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Land-sharing potential of large carnivores in human-modified landscapes of western India

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Abstract
The current protected area (PA) network is not sufficient to ensure long-term persistence of wide-ranging carnivore populations. Within India, this is particularly the case for species that inhabit nonforested areas since PAs disproportionately over-represent forested ecosystems. With growing consideration of human-use landscapes as potential habitats for adaptable large carnivores, India provides a model for studying them in densely populated landscapes, where there is little understanding about human-carnivore interactions in shared spaces. Using key informant interviews and an occupancy modeling framework, we assessed the distribution of three large carnivore species, the leopard *Panthera pardus*, Indian grey Wolf *Canis lupus pallipes*, and striped hyena *Hyaena hyaena*, across a ~89,000 km^2 semiarid multiuse landscape in western India, and quantified ecological drivers of their presence. The three species occupied 57% (leopard), 64% (wolf), and 75% (hyena) of the landscape of which only 2.6% area is protected as national parks or wildlife sanctuaries. The presence of the three carnivores was differentially favored by certain types of agriculture, while populations of domestic livestock supported them in this landscape with low densities of large wild prey. Our results demonstrate the adaptability of large carnivores in human-modified landscapes, and we call for an expansion of the current conservation narratives that currently focus on forested PAs, to include the high potential that anthropogenic landscapes offer as habitats where people and predators can co-adapt and persist.

KEYWORDS
carnivores, human-modified landscape, hyena, India, leopard, wolf

Three large carnivores are present in semiarid landscapes with high human densities and poor wild prey abundance challenging present-day Indian wildlife management narratives.

1 | INTRODUCTION

Human-modified landscapes are increasingly being recognized as potential habitats for many wildlife species that are of conservation concern (Chapron et al., 2014; Gehrt, Riley, & Cypher, 2010). While such landscapes may not be compatible with certain species' ecologies (Karanth, Nichols, Ullas Karanth, Hines, & Christensen, 2010) or species may show statistical avoidance of these areas (Bouyer et al., 2015), they can provide acceptable habitat and facilitate persistence of other species (Prange & Gehrt, 2004; Yirga et al., 2017). Although this challenges traditional approaches to conservation, these landscapes are predicted to become common in the future (Dobrovolski, Loyola, Guilhaumon, Gouveia, & Diniz-Filho, 2013; Lindenmayer et al., 2008). While some species populations have recovered by the creation of unmodified protected areas (PAs) (Walston et al., 2010), land-sharing holds the promise of letting other species persist in the long term by increasing connectivity between PAs and expanding the total size of populations. Many wide-ranging and low-density species that occur outside state-institutionalized reserves cannot be restricted to the current PA network (Chapron et al., 2014; Rodrigues et al., 2004). Exploring alternative approaches is pertinent for accommodating human needs and conservation goals, especially in the face of rapidly changing landscapes (Crespin & Simonetti, 2019).

The wide-ranging nature of large carnivores produces an overlap between their distributions and human-modified areas (Johansson et al., 2016; Sanderson, Redford, Vedder, Coppolillo, & Ward, 2002), potentially posing threats to human lives and livelihoods. This may lead to carnivore population declines and loss of community support for conservation (Treves & Karanth, 2003). However, a congruence of carnivore resilience (Chapron et al., 2014; Mech, 2017), conservation policy (Swenson, Linnell, Swenson, & Andersen, 2015; Treves & Karanth, 2003), and local acceptance of carnivores (Carter & Linnell, 2016) has enabled carnivores to persist in “shared spaces” in many countries (Lindenmayer et al., 2008). While Europe and North America are witnessing recolonization of large carnivores in human-modified landscapes following their mass persecution (Chapron et al., 2014; Smith, Nielsen, & Hellgren, 2016), countries like Australia (Newsome et al., 2014), Ethiopia (Yirga et al., 2017), Brazil (Vynne et al., 2011), Iran (Hosseini-Zavarei, Farhadinia, Beheshti-Zavareh, & Abdoli, 2013), India (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2013), Kenya (Van Cleave et al., 2018), and Israel (Barocas, Hefner, Ucko, Merkle, & Geffen, 2018) have also recorded large carnivore presence in mix-use landscapes. These studies demonstrate the complex and evolving relationships between people and predators, challenging earlier generalizations about co-adaptation in shared spaces (Linnell, Swenson, & Andersen, 2001; Woodroffe, 2000).

Besides being the second most populous country in the world, India is also one of the fastest growing economies in Asia. This entails large-scale land-use conversions with intensive irrigation-assisted agriculture to increase production, industrialization, and urbanization to accommodate economic interests (Sudhira, Ramachandra, & Jagadish, 2004; Tian, Banger, Bo, & Dadhwal, 2014). Despite these conservation challenges, India still retains high diversity and densities of large carnivores (Karanth, 2011). Although high densities of humans and wildlife in India have historically co-occurred in shared spaces, management and research on large-bodied wildlife is mostly focused on populations inside PAs, which cover <5% of the country's land area known (Ghosal, Athreya, Linnell, & Vedeld, 2013). For instance, large carnivores use of human-modified habitats, their interactions with humans, and their life histories in these landscapes are very poorly understood, and there is a need for the conservation discourse to expand to human-modified landscapes (J. R. B. Miller, Linnell, Athreya, & Sen, 2017).

Among the various shared landscapes in India, arid and semiarid regions present a unique set of problems. These have sparse tree cover and could not support taxable livelihoods and the British colonial administration wrongly recognized them as degraded “wastelands.” This designation has shaped their current governance, which rarely regards them as important ecosystems (Ratnam, Tomlinson, Rasquinha, & Sankaran, 2016; Whitehead, 2010), and they are easily converted for agriculture, infrastructure development, and industrial use (P. Singh et al., 2006). Most regions have gradually transformed from rain-fed systems to intensively irrigation-fed permanently cropped lands, or become hotspots of industrial-scale infrastructure, thus creating fragments of semiarid lands. There is an emerging threat from the proposed National Forest Policy of India (F. No. 1-1/2012-FP [Vol.4], 2018), which proposes to increase “forest cover” on semiarid and desert tracts, clearly indicating the lack of ecological understanding of these unique ecosystems.

In this study, we focused on three wide-ranging carnivore species—the leopard *Panthera pardus*, the Indian gray wolf *Canis lupus pallipes*, and the striped hyena *Hyaena hyaena*, to (a) examine the ecological and anthropogenic factors that facilitate their persistence in a large multiuse semiarid landscape (~89,000 km^2) co-inhabited by high-density human populations and (b) determine the patterns of occurrences of these species in this landscape. Among these species, leopards are better represented in research from outside-PAs, most likely because they pose serious management challenges (Athreya et al., 2015; Kshettry, Vaidyanathan, & Athreya, 2017). The ecological requirements of wolves and hyenas in human-use areas, however, remain largely unknown. Based on the observed distribution patterns, we make inferences on the social, management, and policy attributes that could aid in the conservation of these large carnivores in shared semiarid landscapes, outside the PA network.

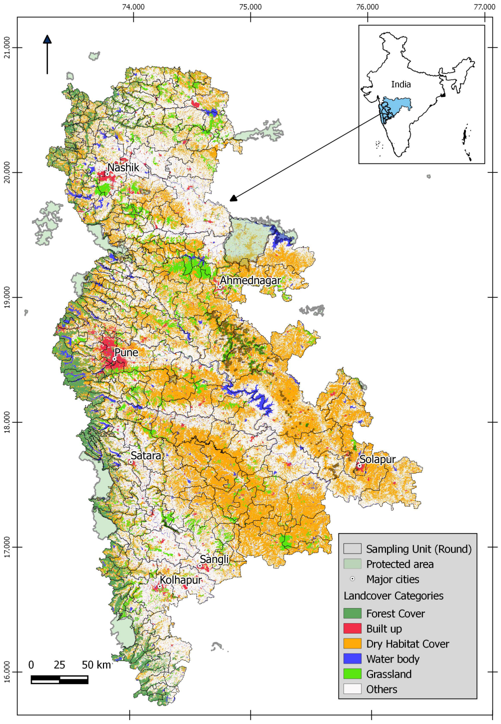

FIGURE 1 A map of the study area depicting land cover with protected areas, major cities and sampling unit boundaries overlaid on it

2 | MATERIALS AND METHODS

2.1 | Study area

We chose seven districts in western Maharashtra (Nashik, Ahmednagar, Pune, Satara, Sangli, Solapur, and Kolhapur), which together cover 89,853 km^2 of primarily semiarid human-dominated landscapes (Figures 1 and 2). District-level human population densities range from 266.48 to 602.63 people/km^2 (2011 India census; https://www.census2011.co.in/census/state/districtlist/maharashtra.html; accessed June 13, 2017). The landscape is highly heterogeneous; the western fringes abutting the Western Ghats are more forested and receive higher rainfall (average monsoon rainfall June–September = 230 mm).The central and eastern parts of the study area receive less rainfall (average monsoon rainfall = 90 mm), and are dominated by arid habitats with a grassland-cropland mosaic (http://hydro.imd.gov.in/hydrometweb/(S(r4sf5srela3ca3zdvw4mkaep))/DistrictRainfall.aspx; accessed June 13, 2017; http://bhuvan.nrsc.gov.in/; accessed February 13, 2016) (Roy et al., 2015).

The region has three large river basins (the Godavari, Krishna, and the Bhima), where agricultural intensification through irrigation has modified arid habitat in the past few decades, where cultivated areas are dominated by sugarcane, millet, grapes, paddy, soya, and other cash crops (District Census Handbook http://censusindia.gov.in/2011census/dchb/DCHB.html; accessed July 17, 2017). Most arid lands and forests under the State Forest Department's control have been progressively converted to monoculture plantations of *Azadirachta indica*, *Gliricidia sepium*, *Eucalyptus spp.*, and *Acaciaspp.* over the past five decades. The region has 11 PAs belonging to National Parks or Habitat/Species Management Area categories (Protected Planet https://protectedplanet.net/country/IND; accessed December 21, 2018) and covering *c.* 2,401.4 km^2 (2.6% of the study area; World Database on Protected Areas https://protectedplanet.net/; accessed June 17, 2017; Protected Areas of India-- ENVIS Centre on Wildlife and Protected Areas http://www.wiienvis.nic.in/Database/Protected_Area_854.aspx; accessed June 17, 2017; Maharashtra Forest department http://www.mahaforest.nic.in; accessed June 17, 2017), mostly which encompass forested lands (including plantations) and poorly represent arid lands. All three large carnivores have been documented outside PAs in this region, generally in the context of livestock losses and attacks on humans (Athreya et al., 2013; Habib & Kumar, 2007). Along with the tiger *Panthera tigris*, which was present in the landscape historically (Karanth et al., 2010), the region originally had a diversity of medium-to-large-sized ungulate herbivores; gaur *Bos gaurus*, sambar *Rusa unicolor*, and chital *Axis axis* in the western parts, and blackbuck *Antilope cervicapra* and chinkara *Gazella bennettii* in the central and eastern parts (Karanth, Nichols, Hines, Karanth, & Christensen, 2009), although these are now sparsely present outside the few PAs and their fringes.

2.2 | Study design

We assessed carnivore distributions in human-dominated areas and excluded protected reserves (national parks and wildlife sanctuaries), which formed less than 3% of the total sampled area. We collected detection/nondetection information on all three carnivores under an occupancy framework (MacKenzie et al., 2018), treating 305 forest administrative units called "rounds" as independent sampling units (hereafter, "sites"). We collected these data through interviews with forest department field staff as our key informants who were active in the field at least during the previous 12 months and were therefore likely to provide reliable information. The average area of the sites was 299.52 km^2 (±19.11 [standard error [SE]). Because we wanted to examine true occupancy and not habitat use, almost all sites were considerably larger than the estimated home range sizes for all species (120–300 km^2 for wolf [Habib, 2007; Jhala & Giles, 1991]; 6–50 km^2 for leopard [Odden, Athreya, Rattan, & Linnell, 2014]; 6–10 km^2 for hyena [Athreya et al., 2013]). We conducted interview surveys from January to July 2015, treating

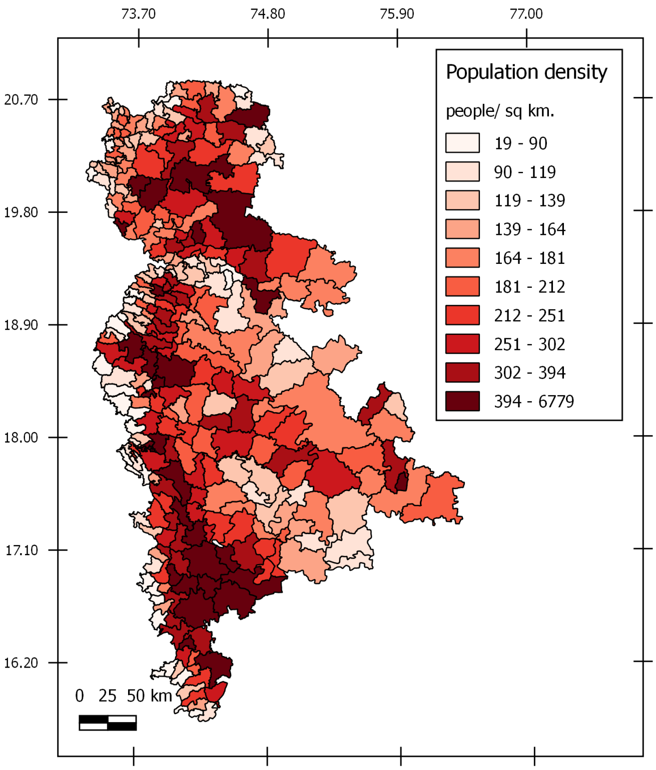

FIGURE 2 A map showing distribution of human densities in the study area (the categories have been fixed to represent equal counts of units)

each interview as an independent replicate (1–18 interviews per site; Srivathsa, Puri, Kumar, Jathanna, & Karanth, 2018). We assumed that a site's occupancy status did not change during the one year for which data were collected (Rota, Fletcher, Dorazio, & Betts, 2009). Relying on administrative boundaries as sites (rather than a grid-based design) allowed us to accurately describe the spatial limits of the sites to the respondents (see Pillay, Johnsingh, Raghunath, & Madhusudan, 2011), and also obtain sufficient number of replicates at this spatial scale.

Our protocol for eliciting interview responses was: (a) We asked all questions in the local language *Marathi*, (b) detection/nondetection records were based only on first-hand sightings of the species (dead or alive) over the past 12 months; indirect signs such as scat, tracks, or calls reported by the respondent were not recorded to avoid potential misclassifications (D. A. Miller et al., 2011), and (c) each respondent was presented with photographs of the focal species for identification. If the respondents identified the species correctly, we further enquired about the morphological and behavioral traits of the species to which if the respondent was unable to give the correct details, their response was discarded. Alternately, for cases where the respondent was unable to identify species altogether from the photograph on the first attempt, we described behavioral and morphological characters of the species to them and a second attempt at identification was allowed. If the species were not identified even after this, their response was discarded. Hence, only those respondents who could describe the species or assign morphological and behavioral traits to each species was considered. In all cases where the respondent reported the presence of a species, we recorded the name of the closest village, habitat where the species was seen, and its behavior as observed by the respondent. Since oral consent was obtained from each respondent prior to the interview, we did not obtain approval from any human ethics committee before the data collection.

2.3 | Covariates for modeling species occupancy and detectability

We collected information on land use/land cover, human population, domestic and wild prey availability as predictors for modeling occupancy probability (ψ; probability of species presence in a site) of leopards, wolves, and hyenas (see Figures S1–S3 in Appendix S1). Similarly, we used information on respondent's field experience, their ability to identify other species and the number of respondents (effort) in each site to model detection probability (*p*; probability of detecting the species, given its presence in the site). For the former, we derived remotely sensed land-use/land-cover information from the Bhuvan–Indian geo-platform of Indian Space Research Organisation (http://bhuvan.nrsc.gov.in [accessed February 13, 2016]) and (Roy et al., 2015). We chose absolute land-use area values as covariates for predicting ψ since the use of proportion of each category within differently sized sites would lead to loss of information on minimum habitat requirements for the species. We obtained site-specific numbers of domestic animals and people from the All India Livestock Census 2012, Government of India and the All India Population Census 2011 (http://censusindia.gov.in/ [accessed January 20, 2015]), respectively. We calculated both abundance and densities of domestic livestock in each site; the former reflects minimum prey requirement and the latter accounts for accessibility of prey per unit area, both of which could be relevant as predictors. We collected information on the presence of the two most widely distributed wild prey species (chinkara and blackbuck) in each site as part of the interview surveys (Table 1). As a surrogate for the abundance of wild prey, we calculated the proportion of respondents who reported a presence for either chinkara or blackbuck for each site.

For all three carnivore species, we selected covariates following a priori predictions based on field observations and published literature concerning their natural history (Table 1). Broadly, we predicted that (a) leopard presence would be positively associated with higher degree of tree cover or permanent crop cover (because of the refuge it provides in human use landscapes) and abundance/densities of medium and large domestic prey, but negatively with urban habitation (Athreya et al., 2015; Kshettry et al., 2017), (b) wolf presence would be positively influenced by open dry habitats including grasslands, seasonal crop cover, abundance of antelope, and medium-sized domestic prey, but negatively by forest cover and urban habitation (Habib & Kumar, 2007; Jethva & Jhala, 2004; M. Singh & Kumara, 2006), (c) hyena presence would be positively influenced by dry habitats with scrub cover, permanent crop cover like has been recorded in parts of the landscape, abundance of medium-sized domestic prey and poultry farms, but negatively by open dry habitats and urban habitation (Athreya et al., 2013; P. Singh, Gopalaswamy, & Karanth, 2010).

We predicted that detection probability would increase with longer field experience of respondents (≥10 years) and with the number of respondents interviewed per site (Guillera-Arroita, 2017). Being the only large felid in the landscape, leopard identification was generally unambiguous. Since this was unlikely for wolf and hyena, we considered that respondents' ability to identify the other carnivore (i.e., identify hyena when recording for wolf and vice versa) would affect detection and used this binary 0/1 index as a reliability score in modeling p.

2.4 | Analytical methods

If a species sighting was confirmed by a respondent in the past year, we recorded it as a single "1" (irrespective of more than one sighting), while nondetection by a respondent was recorded as a single "0" and detection histories were created accordingly for all. We used the program PRESENCE 12.10 (Hines, 2006) to estimate ψ and p using the standard single-season occupancy model (MacKenzie et al., 2018). We used a two-step process to predict the two parameters of interest: ψ and p (Doherty, White, & Burnham, 2012). We first performed model selection to predict p, while keeping a general additive structure for ψ constant. Here, we tested all possible combinations of covariates to examine singular and additive effects. The model with the best relative fit for p was chosen based on Akaike information criterion (AIC; K. P. Anderson & Burnham, 2002), and was kept constant while building models for ψ. In the case of ψ, we first simplified the global model by dropping those predictors whose SE values were higher than their β estimates. We then examined model ranking by building competing models with either singular or additive effects of the remaining covariates which were compared against the null model based on AIC values, and also allowed for assessment of top model performance (Mac Nally, Duncan, Thomson, & Yen, 2017). We concluded on our top models depending on which ranked within ΔAIC of 2.0 of the top most model. However, we calculated averaged occupancy estimates (with associated standard errors) across all models for each site and present the β estimates for each covariate from the top most model it figured in from the entire set. Since differing occupancy probabilities might be a function of unequally sized sampling units, we examined top model performance by additionally including the area of the sampling unit as a covariate provided it was not highly correlated ($r > |0.7|$) with other covariates. Because they represented the same category of predictor, we refrained from using domestic prey "abundance" and "densities" in the same model although these non-nested models were compared together using AIC values (D. Anderson & Burnham, 2006). We standardized all covariates using z-score conversions and examined them for cross-correlations; covariates with a correlation of Pearson's $r > |0.7|$ were not used together in the same model.

3 | RESULTS

We obtained adequate data through interviews (1,626 interviews; 1–18 interviews per site) for only 295 sites out of 305, since for 10 of these respondents were not available. After filtering out data from those respondents who could not identify the species correctly, less than 5% of the remaining respondents required a second attempt at identification for any of the three species. Because of this low proportion, assuming that this category of respondents would have introduced an upward bias in detection estimates due to false positives, we did not consider these separately for explicitly conducting false-positive analysis. We created detection/nondetection matrices with data from 289 sites for leopards, 279 for wolves and 286 for hyenas. Leopard presence was recorded in 150 sites (naive occupancy = 0.51), wolf in 161 sites (naive occupancy = 0.57), and hyena in 179 sites (naive occupancy = 0.62). We compared 20 covariate models for leopards, 26 for wolves, and 18 for hyenas to predict occupancy probability. For all three species, no single model fully supported the data better than other competing models; three models for leopards (cumulative AIC wt. = 0.76), three for wolves (cumulative AIC wt. = 0.78), and four for hyenas (cumulative AIC wt. = 0.85) ranked within ΔAIC ≤ 2.0 (Tables 2–4), indicating that these were similar in their performance. We intended to assess top model performance by including "sampling unit area" as a predictor. But these models either did not converge or the predictor was highly correlated with other covariates and was therefore excluded. Model averaged p for leopards was 0.87 (SE = 0.01) and the model-averaged ψ across all was 0.57 (SE = 0.007) (see Figure 3). For wolves, average p was

TABLE 1 List of covariates used to model occupancy probability ψ and detection probability p for the three carnivores

		Prediction[a]		
Category	**Description**	**Leopard**	**Wolf**	**Hyena**
Occupancy covariates [range of values]				
Natural dry land in km[b]	Current fallow area (agricultural areas which have not been sown for at least a year) [0–1,536.53]	NA	+	−
	Wasteland (predominantly dry areas with little vegetation) [0–249.34]	NA	+	−
	Degraded scrub (areas with scrub vegetation which have undergone soil erosion) [0–53.08]	NA	+	+
Threatened habitat in km[b]	Dry grassland (dry or wet areas predominated by grassy vegetation) [0–157.52]	NA	+	+/−
Forested land in km[b]	Evergreen (forest areas with dense canopy cover year-round) [0–86.99]	+	NA	NA
	Deciduous (forest areas primarily with trees which shed leaves in summer) [0–132.34]	+	−	+
	Plantation (areas with agricultural and nonagricultural tree crops) [0–21.13]	+	−	+
Permanent crop in km[b]	Double/triple crop (lands which have one or more crops sown throughout the year) [0–1,089.38]	+	NA	+
Seasonal agriculture in km[b]	Rabi (crops grown in colder climate between November–March) [0–292.62] Zaid (crops grown in summer between March–June) [0–61.31] Kharif (crops grown in monsoon between June–October) [0–452.58]	NA	+	+/−
Built-up area in km[b]	Cover consisting of buildings, major roads [highways], industries, etc. all used for non-agricultural purposes [0–171.02]	−	−	−
Area of sampling unit in km[b]	Geographical extent of the sampling unit [11.40–3,224.72]	+	+	+
Large wild prey	Chinkara [0–1]	NA	+	NA
	Blackbuck [0–1]	NA	+	NA
Small domestic prey	Poultry fowl [0–294,842]	NA	NA	+
Medium domestic prey	Sheep and goats [10–140,065]	+	+	+
	Dogs [3–53,291]	+	NA	+
	Pigs [0–5,517]	+	NA	NA
Large domestic prey	Cattle [15–206,216]	+	NA	NA
Detection covariates [range of values]				
Years of experience on field (above or below 10 years) [0 or 1]		+	+	+
Identification of other species [0 or 1]		NA	+	+
No. of respondents (effort) [1–18]		+	+	+

[a]*A priori* predictions for each species: "−," negative influence; "+," positive influence; "NA," not applicable, not used to model occupancy for the corresponding species.
[b]Covariates combined into single category for one or more species.

0.75 (SE = 0.01) and model-averaged ψ was 0.64 (SE = 0.01) (see Figure 4). Average p for hyena was estimated at 0.78 (SE = 0.01) and model-averaged ψ across all models was 0.75 (SE = 0.009) (see Figure 5).

Detection probability for leopards was best explained by respondents' experience in the field (10 years and above) (top model estimate $\beta_{exp.10} = 0.51$ [SE = 0.14]). For wolves, p was positively influenced by respondents' field experience and also the number of respondents in each site (top model estimate $\beta_{exp.10} = 1.07$ [SE = 0.13]; $\beta_{no.resp} = 0.28$ [SE = 0.06]). In case of hyenas, p was most explained by the respondents' ability to identify wolves, but correlated poorly with field experience and number of respondents per sampling unit (top model estimate $\beta_{wolf.id} = 0.47$ [SE = 0.21]; $\beta_{exp.10} = 0.24$ [SE = 0.13]; $\beta_{no.resp} = 0.11$ [SE = 0.05]) (Tables 2–4).

Leopard presence was positively influenced by the extent of permanently cropped areas (associated with high degree of irrigation) and densities of cattle, whereas it was negatively influenced by densities and abundance of medium-sized livestock (sheep and goats together; usually present in larger numbers in the drier areas), built-up areas and forested regions; of which the latter two were supported poorly. Wolf presence was strongly favored by abundance as well as densities of medium-sized livestock (sheep and goats), abundance of the chinkara antelope and by area under seasonal agricultural cover (both irrigated and nonirrigated) but negatively favored by dry forests and built-up areas. Hyena presence was strongly favored by sheep and goat densities, abundance of dogs, and broiler fowl (weaker support), while dry plains with sparse vegetation cover and built-up areas had a negative effect (weak statistical support). See Table 5 and Tables S1–S3 in Appendix S1) for β-coefficient values for each covariate and model comparisons, respectively.

4 | DISCUSSION

Nonforest lands outside the purview of state-managed reserves are generally undervalued in supporting large carnivore populations in India. Although most species' geographic ranges overlap with human-dominated landscapes, ecological assessments are disproportionately focused on PAs (Ghosal et al., 2013). We interviewed only trained informants, attempted to eliminate false positives through a fixed protocol (see Methods), and encountered a low proportion of respondents who required a second attempt at identification. Although false positive records likely result in overestimation of state and sampling parameters, we have reason to believe that for our focal species, such biases would be minor (see Pillay, Miller, Hines, Joshi, & Madhusudan, 2013). Using hierarchical occupancy models, we establish that a primarily semiarid landscape spanning over *c.* 89,000 km^2, of which only 2.6% is under wildlife reserves, harbors leopards across 57%, wolves across 64% and hyenas across 75% of its area (see Figures 3–5). Among the 295 sites sampled, 210 (c. 44,000 km^2), 154 (c. 72,000 km^2), and 157 (c. 59,000 km^2) sites had occupancy probabilities higher than the corresponding mean estimates of the same for leopards, wolves, and hyenas, respectively. We interpret areas with high occupancy probability as areas that may support sustainable populations (see Royle & Nichols, 2003). An area of 22, 896 km^2 (25% of the study site) was found to have high probability of occurrence (above estimated mean value of ψ) for all three carnivores species together, which also supported human densities ranging from 59.32 to 1,169.26 people/km^2 (see Figure 6).

4.1 | Agricultural lands as carnivore habitats

Land conversions to agricultural use, accompanied by urbanization, have led to widespread modifications of arid and semiarid lands (Bestelmeyer et al., 2015; Ramankutty, Evan, Monfreda, & Foley, 2008). However, carnivores such as black bears *Ursus americanus*, cheetahs *Acinonyx jubatus*, wolves *C. lupus pallipes*, and jaguars *Panthera onca* have shown resilience and adapted to agricultural landscapes (Behdarvand et al., 2014; Blanco & Cortés, 2007; Boron et al., 2016; Ditmer et al., 2015; Winterbach, Winterbach, Boast, Klein, & Somers, 2015). From what was a primarily arid to semiarid landscape in our case, the crop cover currently stands at 25.2% of seasonal type and 20.9% of permanent type (http://bhuvan.nrsc.gov.in; accessed February 13, 2016). While areas with irrigation-fed year-round crop cover favored leopard presence, wolf presence was supported by areas with seasonal agriculture (irrigated and nonirrigated). Since irrigated land cover has increased from 20,436 km^2 in 2001 to 42,675 km^2 in 2011 in the study area (District Census Handbook; http://censusindia.gov.in/2011census/dchb/DCHB.html; accessed July 17, 2017), this represents a shift from typically wolf-favoring habitats to potentially leopard-favoring habitats. Leopard densities of

TABLE 2 (i) Top additive models run to predict detection probability *p* for leopards while keeping a constant structure for occupancy probability ψ and (ii) top additive model results for predicting leopard occupancy probability ψ against the null model

Models	AIC	ΔAIC	AIC weight	Model likelihood	K (# parameters)	−2logLikelihood
p						
ψ (perm.crop, dog, for), *p* (exp.10)	1,578.38	0	0.5137	1	6	1,566.38
ψ (perm.crop, dog, for), *p* (exp.10,resp)	1,578.5	0.12	0.4837	0.9418	7	1,564.5
ψ (perm.crop, dog, for), *p* (.)	1,589.65	11.27	0.0018	0.0036	5	1,579.65
ψ						
ψ (perm.crop, shpgt), *p* (exp.10)	1,554.28	0	0.2867	1	5	1,544.28
ψ (built, perm.crop, shpgt), *p* (exp.10)	1,554.45	0.17	0.2633	0.9185	6	1,542.45
ψ (built, perm.crop, for, shpgt), *p* (exp.10)	1,554.89	0.61	0.2113	0.7371	7	1,540.89
ψ (.), *p* (exp.10)	1,576.4	22.12	0	0	4	1,568.4

Abbreviations: built, built-up area in km^2; dog, dog abundance; exp.10, experience above 10 years; for, forested area in km^2; perm.crop, permanent crop cover in km^2; resp, no. of respondents per site; shpgt, sheep and goat abundance.

TABLE 3 (i) Top additive models run to predict detection probability *p* for wolves while keeping a constant structure for occupancy probability ψ and (ii) top additive model results for predicting wolf occupancy probability ψ against the null model

Models	AIC	ΔAIC	AIC weight	Model likelihood	K (# parameters)	-2logLikelihood
p						
ψ (grs, dry, chink), *p* (exp.10, resp)	1,505.52	0	0.715	1	7	1,491.52
ψ (grs, dry, chink), *p* (exp.10, resp, hyena.id)	1,507.36	1.84	0.2849	0.3985	8	1,491.36
ψ (grs, dry, chink), *p* (.)	1,606.11	100.59	0	0	5	1,596.11
ψ						
ψ (shpgt, chink, dry.for), *p* (exp.10, resp)	1,469.64	0	0.327	1	7	1,455.64
ψ (built, shpgt, chink, dry.for), *p* (exp.10, resp)	1,470.07	0.43	0.2638	0.8065	8	1,454.07
ψ (shpgt, chink), *p* (exp.10, resp)	1,470.68	1.04	0.1944	0.5945	6	1,458.68
ψ (.), *p* (exp.10, resp)	1,573.83	104.19	0	0	4	1,565.83

Abbreviations: built, built-up area in km^2; chink, measure of chinkara abundance; dry, natural drylands in km^2; dry.for, dry forest cover in km^2; exp.10, experience above 10 years; grs, dry grassland cover in km^2; hyena.id/wolf.id, ability to identify hyena or wolf respectively; resp, no. of respondentsper site; shpgt, sheep and goat abundance.

TABLE 4 (i) Additive models run to predict detection probability *p* for hyenas while keeping a constant structure for occupancy probability ψ and (ii) top additive model results for predicting hyena occupancy probability ψ against the null model

Models	AIC	ΔAIC	AIC weight	Model likelihood	K (# parameters)	-2logLikelihood
p						
ψ (scrub, perm.crop), *p* (wolf.id, resp, exp.10)	1,687.54	0	0.5148	1	7	1,673.54
ψ (scrub, perm.crop), *p* (wolf.id, resp)	1,689.09	1.55	0.2372	0.4607	6	1,677.09
ψ (scrub, perm.crop), *p* (.)	1,701.8	14.26	0.0004	0.0008	4	1,693.8
ψ						
ψ (shpgtdens, dry.plain), *p* (wolf.id, resp, exp.10)	1,663.51	0	0.3269	1	7	1,649.51
ψ (built, shpgtdens, dry.plain), *p* (wolf.id, resp, exp.10)	1,664.19	0.68	0.2327	0.7118	8	1,648.19
ψ (built, broildens, shpgtdens, dry.plain), *p* (wolf.id, resp, exp.10)	1,664.74	1.23	0.1767	0.5406	9	1,646.74
ψ (shpgtdens), *p* (wolf.id, resp, exp.10)	1,665.13	1.62	0.1454	0.4449	6	1,653.13
ψ (.), *p* (wolf.id, resp, exp.10)	1,686.97	23.46	0	0	5	1,676.97

Abbreviations: broildens, broiler fowl densities; built, built-up area in km^2; dry.plain, open dry areas with little vegetation; exp.10, experience above 10 years; hyena.id/wolf.id, ability to identify hyena or wolf respectively; perm.crop, permanent crop cover in km^2; resp, no. ofrespondentsper site; scrub, scrub area in km^2; shpgoatdens, sheep and goat densities.

4.8 (SE = 1.2) have been documented in agricultural areas in this landscape (Athreya et al., 2013), and their presence has been documented in other production landscapes with prey elsewhere in the country (Athreya et al., 2015; Kshettry et al., 2017). Although dry grasslands have been representative habitats for wolves in India (Jethva & Jhala, 2004), seasonal agriculture better favored their presence compared to fragmented dry grasslands in the landscape. Wolf presence in such areas (with no crop cover for certain parts of the year) may stem from their preference for open areas for hunting prey and the associated presence of medium-sized domestic livestock (as prey),which commonly graze in these lands. The presence of hyenas was not significantly associated with any particular land use, but they appeared to avoid large tracts of seasonally fallow arid lands with sparse vegetation.

4.2 | Urban area expansion and degrading wastelands

The expansion of urbanscapes to accommodate rural–urban migration is often at the cost of modifications of grasslands and scrublands (Vanak et al., 2017). Indian policy has often classified savanna ecosystems under human-use as "wastelands" or degraded lands (Ratnam et al., 2016). Hence, such areas are likely to undergo intense alteration because of their

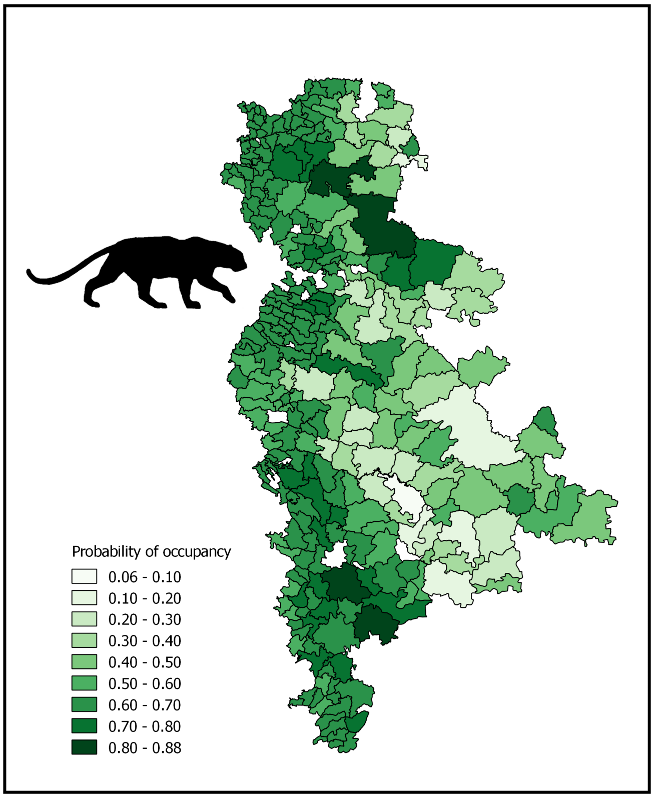

FIGURE 3 Map depicting spatial distribution of occupancy probabilities of leopards in the study area

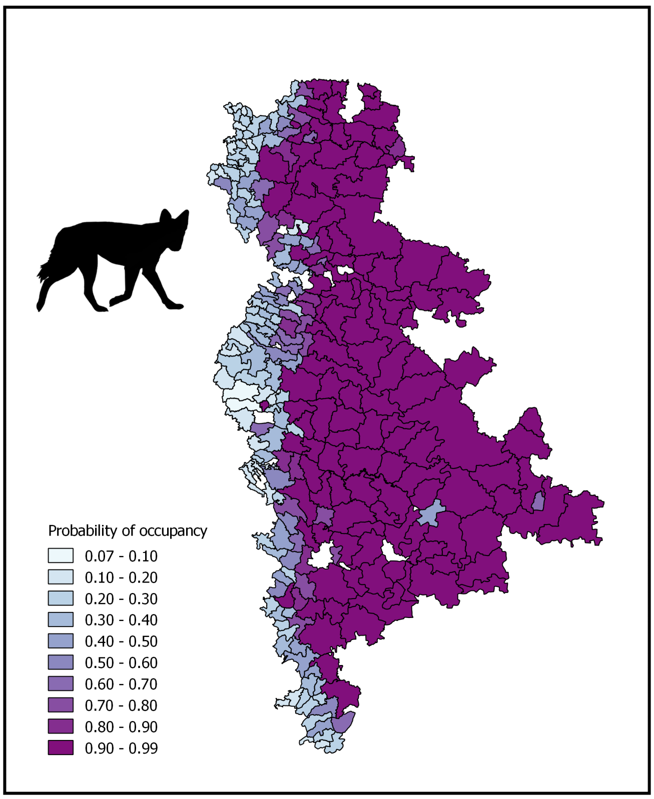

FIGURE 4 Map depicting spatial distribution of occupancy probabilities of wolves in the study area

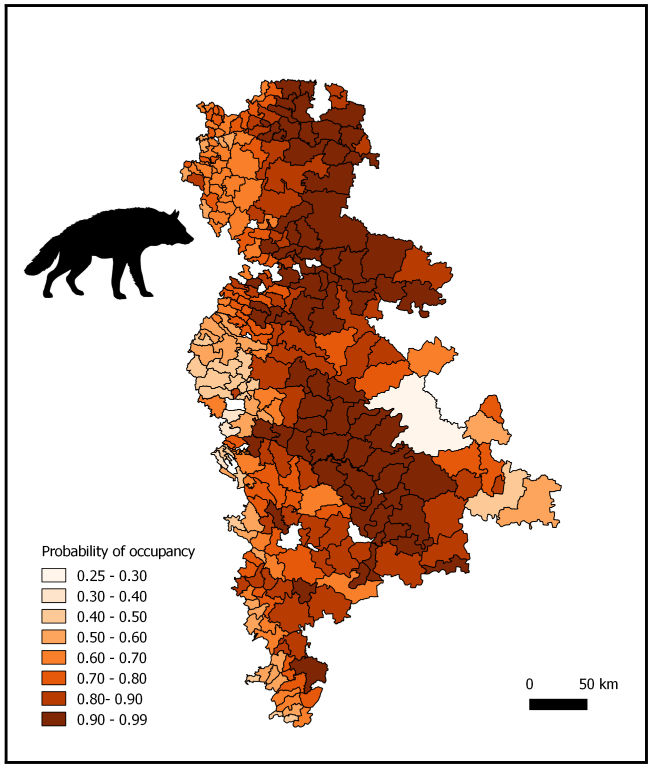

FIGURE 5 Map depicting spatial distribution of occupancy probabilities of hyenas in the study area

conversion to irrigated farmlands, industrial areas with associated infrastructure (e.g., solar farms) and commercial monoculture plantations, all of which is accelerated with government policies and subsidies. Such expansion of urban environments is expected to gain momentum in our study landscape. While urban landscapes may sometimes favor carnivore presence, as with the coyote *Canis latrans* and puma *Puma concolor* in North America (Gehrt et al., 2010) and the spotted hyena *Crocuta crocuta* and African wolf *Canis anthus* in Ethiopia (Yirga et al., 2017), these may also be avoided due to factors like hunting pressure (Abade et al., 2018). All three large carnivores in our study demonstrated statistical avoidance of urbanscapes, this effect being weaker for leopards compared to wolves and hyenas. Leopards in India and some areas of Africa are known to inhabit peri-urban and suburban areas (Athreya et al., 2013; Van Cleave et al., 2018), subsidized by anthropogenic factors, which has enabled them to thrive in considerable densities in close proximity to humans. However, built-up lands are associated with hotspots of human activities and hence, some species such as wolves and hyenas may avoid them. However, even though a statistical avoidance of highly urbanized areas was observed, these species are known to exhibit flexibility in activity patterns, which has enabled them to thrive in other parts of the landscape that have low levels of human activity (Boydston, Kapheim, Watts, Szykman, & Holekamp, 2003; Theuerkauf, 2009).

4.3 | Domestic livestock sustain carnivores outside reserves

Landscapes with no wild prey presence (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2016), or those with very low prey densities or diversity (Khorozyan, Ghoddousi, Soofi, & Waltert, 2015; Pimenta, Barroso, Boitani, & Beja, 2017), have frequently sustained carnivore populations because domestic livestock (as prey or as carrion) serves as a primary source for the wild carnivores in such regions. Livestock losses have sometimes been accepted (Inskip, Carter, Riley, Roberts, & MacMillan, 2016), or have resulted in retaliation especially if accompanied by attacks on humans (Carter & Linnell, 2016). At least one species of domestic prey was associated with the presence of each of the three carnivores in our study area. Cattle densities supported leopard occurrence, a pattern that is consistent with previous observations in this landscape (Athreya et al., 2016). Sheep and goat densities favored wolf and hyena occurrence and just like the leopard's case, wolf diet studies in the landscape have also shown high dependence on livestock (Habib, 2007). Interestingly, hyena presence was associated with abundance of a greater variety of domestic prey, including domestic dogs and poultry fowl. It is possible that hyenas in human-dominated landscape are dependent on poultry and other waste (Yirga et al., 2017), which also attracts dogs, thereby explaining the association between dogs and hyena presence.

4.4 | Carnivore conservation in shared landscapes

In landscapes shared by humans and large carnivores, there is an increased interface that could endanger the welfare of both people and wildlife. In terms of a direct threat to human life, western Maharashtra had 91 officially documented instances of human attacks from 2014 to 2016 (roughly coinciding with our study duration) most of which (93%) were by leopards. Such incidents remain a major challenge in the shared spaces of India, particularly for wide-ranging carnivores that cannot be confined to PAs. Acceptance of losses to carnivores and subsequent large carnivore persistence in the vicinity of humans has strong roots in the socio-political and cultural factors (Dickman, 2010). One such factor is the absence of lethal control of carnivore populations in India, which has perhaps supported shared landscapes. Unfortunately, the cultural and socio-political attributes of people-predator interactions have been examined cursorily at broad spatial scales (Karanth et al., 2009), or, completely discounted because they cannot be quantified in the same way as ecological assessments. It is increasingly evident that the social and cultural factors probably play a much more important role in influencing large carnivore persistence (Aiyadurai, 2016; Athreya et al., 2018; Redpath et al., 2017).

In shared landscapes, the presence of potentially “problematic” carnivores that receive active State protection could create alienation of people (Naughton-Treves & Treves, 2005) and fuel human-human conflict (Redpath et al., 2012). However, in a country such as India, where rural communities have shared space with wildlife for a very long time, we know very little of the socio-cultural mechanisms and behaviors (of both humans and wildlife) that support the sharing of spaces. The human-dominated landscape we consider in this study has hosted human civilizations since at least 200 B.C. (Sontheimer, 1989), while leopards, wolves, and hyenas have inhabited the Indian subcontinent for between 0.4 and 0.1 million years (Rohland et al., 2005; Sharma, Maldonado, Jhala, & Fleischer, 2004; Uphyrkina et al., 2001), and it is clear these landscapes have long supported both together. But several questions about these

TABLE 5 The β estimates with associated standard error values for all covariates from the top models in which they occur (from the candidate set of models run) for each species

	Leopard	Wolf	Hyena
Scrub	--	--	0.13 (0.33)
perm.crop	0.70 (0.21)	--	0.13 (0.31)
dry.plain	--	--	−0.35 (0.20)
broildens	--	--	0.27 (0.25)
broil	--	--	0.88 (0.52)
grass	--	0.45 (0.53)	0.06 (0.27)
dry	--	0.64 (1.27)	--
seas.cover	--	2.67 (0.89)	--
bb	--	0.17 (0.61)	--
dry.for	--	−0.43 (0.27)	0.14 (0.20)
chink	--	1.02 (0.80)	--
pigdens	0.14 (0.14)	--	--
dogdens	−0.04 (0.14)	--	0.23 (0.44)
shpgtdens	−0.54 (0.17)	1.64 (0.57)	1.97 (0.52)
catdens	0.69 (0.17)	--	--
dog	0.09 (0.19)	--	0.84 (0.47)
built	−0.19 (0.15)	−0.31 (0.29)	−0.19 (0.16)
for	−0.17 (0.14)	--	--
shpgt	−0.91 (0.20)	8.60 (1.88)	−0.17 (0.44)

Abbreviations: bb, measure of blackbuck abundance; broil, broiler fowl abundance; broil/cat/dog/pig/shpgtdens, broiler fowl, cattle, dog, domestic pig and sheep and goat densities; built, built-up area in km^2; chink, measure of chinkara abundance; dog, dog abundance; dry, natural drylands in km^2; dry.for, dry forest cover in km^2; dry.plain, open dry areas with little vegetation; for, forested area in km^2; grass, grassland area in km^2; perm.crop, permanently cropped cover in km^2; seas.cover, seasonally cropped area in km^2; shpgt, sheep and goat abundance; scrub, scrub area in km^2.

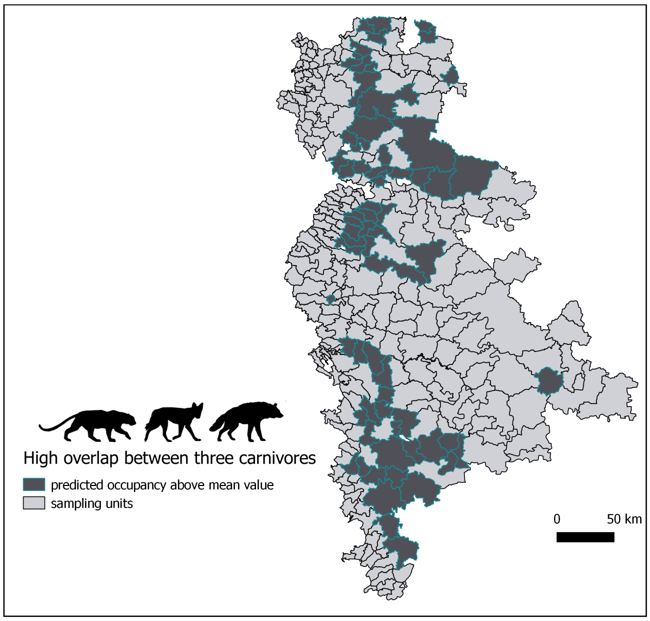

FIGURE 6 Map depicting those overlapping regions in the study area where leopard, wolf, and hyena occupancy estimates were above the averaged values for each

interactions remain unexplored, for example, (a) what kind of agricultural practices are wildlife-friendly, (b) how socio-political changes like agricultural intensification or land abandonment due to human migration affect carnivores, or (c) how will changes in husbandry methods from open grazing to stall-fed practices affect carnivore diet, (d) how will livestock depredation patterns change over time and whether this will affect acceptance of carnivores by people. It is important that policy paradigms, which are currently PA-centric and rely on reactive measures, adapt to incorporating such knowledge so that conflicts between managers and local people can be avoided or reduced and enable conservation on shared lands.

Our results highlight the presence of large carnivores in changing landscapes (Lindenmayer et al., 2008) and that there are species-level consequences to land conversions that are neither fully understood nor integrated into the current paradigm of wildlife management. We call for a shift away from the three dominant narratives in Indian conservation policy–(a) associating sparsely vegetated semiarid landscapes with an absence of biodiversity and subsequent removal of the colonial tag of "wastelands," (b) the urge to expand monocultures to increase tree cover in semiarid landscapes, and (c) ideologically confining large mammals to the extant PAs. In a densely populated country like India, advocating coercive actions such as imposing absolute state control and enforcement of wildlife protection without incorporating power relations, local sentiments, and values (say in the case of criminalizing traditional hunting practices) may not be an ideal strategy in the long term for wildlife that has historically shared space with humans (Redpath et al., 2012).There is a need for (a) an overhaul of obsolete and parochial approaches to conserving large carnivores, especially ineffective management interventions that focus on removal or translocation of animals rather than engaging with local communities on effectively managing shared spaces, (b) thinking of novel frameworks relevant to India's evolving landscapes, like promoting socially responsible interventions that are transparent and focus on measuring conservation performance like wildlife population counts and reduced losses to humans (Mishra, Young, Fiechter, Rutherford, & Redpath, 2017; Ravenelle & Nyhus, 2017; Zabel & Holm-Müller, 2008) or formulating programs which encourage modification of human behavior (Schultz, 2011; Treves & Karanth, 2003) to ensure their safety in shared spaces, and (c) understanding and acknowledging the role of socio-cultural factors that allow for shared spaces to exist and decentralizing the process of conservation with more socially inclusive programs. If large carnivore populations are to be retained in human-use areas, this shift will require an expansion of the skills and tools used by wildlife managers (J. R. B. Miller et al., 2017). Future research will need to augment this with multidimensional assessments that incorporate social and political domains from disciplines like the humanities and social sciences.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

AUTHOR CONTRIBUTIONS

V.A., S.V., and S.L. conceived the idea and V.A., S.V., and S.S. designed the study. I.M. carried out the data collection. I.M., S.V., and S.S. were involved in cleaning, organizing, and collating the data. I.M., A.S., and S.V. conducted the data analysis and arrived at the interpretation. I.M., A.S., S.V., and V.A. were involved in writing the manuscript. S.L. and V.A. facilitated the study by providing required administrative permissions and resource people on field.

DATA ACCESSIBILITY

Data associated with this manuscript were uploaded on Dryad Digital Repository at doi:10.5061/dryad.qs13nt1.

ETHICS STATEMENT

The study did not involve the use of methods requiring collection of any biological material or capture/handling of wildlife. Maharashtra State Forest department provided necessary permits to carry out the interview surveys. Interviews were conducted following verbal consent of Forest department personnel.

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