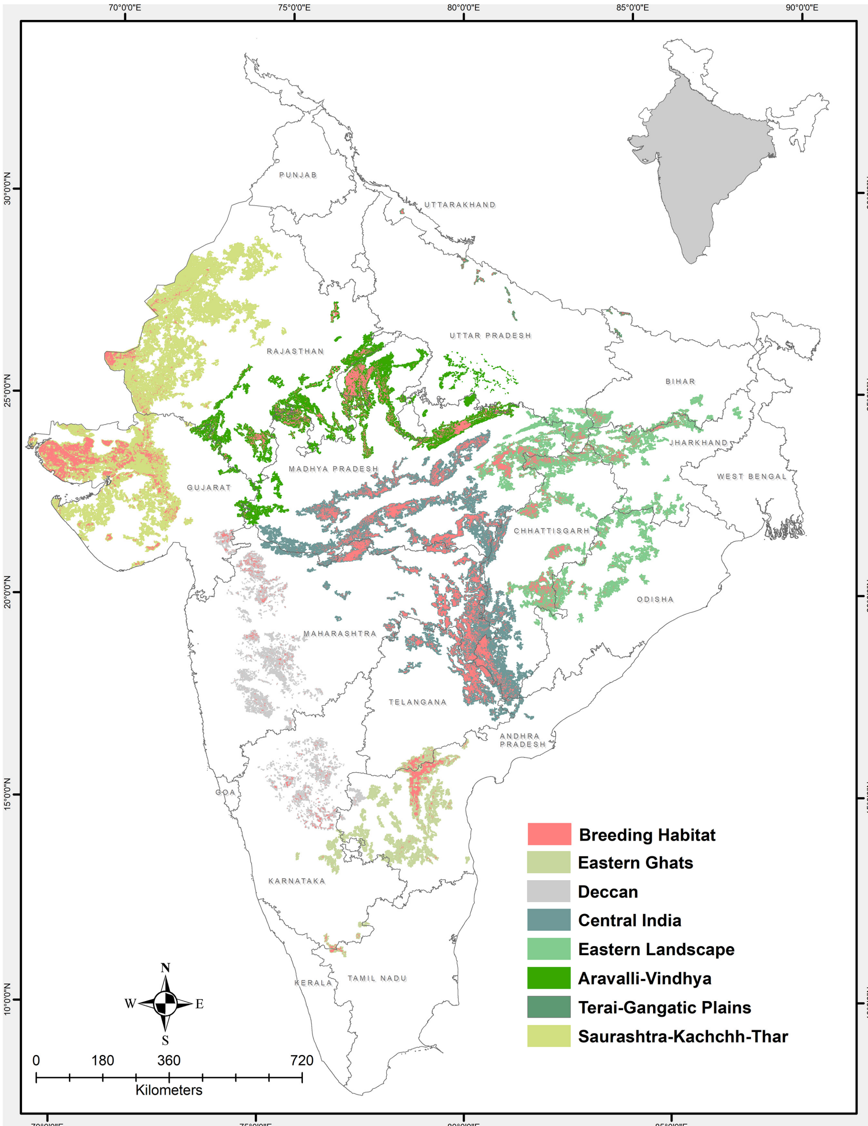

FIGURE 3 | Wolf-occupied landscapes and breeding habitats across India inferred from the MaxEnt models. MaxEnt, maximum entropy framework.

Shahi (1982) estimated the Indian wolf population at ≈800 individuals, while subsequent estimates were higher (2,000–3,000; Jhala, 2003) due to a better understanding of wolf distribution and ecology. The current assessment uses robust quantitative information of occurrence data (from large-scale geo-tagged camera trap, telemetry, and authenticated sightings) in combination with species distribution models with relevant eco-geographic covariates to evaluate wolf status. We use clog-log models with 100 bootstrap runs in MaxEnt (Phillips et al., 2017) to determine the threshold probability below which wolf occurrence was unlikely, to determine wolf-occupied area. Estimates based on models are only as good as the data used to build these models; with an extensive coverage of wolf location data from across their range, from varied habitats, and eco-climatic conditions, we believe that our model predictions are good (as also shown by model evaluation statistics). However, we caution that due to the clog-log threshold used to determine wolf occupancy, there will be some areas where wolves may be present and our model threshold failed to predict them or predicated wolf occupancy in areas of known absence. We believe that at the country scale, these small errors would not matter, but at local scales where conservation measures need to be implemented, deviations from the truth would make a large difference. Therefore, the wolf habitat suitability map provided in this article should be used as a first cut and subsequent ground validation of the model results eventually used for conservation investments and management. The current distribution (**Figures 1**, **2**) and population estimate (**Table 1**) are similar to earlier estimates and validate Jhala (2003) with better information and formal model-based analysis. In the past

TABLE 1 | State-wise estimated wolf population based on the MaxEnt model estimate of potential occupied, breeding habitat, average pack size of 3 (SE 0.24), and territory size of 188 (SE 23) km^2.

State	Occupied habitat (km^2)	Breeding habitat (km^2)	Population estimate (SE range)
Madhya Pradesh	81,734	25,979	772 (626–938)
Rajasthan	73,697	7,097	532 (428–416)
Gujarat	53,891	15,656	494 (401–600)
Maharashtra	40,114	14,453	396 (322–481)
Chhattisgarh	35,310	9,908	320 (259–389)
Andhra Pradesh	20,567	3,582	165 (133–199)
Telangana	15,046	6,165	156 (127–190)
Odisha	11,730	1,107	84 (68–102)
Jharkhand	10,499	1,641	82 (66–99)
Karnataka	9,545	1,238	72 (58–87)
Uttar Pradesh	7,659	1,299	61 (49–74)
Bihar	4,022	758	33 (26–40)

States of Tamil Nadu, Uttarakhand, West Bengal, and Haryana had sporadic wolf occurrence. Range is one SE of the mean.
MaxEnt, maximum entropy framework.

two decades, wolf populations seem to have colonized new areas while losing out in some of their strongholds. Wolves have been recently recorded from several areas from where they had been exterminated or were not known to exist in the recent past [e.g., Rajaji Tiger Reserve (Sharma, 2021), Bangladesh (Muntasir et al., 2021), Indian Sundarbans (Ghai, 2017), Valmiki Tiger Reserve (Maurya et al., 2021), and Kaveri Wildlife Sanctuary (Gubbi et al., 2020)]. While wolves have declined from their stronghold of Kachchh and parts of Rajasthan primarily due to persecution, hybridization with dogs, and development of fast traffic roads. The easternmost limit of the Indian wolf was the Sundarban mangrove forest (Ghai, 2017; Muntasir et al., 2021), there were no records of the Indian wolf from Assam and the North East States. No suitable occupied habitat was predicted in the states of Haryana and Punjab, possibly due to extensive and intensive agriculture, yet it is possible that wolves can also sporadically occur in these two states. It was believed that Indian peninsular wolves rarely used forested habitats (Jhala, 2003), however, as evidenced from the extensive camera trap data, wolves have been recorded from several forested areas of India (**Figure 1**). Notably, the tiger reserves of Mukundara, Kawal, Udanti Sitanadi, Melghat, Panna, Palamau, Bor, Kanha, Satpura, and Pench had a good number of wolf photo captures. Wolf photo captures from these tiger reserves were either from the buffer zone or from parts of the reserve that had relatively open canopied forests and scrubland habitats, and these parts had a relatively low density of tigers. Conserving a large carnivore outside of the realms of a protected area, especially when it has the propensity of predation on livestock, is a formidable task despite being protected by law (Woodroffe et al., 2006). Protected areas targeting wolves as a focal species for conservation were few (e.g., Mahuadanr, Hazaribagh, Gandhi Sagar, and Nauradehi wildlife sanctuaries). Therefore, documenting breeding wolf populations in some well-protected areas of India heralds well for the long-term conservation of Indian wolves. Earlier estimates of wolves from Gujarat and Rajasthan (Jhala and Giles, 1991) mapped their distribution and abundance based on extensive ground surveys and expert knowledge of local pastoral communities. These estimates were lower than the estimates reported herein. The MaxEnt-based analysis identifies habitats that meet the requirements for wolf occupancy based on the covariates used to build the model, human persecution can severely deplete wolf populations within suitable habitats as has been observed in Kachchh in recent times. Therefore, detailed ground surveys and radio-telemetry-based estimates of pack size, territory configurations, and sizes in selected sites are required to validate the population estimates obtained by model-based inference and for monitoring long-term population trends. Telemetry studies from mid-1990s to 2005 in the Bhal and Kachchh regions of Gujarat and Nashik (Jhala, 2007) and Sholapur in Maharashtra (Kumar and Rahmani, 1997; Habib, 2007; Habib et al., 2021) have shown that wolf populations were vulnerable to disease and persecution and fluctuated substantially (Jhala, 2003). Unfortunately, no long-term telemetry-based studies are being implemented on the Indian wolves at specific sites to monitor population dynamics. Source populations of wolves within each of the identified landscapes need to be monitored continuously through radio-telemetry to keep the *pulse of the population,* i.e., ensure that these populations are not declining, and if declining, identify site-specific threats so as to address them in a timely manner. As long as these source populations are secure within each landscape, they will recruit wolves that will disperse and occupy the larger landscapes. Efforts to reintroduce wolves from captive-bred zoo populations should only be considered after appropriate rewilding, evaluation of their behavior, and skills of hunting wild prey. Such wolves (if habituated to humans) can become a major cause of human-wolf conflict (Jhala and Sharma, 1997; Rajpurohit, 1999) and compromise the conservation of the entire species due to community backlash (Treves et al., 2006).

Response curves of wolf occurrence to eco-geographical covariates were in consonance with our hypothesis conforming to their behavioral ecology. Besides climatic and habitat characteristics, top carnivore densities contributed (12.6%) to explaining wolf occurrence. It has long been speculated that Indian wolves have likely been out-competed by other large carnivores that dwell in forested habitats (Jhala, 1993). The alternative hypothesis could be that Indian wolves evolved at a time when India was undergoing a dry spell (Sharma D. K. et al., 2004; Hennelly et al., 2021) and adapted to open semi-arid habitats and therefore now avoid thick forests. Wolves often occurred in the buffer zones of protected areas, but were rarely seen within the core areas of PA's that have high large carnivore densities even though habitats were suitable. For example, the habitats of Gir Protected Area and that of Ranthambore National Park were suitable for wolves (dry open canopied deciduous and thorn forests) and wolves occurred in the periphery of these reserves, but they were rarely seen in the core areas that have high lion and tiger densities, though these core areas abound in prey. While in protected areas, namely, Nauradehi, Gandhi Sagar, and Mukundara, that have similar habitats but do not have tigers or lions and dhole, wolves use most parts of these protected areas. These observations suggest that though Indian wolves may have specialized for open habitats, they were also likely limited by direct competition with other large carnivores. Since we had density estimates of only tigers and lions covering the full extent of these carnivores' range across India, we could use these for modeling wolf occurrence in MaxEnt (**Figure 2**). However, wolves were also likely limited by leopards and dhole. Leopards occur outside of forests as well (Daniel, 1996), while dholes are primarily forest dwellers (Johnsingh and Acharya, 2013) in tropical India. Since leopard, dhole, and wolf photo capture rates were available only from forested habitats, we restricted our analysis on their interactions to this habitat that was extensively camera trapped across India (Jhala et al., 2020). Wolves tended to avoid all three competing large carnivores but were more tolerant of leopards and dhole compared to tigers (**Supplementary Figure 2**).

The peninsular Indian wolf is an ancient lineage endemic to the Indian sub-continent (Sharma L. K. et al., 2004; Hennelly et al., 2021), its status is precarious and with only ≈3,100 adult individuals their population is as big as that of the tiger in India (Jhala Y. et al., 2021). Wolves are persecuted by pastoralists, threatened by diseases spread by dogs, and genetically swamped by a large feral dog population (Jhala, 2003; Vanak and Gompper, 2009; Srivathsa et al., 2019). Conserving wolves is a more formidable task compared to tigers, since the majority of their population resides outside the realm of protected areas and there are currently no focused efforts for conserving the species. For successful recruitment, all that wolves require, within the larger occupied landscapes that include several types of land use and cover, are small patches (5–15 km^2) of safe habitat for denning and rendezvous sites between December to March (Jhala, 2003). Besides the use of poison, the new multi-lane fast-traffic motorways being built through wolf habitats are a death knell for wolves and other threatened species and need careful mitigation to provide safe passage (Dennehy et al., 2021). Ensuring that breeding habitats are well protected would enable wolves to continue to persist in the larger occupied landscape. This study provides the required information for focused efforts to target and assist in their long-term conservation.

DATA AVAILABILITY STATEMENT

The data analyzed in this study is subject to the following licenses/restrictions: Data on pack size, territory size are included in the **Supplementary Material**, location data is provided in the figure. Since the precise location of Schedule 1 species under the Wildlife Protection Act is not possible to be provided in the public domain, therefore, wolf location data will be provided for genuine users based on reasonable requests to the corresponding author. Requests to access these datasets should be directed to corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the manuscript does not involve capture or handling of any animal and depends on secondary data that was generated with appropriate legal approvals as per the wildlife protection act.

AUTHOR CONTRIBUTIONS

YJ conceived the study, collected field data, did the data analysis, and wrote the manuscript. SS conducted data analysis and wrote the manuscript. QQ and SK contributed field data. All authors reviewed and commented on 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.2022.814966/full#supplementary-material

Supplementary Figure 1 | Relationships of wolf occurrence with eco-geographical variables when all variables were considered together in the model and with variables that were considered in explaining wolf occurrence but not used in the final model.

Supplementary Figure 2 | Three-dimensional and two-dimensional scatter plots of wolf relative abundance index (RAI) against tiger **(B,C)**, leopard **(A,B,D)**, and dhole **(A,E)**. Two-dimensional scatter plots show intensity and 95% ellipses of data distribution. Wolf RAI was negatively correlated with all three large carnivores but was statistically significant ($p < 0.01$) only for tigers.

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