



Original investigation

## Large herbivore populations outside protected areas in the human-dominated Western Ghats, India

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### ABSTRACT

Large terrestrial wild herbivores are threatened globally, but scarce information exists on their populations outside of protected areas in South and Southeast Asia. India supports 39 species of wild herbivores, nearly two-thirds of which are threatened. While the protected area network still forms the backbone of large mammal conservation, it occupies less than 5% of India. Yet, remnant habitats outside of parks have received sparse attention to conserve threatened wild herbivores. Our study examined the effects of livestock occurrence, human proximity (distance to nearest village), and habitat factors (percentage habitat available and mean slope) on populations of large wild ungulates in a tropical forest outside of protected areas in the Western Ghats of India. We used a sign-based abundance-occupancy modelling approach to assess the effects of these variables on animal group density ( $\hat{\lambda}$ ) and animal group-specific detection probability ( $r$ ) of three large wild ungulates (gaur *Bos gaurus*, sambar *Rusa unicolor*, and wild pig *Sus scrofa*). Our results reveal that in human-dominated tropical forests, gaur group density increases with larger available habitat and lower occurrence of livestock, while sambar group density increases with higher mean slope and lower occurrence of livestock. Contrary to expectation, sambar group density was higher in smaller available habitat. No variable could reliably explain wild pig group density, but the species is a known generalist. Our results have important implications for conservation of threatened large herbivores and management of remnant tropical forest habitats outside protected areas, especially Reserved Forests in the Indian context. Remnant habitats can support significant populations of large herbivores and need to be protected in developing South and Southeast Asian countries. Gradual improvement in livestock management practices will benefit large herbivore populations in priority regions outside of protected parks in India.

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### Introduction

Terrestrial large wild herbivores play critical roles in forests and ecosystems globally (Ripple et al., 2015). However, large herbivores in the tropics face manifold threats and extinction risks are high for the majority of species in rapidly-developing South and Southeast Asian countries (Ahrestani and Sankaran, 2016; Ripple et al., 2015). India, a mega-diverse country in South Asia, supports 39 species of wild herbivores, two-thirds of which are threatened with extinction (Ahrestani and Sankaran, 2016). Loss of habitat has significantly reduced the distribution range of many large herbivores across the country (Karanth et al., 2010), while hunting is still widespread (Gubbi and Linkie, 2012; Madhusudan and Karanth,

2002; Velho et al., 2012). Moreover, the country's high human population growth (Cohen, 2003) and largely agrarian economy have resulted in a sizeable population of livestock (c. 500 million, Ministry of Agriculture, Govt. of India, 2012), which create severe resource limitation for many native wild herbivores (Madhusudan, 2004; Mishra et al., 2004; Suryawanshi et al., 2010).

Of the 21% of land area in India under forest cover, less than 5% is under the protected area network (ENVIS Centre on Wildlife and Protected Areas, 2016). Almost 60% of these protected areas had resident human populations and were grazed by livestock in the past (Kothari et al., 1989; Singh, 1999), although this has marginally reduced in recent years due to better management of Tiger Reserves in India. Well-protected parks are critical to harbour high densities of large wild herbivores and carnivores (Karanth et al., 2004). Yet, substantial amount of functionally-important forest habitats remain outside of protected reserves in India.

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These habitats include government-controlled Reserved Forests which connect parks (Bennett, 2003; Sharma et al., 2013) and enhance resources for wide-ranging mammalian species (Karanth, 2016; Woodroffe and Ginsberg, 1998). However, these forest commons are also subject to variable intensities of resource use by resident communities of people and their livestock (DeFries et al., 2010). Remnant habitats are increasingly recognized to be important for wide-ranging wildlife (Punjabi et al., 2017; Qureshi et al., 2014; Seidensticker, 2016; Silori and Mishra, 2001), but have received limited conservation focus. This is especially of concern in the context of declining large herbivore populations in 'multiple-use' landscapes, which suffer from intense pressures of local hunting and livestock grazing as they are not explicitly managed for wildlife conservation (Harihar et al., 2014; Pillay et al., 2011).

Land managers require robust assessments of where and how wild herbivore populations can persist in such multiple-use, human-dominated landscapes of South and Southeast Asia (Ripple et al., 2015). Indeed, management efforts to stem the decline in large herbivore populations are constrained by insufficient scientific knowledge for most species in remnant habitats (Sankaran and Ahrestani, 2016). Still, practical limitations (poor sightability, undulating terrain) limit the application of conventional methods such as distance sampling (Buckland et al., 2001) to reliably assess populations of cryptic and low-density herbivores from such habitats, which are important benchmarks for species conservation and management. Also, biotic impacts on wild herbivore populations are difficult to study experimentally across large scales due to multiple constraints (Madhusudan, 2004; Ritchie et al., 2009). From this perspective, newer developments in robust scientific approaches which permit assessments of low-density or cryptic herbivores from sub-optimal habitats are especially valuable (Gopaldaswamy et al., 2012; Rovero and Marshall, 2009; Vongkhamheng et al., 2013).

We conducted a study in the Western Ghats of India to understand how anthropogenic and ecological factors affect populations of large wild ungulates in human-dominated tropical forest landscapes. We used a sign-based occupancy-abundance sampling approach (Gopaldaswamy et al., 2012; Royle and Nichols, 2003) to specifically examine the effects of livestock occurrence, human proximity (distance to the nearest village), and habitat factors (percentage habitat availability and slope) on populations of three large wild ungulates (gaur *Bos gaurus*, sambar *Rusa unicolor*, and wild pig *Sus scrofa*) in a region outside any protected area. Based on known biology and available information, anthropogenic and ecological factors were expected to explain population-level responses of gaur and sambar more reliably as compared to wild pig which is known to be a generalist species and resilient to anthropogenic impacts (Steinmetz et al., 2010).

## Material and methods

### Study area

Our study site spanned an area of c. 325 km<sup>2</sup> around the Tillari river valleys, part of the northern Western Ghats landscape in India. The intensive study area in the state of Maharashtra comprised of Reserved Forests and private forest land, bordering the states of Karnataka and Goa. Majority of forest habitats in our study region are safeguarded as Reserved Forests to prevent illegal tree-felling, but there are minor restrictions on access for resident people and their livestock. The region comprises of Tropical moist deciduous and semi-evergreen forests (Champion and Seth, 1968), and the terrain is undulating with steep escarpments along the main crest of the Western Ghats, with elevation ranging from 50 m to 1030 m

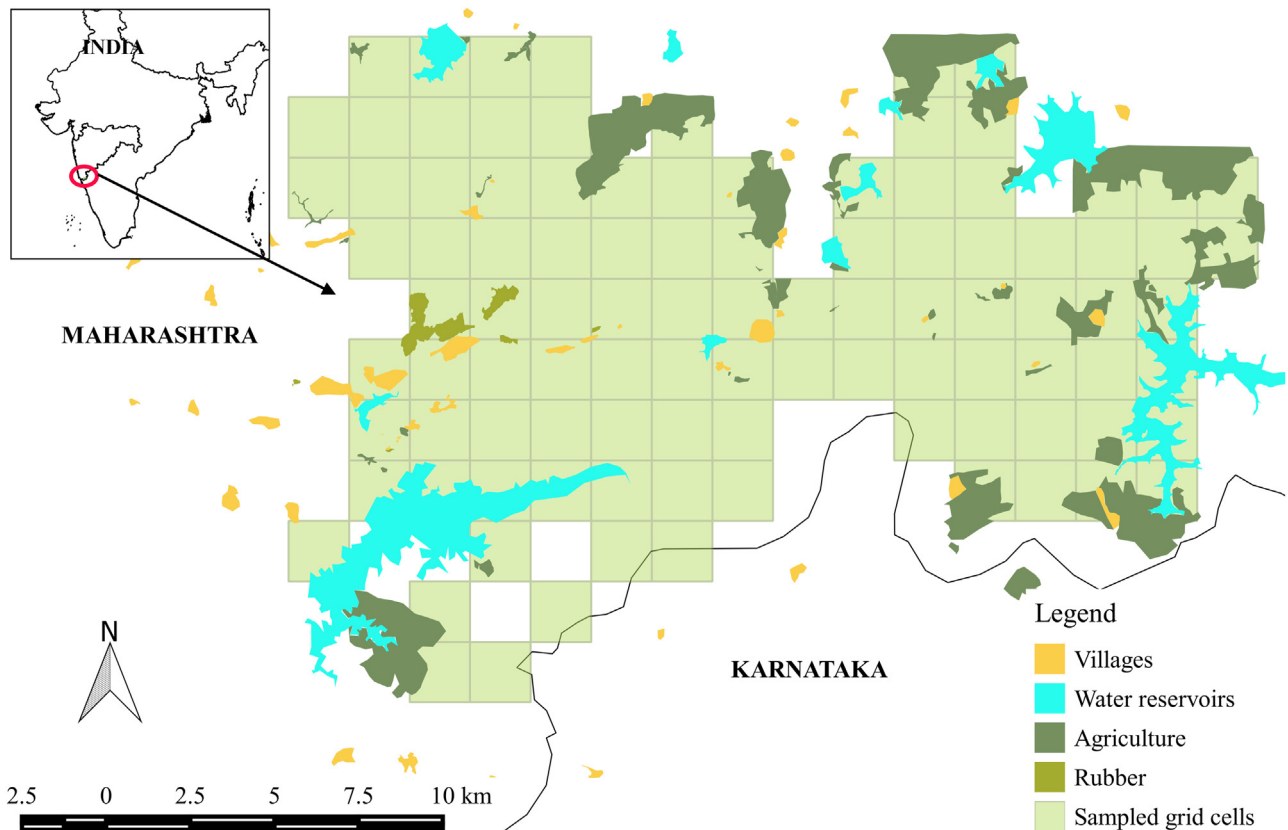
a.s.l. Average rainfall from June to September is c. 3000 mm in the region, and temperatures vary from 16° to 35 °C from the winter to summer months. The region is an important pinch-point in a large mammal corridor between Kali Tiger Reserve in the state of Karnataka and the Radhanagari Wildlife Sanctuary in Maharashtra, the latter being one of the 39 serial sites inscribed in the UNESCO World Heritage list.

Preliminary camera-trapping in the region revealed the presence of the tiger *Panthera tigris*, dhole *Cuon alpinus*, sloth bear *Melursus ursinus*, leopard *Panthera pardus*, and seven species of wild ungulates, which include gaur, sambar, wild pig, Indian muntjac *Muntiacus muntjac*, four-horned antelope *Tetracerus quadricornis*, Indian chevrotain *Moschiola indica* and chital *Axis axis*. Gaur, sambar, and four-horned antelope are categorized as Vulnerable as per the IUCN Red List (Duckworth et al., 2016; Mallon, 2008; Timmins et al., 2015), while the other ungulate species are Least Concern. Four-horned antelope and chital were rarely photographed using camera-traps, indicating that they are particularly uncommon in the region.

Close to 40 villages occur in the study region, with village sizes ranging from 10 to 400 households. A few settlements belong to Gavli dhangars, a traditional resident pastoral community, who rear large number of goat, buffalo, and cattle and rely on communal and Reserved Forest land for grazing (Gadgil and Malhotra, 1982). Six villages were relocated about a decade ago from a part of our study area due to a large irrigation project, creating an inviolate region along one valley of the Tillari River. This gave us an interesting opportunity to assess wild ungulate population in a region devoid of human settlements and livestock, and compare it with other parts of our study region which have human settlements and livestock. Our study region overlapped two administrative districts and human population density varied from 160 people per km<sup>2</sup> to 327 people per km<sup>2</sup>, while livestock density (cattle, buffalo, and goat together) ranged from 47 to 150 livestock per km<sup>2</sup> (Commissionerate of Animal Husbandry, 2012). High densities of livestock, found in much of our study region, graze within forests during day-time and are corralled in villages during night-time. Households in the study region mostly engage in agriculture and cash-crop plantations (sugarcane *Saccharum* sp., cashew *Anacardium occidentale*), and are dependent on forests for livestock grazing, firewood, minor forest produce, and medicinal plants. A few large estates in the study region grow cash crops such as rubber (*Hevea* sp.) and pine-apple (*Ananas comosus*).

### Group density

Since many tropical forest-dwelling herbivores are cryptic, and often exist in low densities outside protected areas, they are notoriously difficult to count using conventional methods such as distance sampling (Buckland et al., 2001). We used an approach developed to assess the relative abundance of herbivores using sign-based occupancy surveys that relies on heterogeneity in detection probability of herbivore signs (Gopaldaswamy et al., 2012; Royle and Nichols, 2003). The key assumption of the method is that heterogeneity in detection probability of signs ( $r$ ) exists as a result of variation in animal abundance (Royle and Nichols, 2003). This modelling approach, termed AOS (abundance–occupancy–spatial), uses detection of herbivore signs on spatial replicates to estimate group density ( $\hat{\lambda}$ , Gopaldaswamy et al., 2012) and not the density of individual animals per unit area, as is the standard. The method is useful to assess the effect of environmental variables on animal populations under certain sampling conditions as it accounts for imperfect detection, and is therefore superior to relative abundance indices (RAIs) which are rarely calibrated in practise (Hayward et al., 2015; Sollmann et al., 2013).



**Fig. 1.** Human-dominated study region in Tillari, Western Ghats, India, overlaid with grid cells (3.24 km<sup>2</sup> each) surveyed for large wild ungulates from January to May 2016. Human modified land-cover types within the surveyed grid cells are shown, the complement of which is available habitat.

We surveyed 100 sampling units (square grid cells, each measuring 3.24 km<sup>2</sup>) for animal signs in the study region (Fig. 1). Each grid cell had nine equally-spaced points, at a distance of 600-m from each other to guide our surveys. Each spatial replicate was a strip of 300 m X 50 m, which we walked and noted animal signs at each consecutive 100 m X 50 m interval (Fig. A.1, Supplementary material). The spatial replicates were strips, as we deviated on either side of the survey route to search for ungulate signs if required. Effort within sampled grid cells varied from a minimum of two spatial replicates to a maximum of 16 spatial replicates, depending on terrain conditions and accessibility. The survey team, comprising of two or three people, noted fresh signs of wild herbivores and domestic livestock, such as ungulate tracks, droppings, and signs of rooting (wild pigs). To avoid false positives, care was taken to ensure that only signs that we could confidently identify from measurements and appearance to the species-level were recorded. Signs were photographed using an appropriate scale and compared with scaled photographs of wild ungulate droppings collected in 2012 from an enclosure in Sanjay Gandhi National Park, Mumbai, India. The first author, a trained researcher, was part of all surveys, ensuring consistency in field identification of animal signs. Signs were identified to be fresh based on appearance, touch, and odour. Each grid cell was surveyed within one-day to control for potential biases due to animal movements. All grid cells were surveyed in the post-monsoon season from 12th January to 7th May 2016 to limit seasonal variations in animal movements or home-range sizes.

The grid cell size of 3.24 km<sup>2</sup> was assumed to be large enough to encompass the expected daily movement of all three large ungulates based on previous field studies (see Gopalaswamy et al., 2012 and references therein). Gopalaswamy et al. (2012) demonstrate that the AOS model using this grid cell size was suitable to assess animal group density for all large ungulate species in

Bhadra Tiger reserve of the Western Ghats. As our study site is ecologically-similar to Bhadra, we assumed that daily movement of large ungulate groups would also be comparable in our study site. Simulations performed by Gopalaswamy et al. (2012) show that the expected daily movement of large herbivores ( $R$ ) has an important bearing on precision of model estimates, and daily movement ranges between 6 and 15% of the length of the grid cell result in favourable model performance. Sample sizes also have a bearing on model performance with larger sample sizes ( $\geq 200$  grid cells) improving precision of mean  $\hat{\lambda}$ .

Likewise, model performance would be optimum if number of animal groups per cell range from 0.5 to 4, and overall number of signs deposited are high ( $> 800$ ), especially important in realistic scenarios under imperfect detection. Cell-specific  $\hat{\lambda}$  was interpreted as group (or cluster) density as all large herbivores in our study region form social groups (Prater, 1971). This is important as the model assumes independence of animals, which does not hold true in the case of animals which show social grouping.

#### *Explanatory variables and group density analysis*

We examined the effect of livestock occurrence, distance to the nearest village, percentage habitat availability and mean slope on  $\lambda$  (animal group density) and  $r$  (animal group-specific detection probability) using the AOS modelling approach.

Livestock occurrence was calculated as an encounter rate per km of livestock signs, which were noted along each 100 m X 50 m interval of a spatial replicate in each grid cell. Detections of signs of all livestock species, which include cattle, buffalo and domestic goat, were combined to make a single covariate to reduce the number of parameters in the interest of parsimony (Burnham and Anderson, 2004). For proximity to nearest village, we created a digitized layer

of villages using high-resolution Google Earth imagery (from 2015–16) of the study region. We ensured accuracy and consistency in the digitization process by viewing the imagery at 3.5 km altitude, which Google Earth provides the viewer. Polygons were created by hand-drawing along the outer boundaries of villages and labelled. The minimum distance (in km) between the centre of each grid cell and boundary of nearest village polygon was calculated using the 'v.distance' tool in GRASS (Version 6.4.3, GRASS Development Team 2014).

Habitat available for large ungulates was considered complementary to the area of human land-use conversion in our study region. To calculate percentage habitat available for large ungulates, we used a similar digitization process as described earlier to create polygons around areas of human land-use conversion, which included man-made water-reservoirs, agricultural fields, fenced plantations (rubber), and villages within each grid cell. The total area of human land-use conversion in each grid cell (in km<sup>2</sup>) was then subtracted from the area of the cell and converted to percentage in Quantum GIS (Version 2.10.1–Pisa, QGIS Development Team 2014). Lastly, to assess the effect of slope, we calculated mean slope per grid cell using ASTER Global Digital Elevation Model data (NASA LP DAAC, 2013; Terra ASTER Global DEM). We used the 'Zonal Statistics' plugin in Quantum GIS to extract mean slope values for each grid cell.

For the sake of numerical stability, all site-specific variables were standardized by calculating z-scores before using them for modelling. Correlations (Pearson's) among variables were examined before constructing candidate model sets, so as to avoid any potential effects of strong collinearity among variables (Dormann et al., 2013). Detection/non-detection data of wild ungulates on surveyed spatial replicates was converted into (1/0) detection histories for each sampling site (grid cell). This detection history was used with site-specific variables in the modelling process.

We conducted our analysis using the Royle and Nichols (2003) heterogeneity model (AOS model in our case) in PRESENCE (Version 9.3, Hines 2006), where the effect of site-specific variables can be examined on  $\log \lambda$  (animal group density) and  $\logit r$  (animal group-specific detection probability). The objective of our study was to examine the effect of environmental variables on  $\log \lambda$  (animal group density) of large ungulates. However, these variables can also affect animal group-specific detection probability by affecting animal group density, therefore it was important to assess their effects on  $\logit r$  in the AOS model. Since the number of additive models using all possible combinations of environmental variables for both  $\log \lambda$  and  $\logit r$  were too large (196 models for each species), we used a two-step approach for modelling. First, by using a fully parameterized  $\log \lambda$  structure (additive model with all four variables), we fixed the variable structure for  $\logit r$  by using all possible additive combinations of explanatory variables as well as a null (intercept-only) model, which were run in PRESENCE. Models were assumed to fit if no convergence errors were reported. For each species, we selected the top-ranked model, based on Akaike's Information Criteria (AIC) scores after an examination of all supported models. We retained the variable structure of  $\logit r$  from this top-ranked model for subsequent analysis. We chose only the top-ranked model for  $\logit r$  so as to not include any uninformative parameters in further analysis (Arnold, 2010). Next, we examined the effect of environmental variables on  $\log \lambda$ , using all possible additive combinations of variables in the models. AIC-ranked models which together had a cumulative Akaike weight of 0.9 ( $w_i$ , model probabilities) were selected as most supported to account for model uncertainty (Burnham et al., 2011).  $\hat{\beta}$ -coefficients and associated standard errors ( $SE$ ) of explanatory variables from most supported models were examined to assess their effect on  $\log \lambda$ . We did not perform model-averaging of coefficients as multicollinearity

among variables renders model-averaging of coefficients untenable (Cade, 2015). Spatially-explicit maps were created in Quantum GIS for group density of large ungulates using estimates from the top models.

## Results

Signs of gaur, sambar, and wild pig were detected in 59, 72, and 48 grid cells, respectively. A total survey effort of 203.7 km was invested to sample 100 grid cells in the study.

### Group-specific detection probability

For gaur, the model where  $\logit r$  was a function of percentage habitat available was top-ranked; whereas for sambar and wild pig the top-ranked model was one where  $\logit r$  was a function of the null (intercept-only) (Table 1). To exclude uninformative variables, we dismissed other competing models for gaur (cumulative  $w_i$  of 0.9,  $\Delta AIC < 4$ ) as all of them included percentage habitat available as a covariate. For sambar and wild pig, distance to nearest village was not used as an explanatory variable for  $\logit r$  as all the models with the variable failed to converge. For both sambar and wild pig, competing models with other predictor variables for  $\logit r$  were dismissed as the null model was top-ranked, indicating that other models did not explain enough variation in  $\logit r$ .

### Group density

Five models received most support (cumulative  $w_i$  of 0.9,  $\Delta AIC < 4$ ) in explaining group density ( $\log \lambda$ ) for gaur, two models were most-supported for sambar, while 12 models received support for wild pig (Table 2). All four explanatory variables were included in most-supported model sets for the three ungulates, which enabled us to test their effect for each species.

Livestock occurrence had a negative influence on group density of gaur and sambar (Table 3). Percentage habitat available had a positive influence on gaur, but a negative influence on sambar group density; whereas slope had a positive influence on sambar group density (Table 3). Livestock occurrence and percentage habitat available were less reliable in explaining group density for wild pig; slope was less reliable in the case of gaur and wild pig, while distance to nearest village was less reliable in explaining group density for all three species due to large errors associated with estimated beta-parameters.

Estimates of group density ( $\hat{D}_s \pm \hat{SE}$ ) per km<sup>2</sup> from the AOS model (null) for the three large ungulates are compared with those from ecologically-similar, but better-protected Bhadra Tiger Reserve (Gopaldaswamy et al., 2012) in south India (Table A.1, Supplementary material). Fig. 2 shows spatially-explicit maps of mean  $\hat{\lambda}$  ( $SE$ ) values from top-ranked models for all three large ungulates in the study region. Grid cells where survey effort was low had larger errors associated with the estimate (Fig. 2).

## Discussion

Conservation and management of threatened large herbivores in South and Southeast Asia require robust assessments of population status, threats, and factors that allow persistence in human-dominated landscapes (Hoffmann et al., 2015; Sankaran and Ahrestani, 2016). We found that in our human-dominated study region, gaur group density was higher in sampling units with larger available habitat and lower occurrence of livestock, while sambar group density was higher in sampling units with higher mean slope and lower occurrence of livestock. Contrary to expectation, sambar group density was negatively associated with higher



**Table 1**

Candidate models used to assess the effect of covariates on logit  $r$  (group specific detection probability) of large ungulates, using a fully parameterized structure for log  $\lambda$  (group density) in the Tillari region, Western Ghats, India. In the case of gaur, models with  $\Delta$  AIC < 7 have been shown.

Species	Model	AIC	$\Delta$ AIC	$w_i$	Mod.lik	K	
gaur	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat)	639.65	0	0.32	1	7	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + dist.vil)	641.08	1.43	0.16	0.49	8	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + lvs)	641.17	1.52	0.15	0.47	8	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + slope)	641.37	1.72	0.14	0.42	8	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + lvs + dist.vill)	642.33	2.68	0.08	0.26	9	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + lvs + slope)	642.4	2.75	0.08	0.25	9	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + dist.vil + lvs + slope)	644.12	4.47	0.03	0.10	10	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (.)	646.46	6.81	0.01	0.03	6	
	sambar	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (.)	706.2	0	0.25	1	6
		$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs)	706.45	0.25	0.22	0.88	7
$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat)		707.33	1.13	0.14	0.57	7	
$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs +%_habitat)		707.9	1.7	0.11	0.43	8	
$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (slope)		708.11	1.91	0.09	0.38	7	
$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs + slope)		708.33	2.13	0.08	0.34	8	
$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_hab + slope)		709.32	3.12	0.05	0.21	8	
$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs +%_hab + slope)		709.75	3.55	0.04	0.17	9	
wild pig		$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (.)	490.34	0	0.35	1	6
		$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat)	492.02	1.68	0.15	0.43	7
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (slope)	492.1	1.76	0.14	0.41	7	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs)	492.24	1.9	0.13	0.39	7	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs + slope)	493.42	3.08	0.07	0.21	8	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (%_habitat + slope)	493.87	3.53	0.06	0.17	8	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs +%_habitat)	493.96	3.62	0.06	0.16	8	
	$\lambda$ (lvs + dist.vil +%_habitat + slope), $r$ (lvs +%_habitat + slope)	495.34	5	0.03	0.08	9	

AIC, Akaike's Information Criteria;  $\Delta$  AIC, difference in AIC scores;  $w_i$ , Akaike weight; Mod.lik, Model likelihood; K, number of parameters;  $\lambda$ , group density;  $r$ , group specific detection probability; lvs, livestock encounter rate; dist.vil, distance to nearest village; %\_habitat, percentage available habitat; slope, mean slope.

**Table 2**

Candidate models used to assess the effect of covariates on log  $\lambda$  (group density) of large ungulates in the Tillari region, Western Ghats, India. Most-supported models are shown in bold for each species. For all species, models with  $\Delta$  AIC < 7 have been shown.

Species	Model	AIC	$\Delta$ AIC	$w_i$	Mod.lik	K	
gaur	$\lambda$ (lvs +%_habitat), $r$ (%_habitat)	<b>639.33</b>	<b>0</b>	<b>0.25</b>	<b>1</b>	<b>5</b>	
	$\lambda$ (lvs + dist.vill +%_habitat + slope), $r$ (%_habitat)	<b>639.65</b>	<b>0.32</b>	<b>0.21</b>	<b>0.85</b>	<b>7</b>	
	$\lambda$ (lvs + dist.vill +%_habitat), $r$ (%_habitat)	<b>639.68</b>	<b>0.35</b>	<b>0.21</b>	<b>0.84</b>	<b>6</b>	
	$\lambda$ (lvs +%_habitat + slope), $r$ (%_habitat)	<b>639.87</b>	<b>0.54</b>	<b>0.19</b>	<b>0.76</b>	<b>6</b>	
	$\lambda$ (dist.vill +%_habitat), $r$ (%_habitat)	<b>642.95</b>	<b>3.62</b>	<b>0.04</b>	<b>0.16</b>	<b>5</b>	
	$\lambda$ (lvs), $r$ (%_habitat)	643.91	4.58	0.03	0.10	4	
	$\lambda$ (lvs + dist.vill), $r$ (%_habitat)	644.28	4.95	0.02	0.08	5	
	$\lambda$ (lvs + slope + dist.vill), $r$ (%_habitat)	644.92	5.59	0.01	0.06	6	
	$\lambda$ (lvs + slope), $r$ (%_habitat)	645.09	5.76	0.01	0.05	5	
	$\lambda$ (%_habitat), $r$ (%_habitat)	646.2	6.87	< 0.01	0.03	4	
	sambar	$\lambda$ (lvs +%_habitat + slope), $r$ (.)	<b>704.38</b>	<b>0</b>	<b>0.64</b>	<b>1</b>	<b>5</b>
		$\lambda$ (lvs + dist.vill +%_habitat + slope), $r$ (.)	<b>706.2</b>	<b>1.82</b>	<b>0.26</b>	<b>0.4</b>	<b>6</b>
		$\lambda$ (lvs +%_habitat), $r$ (.)	709.59	5.21	0.05	0.07	4
		$\lambda$ (lvs + slope), $r$ (.)	711.18	6.8	0.02	0.03	4
wild pig		$\lambda$ (%_habitat), $r$ (.)	<b>486.34</b>	<b>0</b>	<b>0.18</b>	<b>1</b>	<b>3</b>
		$\lambda$ (lvs +%_habitat), $r$ (.)	<b>487.15</b>	<b>0.81</b>	<b>0.12</b>	<b>0.67</b>	<b>4</b>
	$\lambda$ (%_habitat + slope), $r$ (.)	<b>487.27</b>	<b>0.93</b>	<b>0.11</b>	<b>0.63</b>	<b>4</b>	
	$\lambda$ (dist.vill +%_habitat), $r$ (.)	<b>487.31</b>	<b>0.97</b>	<b>0.11</b>	<b>0.62</b>	<b>4</b>	
	$\lambda$ (dist.vill), $r$ (.)	<b>487.84</b>	<b>1.5</b>	<b>0.09</b>	<b>0.47</b>	<b>3</b>	
	$\lambda$ (lvs), $r$ (.)	<b>487.94</b>	<b>1.6</b>	<b>0.08</b>	<b>0.45</b>	<b>3</b>	
	$\lambda$ (lvs +%_habitat + slope), $r$ (.)	<b>488.67</b>	<b>2.33</b>	<b>0.06</b>	<b>0.31</b>	<b>5</b>	
	$\lambda$ (dist.vill +%_habitat + slope), $r$ (.)	<b>488.69</b>	<b>2.35</b>	<b>0.06</b>	<b>0.3</b>	<b>5</b>	
	$\lambda$ (slope), $r$ (.)	<b>488.77</b>	<b>2.43</b>	<b>0.05</b>	<b>0.3</b>	<b>3</b>	
	$\lambda$ (lvs + dist.vill), $r$ (.)	<b>489.32</b>	<b>2.98</b>	<b>0.04</b>	<b>0.22</b>	<b>4</b>	
$\lambda$ (slope + dist.vill), $r$ (.)	<b>489.78</b>	<b>3.44</b>	<b>0.03</b>	<b>0.18</b>	<b>4</b>		
$\lambda$ (slope + lvs), $r$ (.)	<b>489.91</b>	<b>3.57</b>	<b>0.03</b>	<b>0.17</b>	<b>4</b>		
$\lambda$ (lvs + dist.vill +%_habitat + slope), $r$ (.)	490.34	4	0.02	0.14	6		
$\lambda$ (lvs + dist.vill + slope), $r$ (.)	491.32	4.98	0.01	0.08	5		

AIC, Akaike's Information Criteria;  $\Delta$  AIC, difference in AIC scores;  $w_i$ , Akaike weight; Mod.lik, Model likelihood; K, number of parameters;  $\lambda$ , group density;  $r$ , group specific detection probability; lvs, livestock encounter rate; dist.vil, distance to nearest village; %\_habitat, percentage available habitat; slope, mean slope.

percentage habitat available. Distance to nearest village was less reliable in explaining patterns of group density for gaur and sambar. In the case of wild pig, no variable we assessed could reliably explain group density. We discuss our findings for those variables which found support in explaining group density of large herbivores.

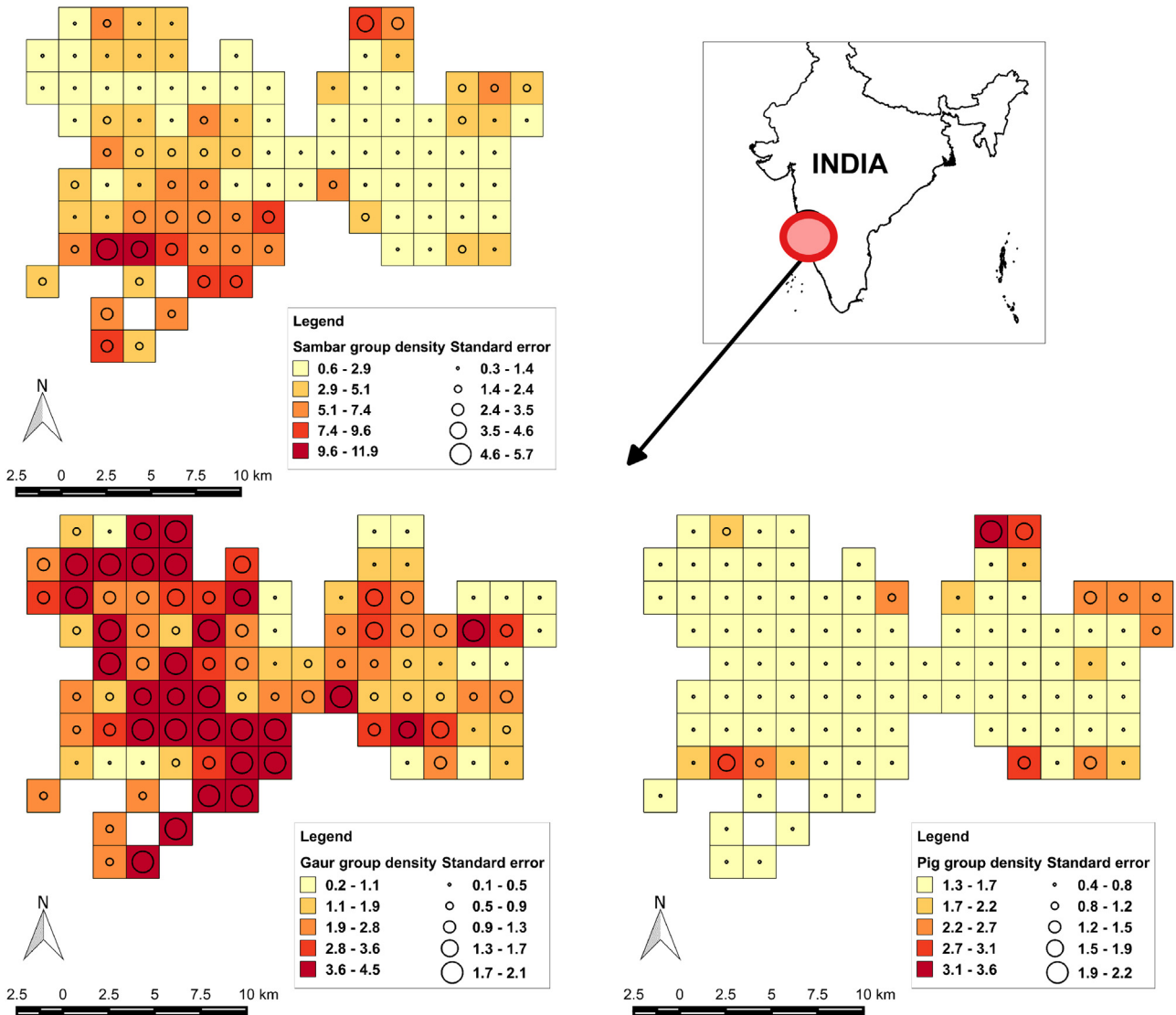
Both gaur and sambar had lower group densities in areas where livestock occurred within remnant forests in our study region. This

was expected as livestock heavily outnumber wild ungulates in much of our study region, suggesting severe competitive limitation for resources. The most likely cause for competitive resource limitation would be similarity in diets among domestic and wild ungulates (Bagchi et al., 2004; Mishra et al., 2004). In Bandipur, south India, Madhusudan (2004) found spatial avoidance by gaur in response to free-grazing cattle due to the effects of resource limitation, although sambar deer showed no clear effects. We found that

**Table 3**  
 $\hat{\beta}$ -coefficients ( $\pm SE$ ) from most-supported models used to assess the effect of variables on  $\log \lambda$  (group density) of large ungulates in the Tillari region, Western Ghats, India.

Species	Models	$\hat{\beta}_{int,\lambda}$ (SE)	$\hat{\beta}_{vs,\lambda}$ (SE)	$\hat{\beta}_{dist\_vill,\lambda}$ (SE)	$\hat{\beta}_{\%habitat,\lambda}$ (SE)	$\hat{\beta}_{slope,\lambda}$ (SE)
gaur	Model 1	0.71 (0.34)	-0.39 (0.14)	-	0.61 (0.25)	-
	Model 2	0.7 (0.35)	-0.41 (0.16)	0.18 (0.12)	0.68 (0.25)	-0.21 (0.15)
	Model 3	0.71 (0.34)	-0.33 (0.15)	0.15 (0.12)	0.62 (0.25)	-
	Model 4	0.7 (0.35)	-0.47 (0.16)	-	0.66 (0.25)	-0.17 (0.15)
	Model 5	0.58 (0.28)	-	0.26 (0.11)	0.58 (0.23)	-
sambar	Model 1	1.13 (0.34)	-0.42 (0.13)	-	-0.34 (0.11)	0.31 (0.11)
	Model 2	1.13 (0.35)	-0.43 (0.14)	-0.04 (0.10)	-0.34 (0.11)	0.33 (0.11)
wild pig	Model 1	0.41 (0.33)	-	-	-0.23 (0.13)	-
	Model 2	0.42 (0.34)	-0.16 (0.15)	-	-0.24 (0.13)	-
	Model 3	0.45 (0.34)	-	-	-0.28 (0.14)	0.16 (0.16)
	Model 4	0.41 (0.34)	-	0.13 (0.13)	-0.23 (0.13)	-
	Model 5	0.32 (0.30)	-	0.15 (0.14)	-	-
	Model 6	0.32 (0.31)	-0.16 (0.16)	-	-	-
	Model 7	0.45 (0.35)	-0.12 (0.16)	-	-0.27 (0.14)	0.12 (0.17)
	Model 8	0.45 (0.34)	-	0.10 (0.14)	-0.27 (0.14)	0.13 (0.16)
	Model 9	0.32 (0.30)	-	-	-	0.07 (0.15)
	Model 10	0.32 (0.31)	-0.11 (0.16)	0.11 (0.14)	-	-
	Model 11	0.32 (0.30)	-	0.14 (0.14)	-	0.04 (0.15)
	Model 12	0.32 (0.31)	-	-	-0.15 (0.16)	0.02 (0.16)

AIC, Akaike's Information Criteria;  $\lambda$ , group density;  $r$ , group specific detection probability;  $\hat{\beta}_{int,\lambda}$ , Beta coefficient for intercept of  $\lambda$ ;  $\hat{\beta}_{vs,\lambda}$ , Beta coefficient for the effect of livestock on  $\lambda$ ;  $\hat{\beta}_{dist\_vill,\lambda}$ , Beta coefficient for the effect of distance to nearest village on  $\lambda$ ;  $\hat{\beta}_{\%habitat,\lambda}$ , Beta coefficient for the effect of percentage habitat on  $\lambda$ ;  $\hat{\beta}_{slope,\lambda}$ , Beta coefficient for the effect of slope on  $\lambda$ ; SE, estimated standard error.



**Fig. 2.** Spatially-explicit maps of estimated group density of large ungulates in sampled grid cells; sambar *Rusa unicolor* (top left), gaur *Bos gaurus* (bottom left), and wild pig *Sus scrofa* (bottom right) in the Tillari region, Western Ghats, India. Standard errors associated with estimated group densities are shown as circles within each grid cell.

sambar group density is also negatively affected by livestock occurrence in our study region. High densities of domestic goat in our study region likely compete heavily with sambar, a predominant browser and intermediate feeder (Johnsingh and Sankar, 1991; Semiadi et al., 2009). In contrast, wild pig possibly faces much lesser competition for forage from livestock due to its broad omnivorous diet, which includes agricultural crops (Ballari and Barrios-García, 2014). Further research using experimental studies may help better explain these patterns observed in our study.

Group density of gaur, the largest of the three wild herbivores in our study, increased in grid cells with higher percentage habitat. This finding is significant given that current rates of habitat loss are high in South Asia, both within and outside of protected areas (Clark et al., 2013). The population of gaur has declined considerably due to habitat loss and hunting over the last few decades across India (Duckworth et al., 2016; Karanth et al., 2010). The species now survives in three discontinuous regions in India (Western Ghats, Central India, and North-east India) and habitats are largely fragmented outside parks (Choudhury, 2002). However, gaur populations fare considerably well in some well-protected parks (Choudhury, 2002; Duckworth et al., 2016), and efforts to reintroduce gaur in areas of former occurrence have been attempted (Sankar et al., 2013). On the other hand, sambar group densities were found to be higher in grid cells with higher mean slope and lower percentage available habitat. This indicates that even smaller undulating habitats can support higher densities for this species, at least in our study region. Sambar has been noted to prefer undulating terrain (Schaller, 1967; Timmins et al., 2015), however the species could be more susceptible to hunting pressures in smaller habitats, especially if males are selectively removed from a population (Steinmetz et al., 2010). No variable reliably explained wild pig group density, which is not completely surprising given that the wild pig shows flexible habitat selection (Chauhan et al., 2009) and can persist even under high anthropogenic impacts (Steinmetz et al., 2010).

Overall, estimates of group density per km<sup>2</sup> using the AOS (null) model for gaur ( $0.51 \pm 0.21$ ), sambar ( $0.64 \pm 0.25$ ), and wild pig ( $0.42 \pm 0.22$ ) in our human-dominated study region are lower than those from ecologically-similar but better-protected Bhadra Tiger Reserve in south India (Gopaldaswamy et al., 2012). Robust estimates of threatened large herbivores are scarce from areas outside of protected areas in India, and our study is one of the few to assess the status of these species (gaur and sambar) outside of protected area boundaries. The approach used in our study is useful as the AOS modelling approach accounts for issues such as imperfect detection when using presence-absence data (Royle and Nichols, 2003). The use of uncalibrated indices (RAIs) to assess either of these parameters is problematic as it can result in flawed inference (Hayward et al., 2015; Sollmann et al., 2013).

#### Limitations of study

Some limitations of our study include the inability to check for violations of model assumptions such as daily movement rate of herbivores ( $R$ ), which has an important bearing on model precision. Nevertheless, the AOS approach is still effective to derive at least a practical ‘relative abundance index’ of animal populations as the direction of bias is predictable and can be corrected for, once information on daily movement rates becomes available (Gopaldaswamy et al., 2012). As the approach relies on surveying adjacent spatial replicates, potential biases in our estimates may have also occurred from spatial dependence among detections (Gopaldaswamy et al., 2012). However, we note that methods to estimate density directly using presence-absence data are still improving, and newer approaches that incorporate spatial dependence of detections as a source of information, rather than a source

of bias look promising (e.g. Ramsey et al., 2015). Future improvements can enable us to account for any biases in estimates resulting from spatial dependence among detections.

#### Conclusions

Although correlational, our study still has important implications for conservation and management of large wild ungulates outside protected parks in India. Human populations in biodiversity hotspots such as the Western Ghats are predicted to increase, further elevating threats to biodiversity (Cincotta et al., 2000). Robust assessments of threatened wildlife populations can help better protect and manage priority habitats outside protected areas and set realistic recovery targets (Harihar et al., 2014). Our study reveals that remnant habitats can support significant populations of threatened large herbivores (gaur and sambar) and need to be better protected. This is especially important in the context that remnant habitats are rapidly fragmenting in developing South and Southeast Asian countries (Clark et al., 2013; Sankaran and Ahrestani, 2016; Sodhi et al., 2010). As large herbivores also form preferred prey for endangered large carnivores such as the tiger and dhole (Hayward et al., 2014), protection of remnant habitats will aid the persistence of these carnivores in larger landscapes (e.g. Tiger Conservation Landscapes, Wikramanayake et al., 2011).

Measures to gradually improve livestock management, if designed through field-testing and local community support, could benefit large herbivore populations in critical habitats in India (e.g. Mishra et al., 2003). For instance, studies such as ours can be a starting point to determine stocking rates for livestock in remnant habitats, so as to design effective measures for livestock management through local community support. This reiterates the need for a scientific framework for conservation and management practices even outside of parks in India, which takes into account social, economic, and ecological considerations. Vitality, relationships between humans and large herbivore species have changed dramatically (Gordon, 2009), and large herbivores are prone to conflict where they occur in forest-agriculture mosaics (Karanth et al., 2013). Therefore measures which actively focus on improving tolerance in rural populations and reducing human impacts on large wildlife through innovative approaches will reap larger conservation benefits for many threatened species outside protected areas.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2017.05.004>.

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