1**Title: Seasonal patterns of density distribution of ungulates in the tropical deciduous**

2**forest of central India**

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14ABSTRACT:

151. Tropical deciduous forests show strong seasonal variations due to temporal dynamics of 16precipitation and temperature and therefore, resource availability for animals are also limited 17accordingly. Certain harsh environment even pushes animals to seasonal movements towards 18available resources.

192. We hypothesize that the density distribution of four sympatric ungulate species is 20structured by habitat covariates but more affected by seasonality. We then investigated 21density gradient of these species between contrasting season and correlated with 22environmental covariates.

233. We used distance-based density surface modelling with survey effort of 518 km in winter 24and 356 km in summer and with count data as a function of environmental variables in 25generalised additive modelling framework. We extrapolated seasonal abundance of each 26species and calculated coefficient of variation to ensure precision for the entire study area.

274. We observed a clear seasonal shift in the density distribution of all four species between 28summer (more abundant in valley) and winter (evenly distributed), significantly influenced 29by anthropogenic and topographic factors. Solitary species were congregated in larger groups 30during summer while group living species were in larger groups during winter.

315. Our study provides a clear understanding of species-habitat relationship as a function of 32seasonality in tropical forest and is useful in spatial prioritization of the habitats for relevant 33management inputs.

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38**1. INTRODUCTION**

39Tropical dry deciduous forests are highly seasonal due to the effect of monsoon and climate

40(Singh & Chaturvedi, 2017). The amount and period of annual rainfall, length of the dry

41season and the mean temperature of the coldest month are the major seasonal drivers which

42cause extreme variations in the forest attributes (Meher-Homji & Fontanel, 1978). Tropical

43dry deciduous forest witnesses a very short period of growth during monsoon after a very

44long dry season of around six months and hence making every taxa completely dependent on

45the monsoonal rainfall directly or indirectly. Strong seasonality of dry deciduous forests leads

46to seasonal variation in phenology of different floral species (Singh & Singh, 1992) and

47accordingly, the deciduousness of tree leaves during dry season is an important event shaping

48animals distribution. Water availability limits the growth of deciduous trees (Reich and

49Borchert 1984) and hence, drier regions have greater proportion of the deciduous trees.

50Topography in such scenario plays a major role in establishing moisture gradient across

51regions. Most of the monsoonal water sink to the river valley, leaving plateaus drier and thus

52triggering deciduousness of trees which in turn allow more sunlight penetration making these

53regions warmer. In contrasts, valleys retain most of the monsoonal water, allow evergreen

54tree species to flourish makes them shady habitats and cooler all throughout the year. The

55phenological variations changes the microclimatic conditions and availability of food

56resources. In dry season, soil also becomes dry due to wind and insolation (Kapos, 1989) and

57reduce plant productivity (Ceballos, 1990). Consequently, mammals in dry deciduous forest

58either becomes generalists that adapt or change the diet in different seasons or become diet

59specialists that move to preferable habitats when resources are abundant or scarce (Stoner &

60Timm, 2004).

61Animal species cope with the environmental seasonality by variety of behavioural

62adaptations such as; dietary flexibility, local movements, short-distance migration, long-

63distance migration, change in activity patterns and seasonality of reproduction (Stoner &

64Timm, 2004; Wall, González, & Simmons, 2011) which allow them to survive in harsh

65environment. These adaptations allow animals to obtain sufficient resources, cope with the

66hot and dry environmental conditions and reduce competition. Variation in the forest attribute

67pushes animals to make their preferences across habitats in different seasons. Ungulates

68preference of different habitats in different seasons (Lamprey, 1963) is then guided by abiotic

69factors such as topography, water availability and weather and biotic factors such as forage

70availability (Bailey & Provenza, 2008). As previous studies suggest, animals prefer higher

71elevation and ridges in colder temperatures (Harris, Johnson, George, & McDougald, 2002)

72and seek shade during hot weathers (McIlvain & Shoop, 1971). Ungulates migrate from one

73region to another is also a result of the lack of forage and water (Fryxell & Sinclair, 1988;

74Payne et al., 2020). In dry season, sources of water and shade is often limited and forage

75availability becomes scarce. In the dry deciduous forests, trees in riverine and cliff habitat

76retain their leaves and are more humid (Moura, 2007) and are the best refugee. In such

77scenario, dispersal allows them to survive despite the harsh climatic variations (Boone,

78Burnsilver, Worden, Galvin, & Hobbs, 2008) and help fulfil their nutritional requirements

79(Coppedge & Shaw, 1998; Scott, Provenza, & Banner, 1995; Senft, Rittenhouse, &

80Woodmansee, 1985). Human settlements and agricultural field also affect their distribution

81patterns (Mysterud, Lian, & Hjermann, 1999).

82Understanding the seasonal movement patterns is of much benefit for conservation and

83habitat management as it particularly improves our understanding of habitat important for

84wildlife in space and time (Hebblewhite & Haydon, 2010) which further help in maintaining

85connectivity within the landscape and identifying the probable threats (Allen & Singh, 2016).

86With advancements in the methodology, it is now comparatively easier to understand these

87ecological patterns particularly by building spatial models which allow habitat heterogeneity

88as well as identify environmental variables that influence density distribution in space and

89time. Density Surface Modelling (DSM) (Miller, Burt, Rexstad, & Thomas, 2013) combines

90spatial modelling techniques with distance sampling (Buckland et al., 2001, 2004) taking into

91account the probability of detecting an animal at each sampling unit and build maps of the

92population abundance distributions. These maps are extremely useful due to their scale

93flexibility and simple interpretation of complex scientific algorithm and thus easy to

94communicate results to the non-specialists (Miller et al., 2013). DSM also propagates

95uncertainty from detection function to spatial model depending on the environmental

96variables and estimate the variance for each sampling unit to ensure precision of the

97population estimates (Hedley & Buckland, 2004). DSM has recently been used for many

98different taxa, i.e. marine mammals (Mannocci, Roberts, Miller, & Halpin, 2017; Redfern et

99al., 2017; Sigourney et al., 2020), seabirds (Fifield et al., 2017), marine benthos

100(Katsanevakis, 2007), terrestrial plants (Dias et al., 2016) and terrestrial ungulates (Valente,

101Marques, Fonseca, & Torres, 2016). However, a holistic approach of comparative seasonal

102abundance distribution with detailed information on the environmental variables influencing

103these patterns remains pioneering in tropical forests.

104Most of the studies on seasonal movements are mostly based on radio-telemetry data and

105concentrated on the African savannah (Fryxell & Sinclair, 1988; Owen−Smith et al., 2020;

106Yoganand & Owen-Smith, 2014) and Neotropical forests. Studies based on radio-telemetry

107data give precise estimates however, have limitations such as, observations restricted to a

108small number of individuals and are not very cost-effective. In contrasts, distance sampling

109based on line transect data is cost-effective and includes the population for observations.

110Given the strong seasonality of tropical dry deciduous forests, studies describing the role of

111seasonality in mediating the ungulates distribution is gravely lacking. Therefore, we built our

112hypothesis based on the above theories so as to understand the seasonal movement by

113establishing density gradient in the whole study area for four ungulate species in two different

114seasons and to investigate the relationship between environmental covariate and population

115density.

116

117**2. METHODOLOGY:**

118**Study area**

119This study was undertaken in Panna Tiger Reserve (PTR) (Figure 1) situated in the Vindhyan

120mountain ranges in Madhya Pradesh, central India, between 24°27′N to 24°46′N latitude and

12179°45′E to 80°09′E longitude. PTR is uniquely characterized by its 'terraced topography' and

122presents two tabletop mountains and a valley formed by the Ken River. The transition from

123one plateau to another forms rocky and steep escarpments ranging from 10 to 80 m in height.

124The Ken River cuts through the reserve from south-west to north-east and serves as a major

125water source for most lives in the reserve.

126PTR is mostly dependent on monsoon rainfall during July–September. The average annual

127rainfall is approximately 1100 mm. Following the monsoon, there is the winter season from

128November-February when the minimum temperature drops down to 5°C, followed by dry

129summer in April-June when the maximum temperature often exceeds 45°C (Karanth,

130Chundawat, Nichols, & Kumar, 2004). There are six species of ungulates which are Chital

131(*Axis axis*), Sambar (*Rusa unicolor*), Nilgai (*Bocephalus tragocamelus*), Wild pig (*Sus*

132*scrofa*), Four-horned Antelope (*Tetracerus quadricornis*) and Chinkara (*Gazella bennettii*)

133although the latter two are highly restricted in distribution and only occasionally sighted. The

134major forest type is tropical dry deciduous (Meher-Homji, 1990) shows exceptional

135seasonality with the scarcity of resources during summer.

136**Field sampling**

137We followed distance sampling protocol (Buckland et al., 2004) for ungulate data collection.

138A total of 66 spatially distributed line transects were walked covering the whole core area of

139PTR and sampling was done in both Summer and Winter. Data were collected for two

140sampling seasons of winter 2015-2016 and 2016-2017 and two sampling seasons of summer

1412016 and 2017. Line length was kept 1.5 km to 2.0 km depending upon the habitat and terrain

142complexity. We walked transects in the early morning hours at the time of peak activity of

143the ungulates. All the transects were subjected to repeated sampling of up to thrice in each

144sampling season.

145We used laser range finder to estimate the distance from the observer to the animal, GPS

146device for coordinates and Suunto compass to calculate the angle. Ungulate species ID,

147number of individuals, sighting angle, GPS coordinates and sighting distance were recorded

148in the field.

Figure 1: Map showing the spatial distribution of line transect survey in the study area, Panna Tiger Reserve overlaid on the digital elevation model data. Elevation divides the whole area into three distinct boundaries viz; upper Panna plateau (south), middle Hinota plateau and lowest Ken river valley (north).

Statistical analysis

a) Data preparation:

Two years data was compiled for both seasons for each species separately. We divided all transects into 400 meters bin and accordingly yielded spatio-temporal replicates of 1286 for summer and 892 for winter. We used both geographical and local habitat variables to model spatial density-distribution of the ungulate species (Figure 11; Appendix A). We derived covariates value either directly from remotely sensed data or derived from remote sensing data to calculate Euclidean distance (Table 1). We used two geographic covariates consisted of Elevation and Terrain Ruggedness Index (TRI); vegetation index consisted of Normalised

163Difference Vegetation Index (NDVI), Habitat parameter consisted of distance to water source

164(water) and one parameter for anthropogenic pressure was distance from the forest edge

165(Distedge). We also incorporated bivariate smooth of spatial coordinates to address the

166spatial variations. Due to dynamic seasonality of the dry deciduous forest, we calculated

167NDVI and distance from water source for summer and winter separately. Prediction grids

168were formed by dividing the whole study area into square grids of 200m X 200m and

169covariates values were extracted for the centroid of the grid for both seasons.

Variable	Data Source and processing details	Spatial resolution and time period	Description
Latitude, Longitude (x, y)	Survey location		
Elevation (dem)	Digital elevation- Shuttle Radar Topography Mission data https://earthexplorer.usgs.gov	30 meter	
Topographic Ruggedness index (TRI)	Calculated from SRTM – digital elevation data (Riley, DeGloria, & Elliot, 1999)	30 meter	This is a measure of roughness in the terrain.
Distance from the water source (water)	Sentinel-2A https://earthexplorer.usgs.gov First, generated a layer of water bodies for two seasons using normalized difference water index (NDWI)	10 meter; Winter data: Dec 2016 – Jan 2017; Summer data: April 2016 – May 2016	This provides a measurable distance from the water that may affect distribution in dry season.

	(McFEETERS, 1996) in ERDAS-Imagine tools. We then calculated as Euclidean distance from the water source.		
Normalized difference vegetation index (NDVI)	Sentinel-2A https://earthexplorer.usgs.gov	10 meter; Winter data: Dec 2016 – Jan 2017; Summer data: April 2016 – May 2016	This is used as vegetation cover in both summer and winter season.
Distance from the Forest Edge (distedge)	Calculated as Euclidean distance from the forest boundary.		This variable represents distance from the human settlements, metal roads and agricultural field present at the periphery. It will also serve as an calculative measures to the access of local people to the forest produces.

170Table 1: Predictor variables to function count data in generalised additive modelling

171framework for spatial modelling.

172**b) Density surface modelling:**

173For each analysis, we used count per segment as a response variable which was modelled

174given habitat variables using GAM approach. The model for count per segment is:

175

176The initial part of the equation ⌐ defines the detection probability in each segment

177multiplied by the area of each segment whereas, the later part defines the intercept and

178smooth functions of covariate (Miller et al., 2013). The modelling process is implemented

179using a two-stage approach. The first step is to fit the detection function to the distance data

180and the second step is to construct the generalised additive modelling (GAM) with per-

181segment counts as a response variable.

182To model the density, we used conventional distance sampling (CDS) which models

183detection probability as a function of observed perpendicular distances. Three key detection

184functions i.e. Uniform, Half-normal and Hazard-rate were fitted to the distance data along

185with and without cosine, polynomial and Hermite-polynomial adjustment terms (Appendix:

186B). The best detection function was selected using Akaike's Information Criteria (AIC). Data

187was truncated for the farthest observations up to 9% from the line of sighting based on visual

188inspection of the detection function superimposed on the histogram of distances (Buckland et

189al., 2001). We chose to keep same truncation distance for one species in both seasons to

190optimise variations in detection probability due to seasonal changes in the habitat. This

191analysis was implemented using the Distance package version 1.0.0 (Miller, Rexstad,

192Thomas, Marshall, & Laake, 2019) for R version 3.6.0 (R Core Team, 2019)

193To model spatial abundance of each species per season, count per segment was modelled as a

194smooth function of predictor variables. Segment area was used as an offset term obtained

195from ⌐ ⌐ where ⌐ is truncation distance and the ⌐ is the segment length. We used default

196thin plate regression spline smoother in GAM. The term selection was performed by checking

197smoother p-value significance and zero effect (Wood, 2006). An extra shrinkage term was

198imposed in the model allowing smooth terms to be removed from the model during fitting

199(Wood, 2011). Data were assumed to follow a Poisson distribution. The mean-variance

200relationship was allowed to vary with advanced distribution Tweedie and Quasi-Poisson

201(Candy, 2004; Foster & Bravington, 2012). Dispersion parameter was investigated for each

202family distribution and model was refitted if data was highly under-dispersed or over-

203dispersed. The basis dimensions in the model were chosen by a repetitive process, in which

204analysis was rerun to make the model wiggly enough to capture the relationship in the data

205and not too wiggly to capture the noise in the data. A decision was made for basis dimensions

206by comparing the effective degree of freedom and random patterns in residuals for each

207smoother (Pedersen, Miller, Simpson, & Ross, 2019). This analysis was implemented using

208'dsm' package version 2.3.0 (Miller, Rexstad, Burt, Bravington, & Hedley, 2020) for R

209version 3.6.0 (R Core Team, 2019). All the models were checked and selected by the iterative

210process (Appendix A).

211**c) Abundance prediction and variance estimation:**

212Response distribution obtained from DSM was then used to predict abundances over the

213whole study area with 200m X 200m prediction cells. Predictions were made for each cell

214based on predictor variables used to fit the model. We assume that detection function and

215spatial models are independent (detection probability is constant across whole study area for

216each analysis) therefore, we estimated coefficient of variance (CVs) for detection function

217parameters and GAM parameters. To measure CVs for abundance prediction, squared

218coefficient of variation from both parameters vis; GAM and detection function were added on

219a per-cell basis following the approach described in (Miller et al., 2013). To visualize the

220CVs, we produced maps for the prediction cells overlaid by the CV values.

221

222**3. RESULTS:**

223The total survey effort in summer was 356 km and in winter was 518 km. Animal sightings
224were frequent in summer due to increased visibility and thinner understorey vegetation.
225Sambar was the most frequently sighted animal in both seasons followed by Nilgai and
226Chital. However, sambar was sighted mostly as solitary species. Most commonly selected
227predictor for abundance was distance from the forest edge and TRI. Seasonal distribution of
228abundance showed a difference in the group size formation. Sambar, Nilgai and Wild pig
229formed larger groups during summer and more evenly distributed during winter whereas,
230Chital were more dispersed during summer and forming larger groups in winter.

231**Sambar (*Rusa unicolor*):**

232Sambar followed the Half-normal and Hazard-rate distribution in summer and winter
233respectively (Table 2). Quasi-Poisson and Poisson family distribution explained the mean-
234variance relationship in summer and winter respectively. Sambar winter abundance was
235predicted to increase with elevation (Figure 2). They were more likely to prefer upper and
236middle plateau regions that also offer dense vegetations and complex topography. Their
237distributions seem to be adjusting with distance to the forest edge throughout the year that
238offers forage resources in the form of agricultural crops in winter also comes with some costs
239of anthropogenic pressure in terms of settlements and road. While in summer, Sambar was
240predicted to be abundant in middle plateau offering less rugged terrain and valley offering
241highly rugged terrain. They seemed to avoid human proximity in summer as forest edge does
242not offer many resources in that season. Our results show a clear seasonal shift in abundance
243gradient of the species (Figure 3 & 4). Sambar is forming larger groups in summer while in
244winter, distribution is more dispersed with smaller group size (0-6 individuals/cell) depicting
245its behaviour modification with harsh climatic conditions. In summer, distribution shrinks to
246more suitable habitats which offer shade as well as food resources. We recorded low CVs in

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247most of its distributional ranges in both seasons except the riverine area in winter and near the

248forest edges in summer.

249**Nilgai (*Bocephalus tragocamelus*) :**

250Nilgai followed the Half-normal and Hazard-rate distribution in summer and winter

251respectively (Table 2). Poisson family distribution explained the mean-variance relationship

252in both seasons. Nilgai winter abundance was predicted to increase away from the forest edge

253and in less rugged terrain (Figure 2). They avoid dense vegetations preferring open habitats

254whereas, in summer, terrain ruggedness elevation does not affect their distribution much.

255Nilgai majorly prefers proximity to the water source in both seasons. Their distributions were

256much restricted to the valley forming larger groups (0-11 individuals/cell) in summer while

257they are distributed to the valley and middle plateau in winter forming smaller groups (0-6

258individuals/cell). Nilgai showed a clear seasonal shift in the distribution with habitat

259preference of middle plateau and valley in the winter and completely shifted to the valley in

260summer (Figure 5 & 6). We recorded low CVs in most of the distributional ranges in both

261seasons except the area away from water in winter and away from the forest edge in summer.

262**Chital (*Axis axis*):**

263Chital followed the Uniform and Hazard-rate distribution in summer and winter respectively

264(Table 2). We recorded higher detection probability in summer due to increased visibility.

265Poisson family distribution explained the mean-variance relationship in both seasons. Chital

266abundances were predicted to increase away from the forest edge and in moderately rugged

267terrain in both seasons. Chital was found most abundant in the valley and preferring dense

268vegetations in winter. Response curve with elevation in summer clearly shows its higher

269abundance in the valley and middle plateau, avoiding ridge areas and upper plateau (Figure

2702). Chital forms larger groups in winter when resources are abundant while more dispersed in

271summer forming relatively smaller groups when resources are scarce. This might act as an

272anti-predatory strategy for group-living animals to congregate in larger groups to increase

273safety when visibility is less and the cost of living in the group due to resource sharing could

274be minimised. We observe a seasonal shift in the abundance distribution as a larger chunk of

275abundances were distributed to the valley and middle plateau in summer (Figure 7 & 8). We

276observe low CVs in summer however, CVs were large in winter due to sampling limitation of

277detecting animals near the sighting line.

278**Wild pig (*Sus scrofa*):**

279Wild pig is the least sighted ungulate however, data fulfilled the model assumptions and

280hence were sufficient enough to perform the analysis. Data followed Half-normal distribution

281in both seasons. Poisson and Tweedie family distributions explained the mean-variance

282relationship in summer and winter respectively (Table 2). Wild pig winter abundances were

283predicted to increase in less rugged terrain avoiding highly rugged terrain (Figure 2). While

284in summer, abundance distribution show species water independence. They avoided

285proximity to the forest boundary and were more evenly distributed in each type of terrain.

286Abundance maps of both seasons show their complete seasonal shifts to the valley in summer

287(Figure 9 & 10). They make larger groups in summer as there is lesser number of niche

288available due to resource scarcity. Whereas in winter, animals were more evenly distributed

289to the plateau in smaller groups. We observe low CVs in most of the distributional range in

290both seasons except the area where detections were less.

291

292**4. DISCUSSION:**

293This study majorly focuses on the seasonal movement of four ungulate species. Tropical dry

294deciduous forests show strong seasonality which in turn cause a difference in resource

295distribution across habitats (Singh & Chaturvedi, 2017). Seasonal dynamics is so evident that

296it causes the animals to shift their habitat as per the resource availability. Our results show a

297clear seasonal shift in the abundance distribution of all ungulate species, more abundant in

298the valley region during summer.

299The topography of dry deciduous forests plays a major role in driving the abundance

300distribution of ungulates. Topography defines the ascending moisture gradient from plateau

301to the valley which is further related to the forage availability (Moura, 2007; Singh &

302Chaturvedi, 2017). Thus in summer when resources become scarce, valley fulfil all the

303habitat requirements such as shade to escape the heat, water and green foliage as forage

304(Johnsingh & Manjrekar, 2015; McKay & Eisenberg, 1974; Schaller, 1974). Whereas in

305winters, when moisture does not limit resource distribution across habitats cause animals to

306be distributed more evenly. Elephants (Bohrer, Beck, Ngene, Skidmore, & Douglas-

307Hamilton, 2014) and other large herbivores in Kenyan savanna landscape showed similar

308pattern and migrated along the elevational gradient in response to water and forage

309availability (Hobbs & Gordon, 2010) concurring with our hypothesis and observations of

310movement of herbivores in response to resource distributions. Abundance distribution due to

311terrain ruggedness is also associated with the resources it has to offer in different seasons.

312The drier environment of plateaus harbours greater proportion of trees of deciduous habit

313which shed leaves early winters, receives more sunlight hence warmer, helps animals to

314escape cold forest nights. On the other hand, the valley habitats provide more shades with

315thick canopy and hence relatively colder. Consequently, we found all four species to be

316distributed on the plateaus during winters.

317Ungulates seasonal distribution is largely influenced by the availability of suitable habitat,

318vegetation cover, water and lack of disturbance (Johnsingh & Manjrekar, 2015; Neumann et

319al., 2015). Varying response with distance from the forest edge highlights the unsegregated

320effects of human presence in terms of settlements, local people access to the forest and road

321cause disturbance and agricultural fields offer forage resources. In winter, forest edge at some

322places benefits the species offering forage whereas, in summer, forest edge majorly cause a

323disturbance which in turn pushes species to modify its behaviour throughout the study area in

324a given season. Nilgai in central India is considered as a serious crop-raider since it is

325distributed in the fringe area (Sankar, 1994). Accordingly, Awasthi et al., (2016) and

326(Harihar, Pandav, & Macmillan, 2014) found Nilgai to be abundant in human-dominated

327landscape. Nilgai's positive relationship with distance from the forest edge in our study can

328be explained by its preferences to less dense vegetations. Relocated villages in PTR inhabits

329many fruiting trees and ample amount of grasses in winters provide excellent habitats for

330such mixed feeders (Sankar, 1994). However, positive relationship of Chital, Sambar and

331Wild pig with the distance from the forest edge explains their habitat preferences to the

332undisturbed forest.

333Plateaus are the most preferable habitats in winter as they provide an ample amount of

334resources due to availability of water post-monsoon. In winter, streams and waterholes retain

335monsoonal water and thus support higher abundance than the valley. As summer approaches,

336water shrinks measurably in waterholes and streams. Being an antelope, Nilgai distributions

337is independent of water and can tolerate larger distances with water sources (Figure 2)

338(Prater, 1990). However Wild pig, being water-dependent species prefer to stay near

339permanent water sources (Johnsingh & Manjrekar, 2015; Roberts, 1997) and moved to those

340areas where river waters are easily accessible (Figure 2). Local movements and migration

341activities in response to water limitations in dry season have been recorded in White-eared

342kob (Fryxell & Sinclair, 1988), Khulan (Payne et al., 2020),African Elephants (Purdon, Mole,

343Chase, & van Aarde, 2018) and in different ungulate species in Serengeti. However, browsers

344and grazers were found to have similar water requirements (Kihwele et al., 2020), while in

345contrast, few other mammals such as bats (Heithaus, Fleming, & Opler, 1975) and primates

346(Brown & Zunino, 1990) are found to have shift in their diet to increase intake of water

347through forage as well as reduce competition when resources are scarce (Galetti & Pedroni,

3481994). Although we did not include the diet preferences of any of four ungulates in this study,

349we suspect that Chital and Sambar rely more on dietary flexibility for water requirements in

350dry season as there were no significant relationship of water and population density for both

351of the species (Figure 2).

352Our results also bring insights that Sambar habitat preferences match to the Chital in both

353seasons and they found in common presence while it shows spatial abundance segregations

354with Nilgai. Chital and Sambar prefer dense vegetations in winter while Nilgai prefers open

355habitats. Our study also highlights that group-living animals such as Chital formed larger

356groups in winter when resources are abundant. This act as their anti-predatory behaviour

357helps them to stay more vigilant when visibility is less and the cost of resource sharing could

358be minimised (Johnsingh & Manjrekar, 2015). However, solitary species such as Sambar and

359Nilgai are pushed to stay in groups during summer as resources become scarce and less

360number of suitable habitats are available. Wild pig, on the other hand, does not show much

361differences in group size formation confirms its behaviour, not as an obligatory group-living

362animal.

363**Conservation implications:**

364Our study builds a robust spatial model to elaborate seasonal shifts in ungulates densities over

365a large spatio-temporal scale. This study also highlights the species-specific and season-

366specific roles of environment variables in defining the density gradients. Spatial distribution

367maps elaborating the density gradients between seasons is useful in communicating the

368results to non-experts and conservation managers. The results can be used to plan habitat

369management including the opportunity for increasing ungulate abundance as the current

370requirement demands increasing prey abundance as the large predator population is showing

371spill-over effects in the reserve. The spatially explicit patterns also serve the options to devise

372appropriate monitoring strategies and managing the habitats for these species, while also

373planning tourism opportunity suitably with minimal effect on the conservation values of the

374reserve.

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385**Author Contribution Statement**

386R.K. developed the larger project, secured funding and facilitated field data collection; D.G.

387and R.K. designed the experiment and data collection protocols. D.G. conceived the idea,

388collected data, performed statistical analyses and wrote the article; both authors discussed the

389results, and reviewed the manuscript.

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391**Data availability statement:**

392The data was collected as a part of large conservation project involving Tiger Reintroduction

393in Panna Tiger Reserve and most are confidential due to the location of endangered species,

394but the data may be shared by the Principal Investigator of the project (R.K.) upon reasonable

395request for any important purpose.

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Species	Season	Detection function	Detection probability	Response	Terms (p-value < 0.01)	Dispersion parameter	Deviance explained	Estimated abundance	CV
Sambar	Summer(n=131)	Half-Normal with cosine adjustments	0.32	Quasi-Poisson	s(x,y, 28.5), s(distedge, 13.6), s(TRI, 5.66)	1.09	28.6%	6486±937	0.14
	Winter(n=172)	Hazard-rate with no adjustment	0.33	Poisson	s(x,y, 21.1), s(distedge, 9.04), s(dem, 5.09), s(ndvi, 3.76)	0.91	23.7%	5817±690.8	0.11
Nilgai	Summer(n=93)	Half-Normal with cosine adjustment	0.28	Poisson	s(x,y, 21.5), s(distedge, 6.68), s(TRI, 3.01), s(water, 3.05), s(dem, 4.93)	1.02	30.2%	4270±782	0.18

	Winter(n=138)	Hazard-rate with no adjustment	0.26	Poisson	s(x,y, 25.7), s(distedge, 1), s(water, 6.42), s(TRI, 2.55), s(ndvi, 1)	0.76	20.8%	4176±892	0.21
Chital	Summer(n=94)	Uniform with cosine adjustment	0.39	Poisson	s(x,y, 20.3), s(distedge, 7.23), s(TRI, 6.8), s(dem, 5.2)	1.73	29.1%	7519±884	0.11
	Winter(n=103)	Hazard-rate with cosine adjustment	0.28	Poisson	s(x,y, 20.6), s(distedge, 7.13), s(dem, 2.33), s(TRI, 7.05), s(ndvi, 1)	0.71	37.1%	4866±733	0.15
Wild pig	Summer (n=68)	Hazard-rate with cosine adjustment	0.32	Poisson	s(x,y, 23.8), s(distedge, 5.26), s(TRI, 3.41), s(water, 6.57)	0.73	37.2%	2305±481	0.20

| | Winter (n=45) | Hazard-rate with cosine adjustment | 0.32 | Tweedie | s(x,y, 15.2), s(TRI, 1.96) | 0.73 | 21% | 2138±475 | 0.22 |

593 Table 2: Model parameters for detection function and Generalised additive modelling of spatial model for each species in each season.

594

|		s(x,y)	s(distedge)	s(TRI)	s(dem)	s(ndvi)	s(water)
Sambar	Winter			--------			--------
Sambar	Summer				--------	--------	--------
Nilgai	Winter				--------		
Nilgai	Summer					--------	
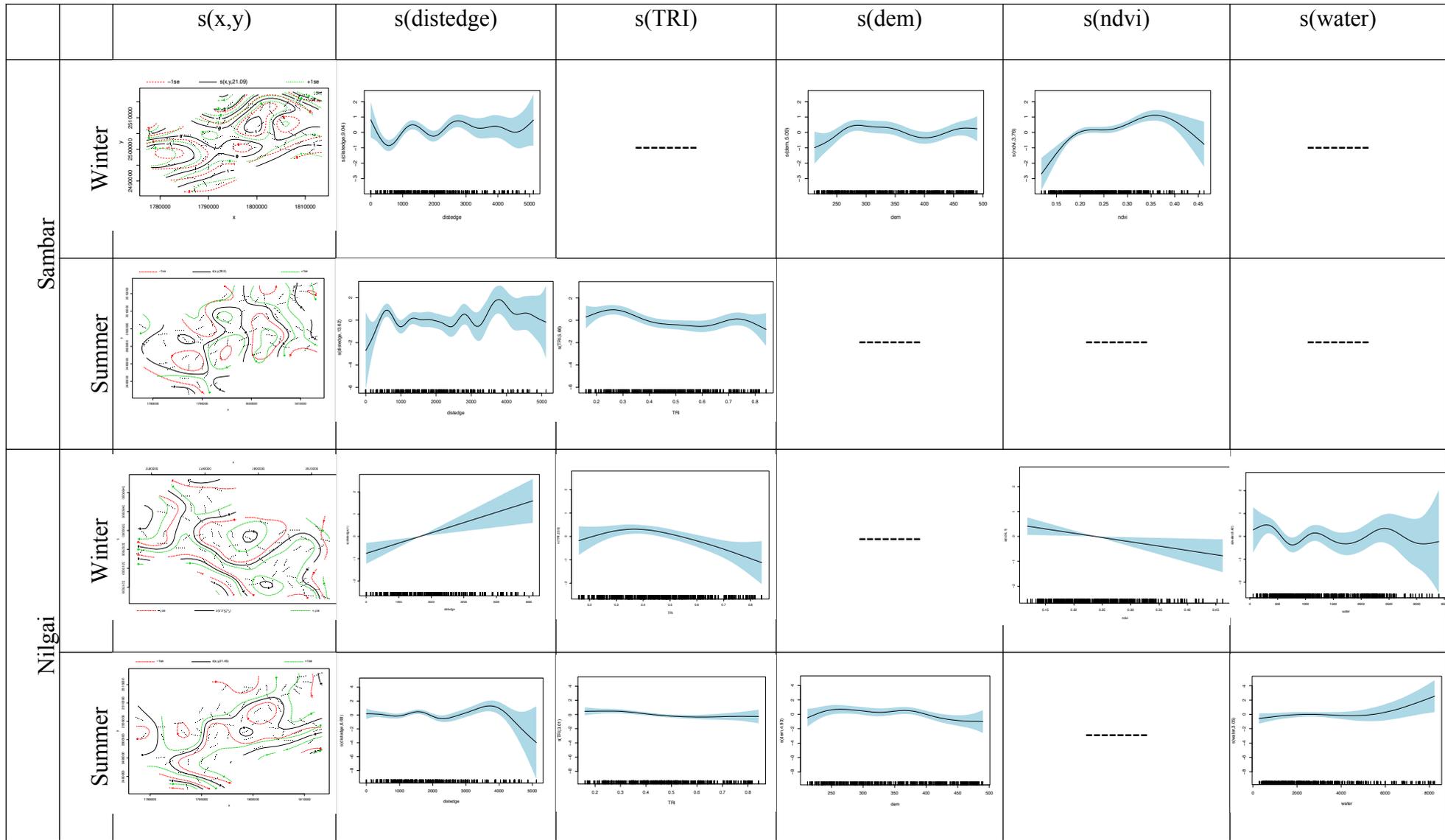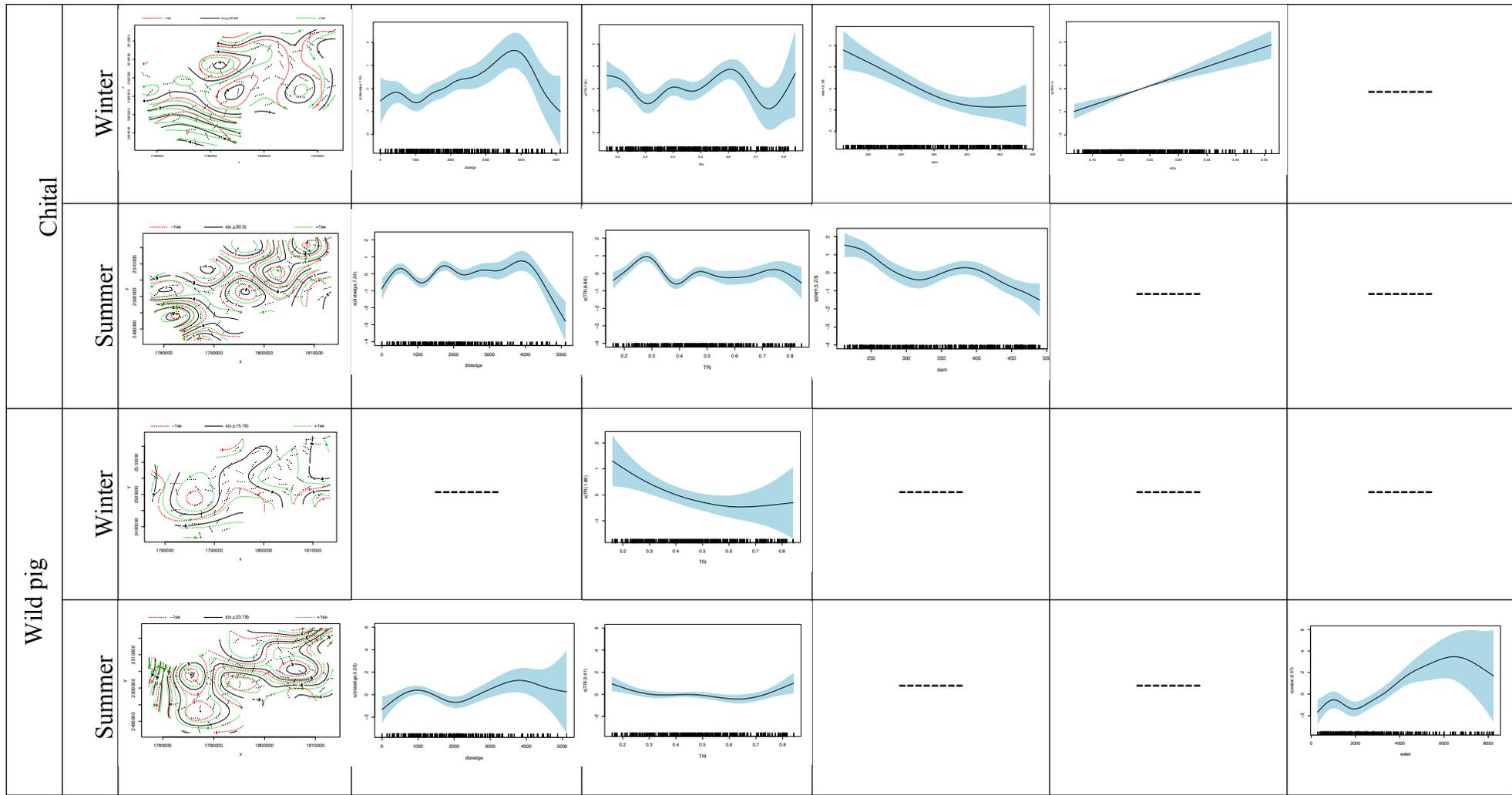
595 Figure 2: Generalised response curve of significant predictor variable with 95% confidence interval (blue fills) for each species in each season.

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599Figure 3: Map of Sambar a) predicted density (individuals / 4hactares) and b) coefficient of variations

600calculated from both detection function and GAM parameters of the model for the Summer season.

601

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603Figure 4: Map of Sambar a) predicted density (individuals / 4hactares) and b) coefficient of variations

604calculated from both detection function and GAM parameters of the model for the Winter season.

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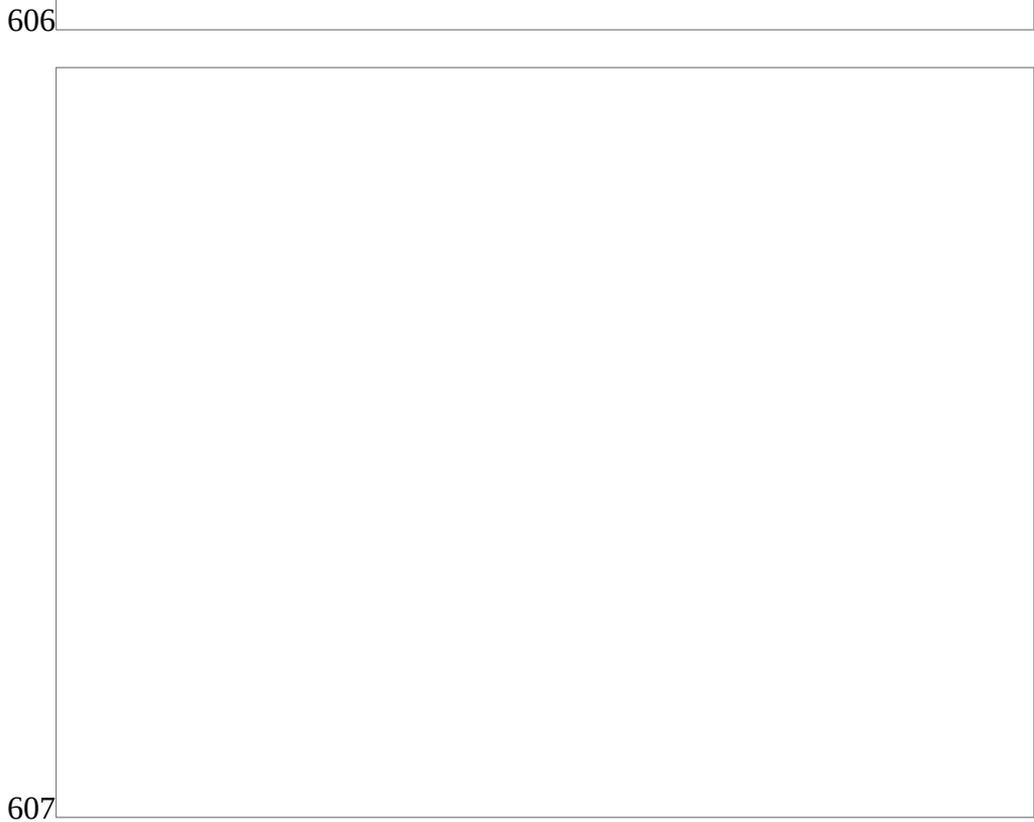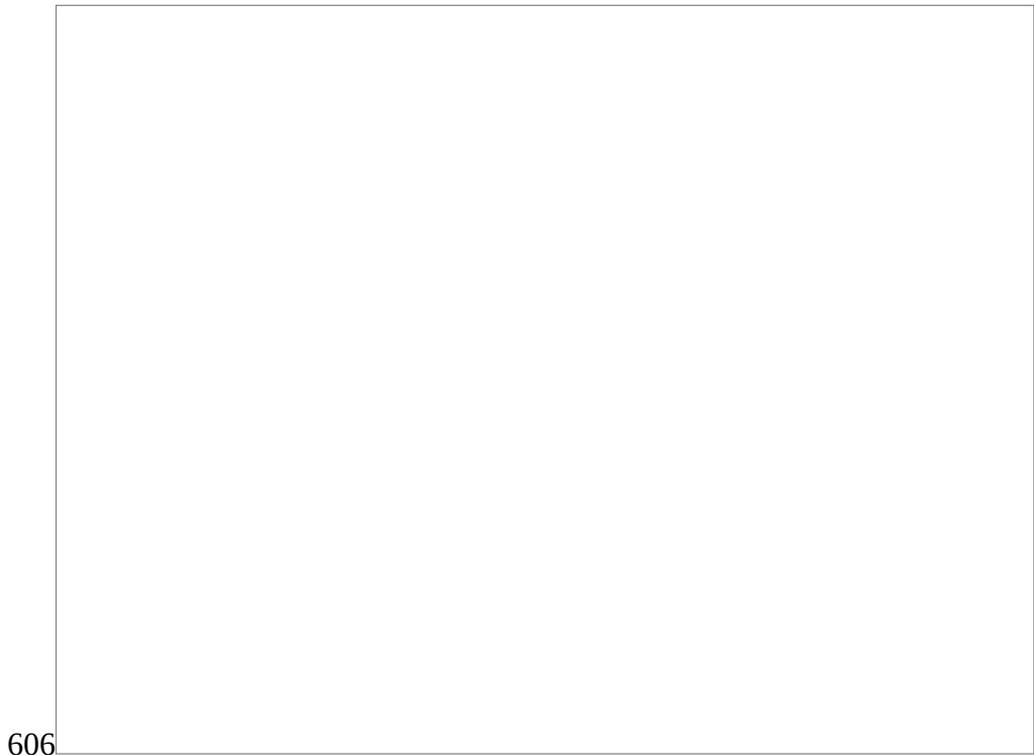
608Figure 5: Map of Nilgai a) predicted density (individuals / 4hactares) and b) coefficient of variations

609calculated from both detection function and GAM parameters of the model for the Summer season.

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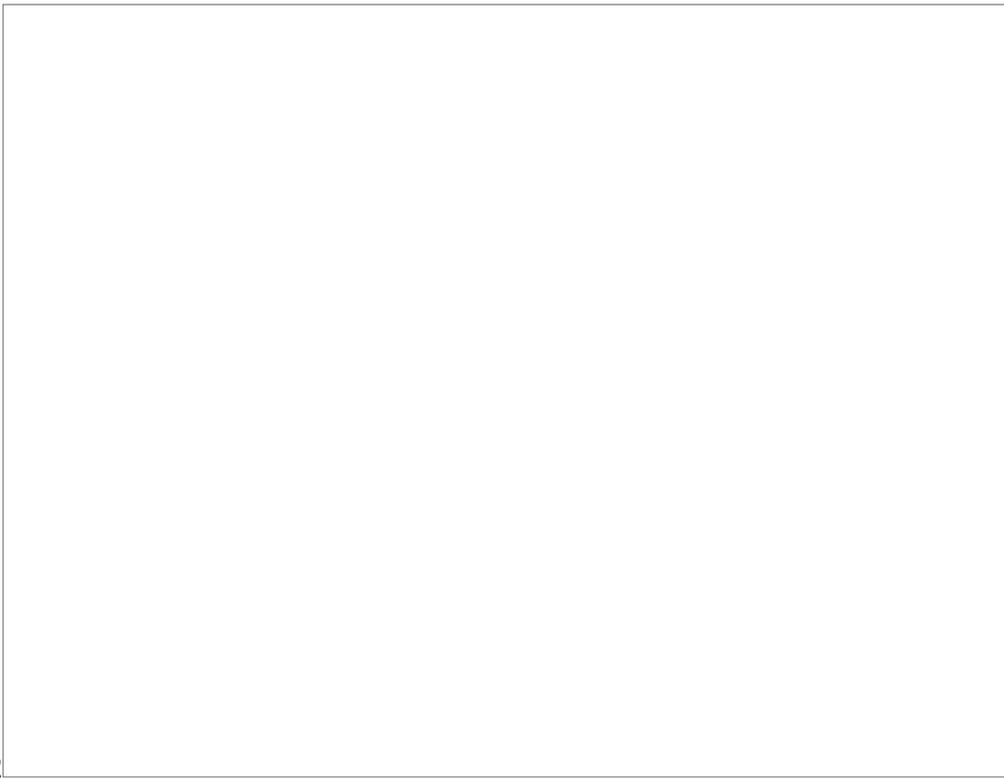
613Figure 6: Map of Nilgai a) predicted density (individuals / 4hactares) and b) coefficient of variations

614calculated from both detection function and GAM parameters of the model for the Winter season.

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618Figure 7: Map of Chital a) predicted density (individuals / 4hactares) and b) coefficient of variations

619calculated from both detection function and GAM parameters of the model for the Summer season.

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623Figure 8: Map of Chital a) predicted density (individuals / 4hactares) and b) coefficient of variations

624calculated from both detection function and GAM parameters of the model the for Winter season.

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628Figure 9: Map of Wild pig a) predicted density (individuals / 4hactares) and b) coefficient of variations

629calculated from both detection function and GAM parameters of the model for the Summer season.

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633 Figure 10: Map of Wild pig a) predicted density (individuals / 4hactares) and b) coefficient of variations

634 calculated from both detection function and GAM parameters of the model for the Winter season

635

636 **Appendix: A**

637 **Density Surface Modelling: Data exploration and Model selection procedure**

638**A. Data exploration:**

639Data exploration was performed in R program using package 'lattice' (Sarkar, 2008) and

640'latticeExtra' (Sarkar & Andrews, 2019) packages following Zuur, Ieno, & Elphick (2010).

641Cleveland dot plots were used to inspect predictor variables for extreme observations. Pair

642plot and VIF values were used to assess collinearity. Multi-panel scatterplots with LOESS

643smoother were used to visualize relationships between predictor and response variables. Data

644were checked for zero-inflation and correlation structures. We found non-linear relationships

645between predictor and response variable with no correlation structure. Hence, we used

646Generalized Additive Modelling (GAM) (Wood, 2006, 2017) approach in Density Surface

647Modelling (DSM)(Miller, Burt, Rexstad, & Thomas, 2013) framework. Cluster size for each

648species in both seasons along with the transect lines were overlaid on the predictor variables

649to visualize the spatial distribution of observations.

650**B. Model checking and selection:**

651Models were selected based on restricted maximum likelihood (REML) scores, deviance

652explained. We chose REML score over generalised cross validation and unbiased risk

653estimators because REML provides a fitting criteria with a more pronounced optima that

654avoids some problems with parameter estimation (Miller et al., 2013). However, we did not

655rely solely on REML score and deviance explained due to their sensitivity, though both

656values played an important role in our model selection process. We calculated dispersion

657parameter to understand the mean-variance relationship explained by the model. We check

658the models with standard GAM diagnostic plots and smoothing parameter estimation

659convergence information (Wood, 2017). The standard GAM diagnostic plots correspond to

660the various residual plots visualising if residual patterns remained in the model. Slight

661departure from the assumed distributions were not considered problematic if dispersion

662parameter was accurate (Augustin, Sauleau, & Wood, 2012; Heyde, 1997).

663We further investigated our model for data independency due to model misfit by plotting

664residuals versus each covariate in the model and also versus each covariate not in the model.

665Any patterns in these plots were considered dependency due to model misfit caused by

666covariate and model were corrected for the variation.

667When models were fitted with multiple smooth we check our model for concurvity.

668Concurvity measures how well one smooth term can be explained by some combination of

669the other smooth terms in the model (Pedersen, Miller, Simpson, & Ross, 2019). We removed

670one of the two variables if the two have concurvity value >0.8. We check our model for

671influential observations by plotting cook's distance and influential observations were

672removed. Spatial auto-correlation was checked by using semi-variogram and residual box

673plot for each sampling sites. Our data did not show any correlation structure therefore, we

674stick to generalised additive modelling and did not incorporated generalised additive mixed

675modelling. We again performed GAM with model residuals and covariates to check if there is

676any residual structure left in the model. Patterns were considered systematic if we got

677smoothers p-value significant and in such scenario, main model was rerun with adjusted

678parameters.

679**Reference:**

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699
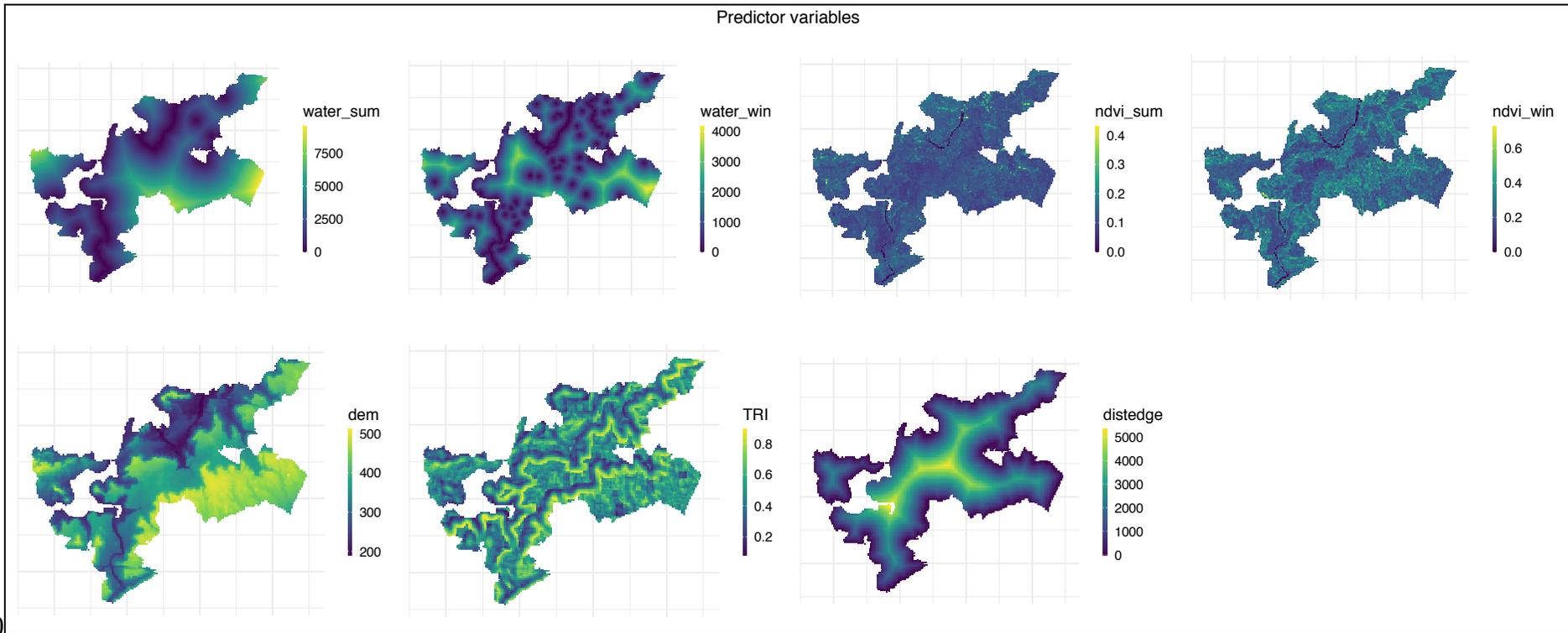
Figure 11: Maps showing all predictor variable for Winter and Summer season across study area. Here, water_sum (Distance from the water source in Summer, water_win (Distance from the water source in winter), ndvi_sum (NDVI in summer), ndvi_win (NDVI in winter), dem (Digital Elevation model), TRI (Terrain Ruggedness Index) and distedge (Distance from the forest edge).

**Appendix: B**
Histograms of fitted detection function using Distance sampling methods
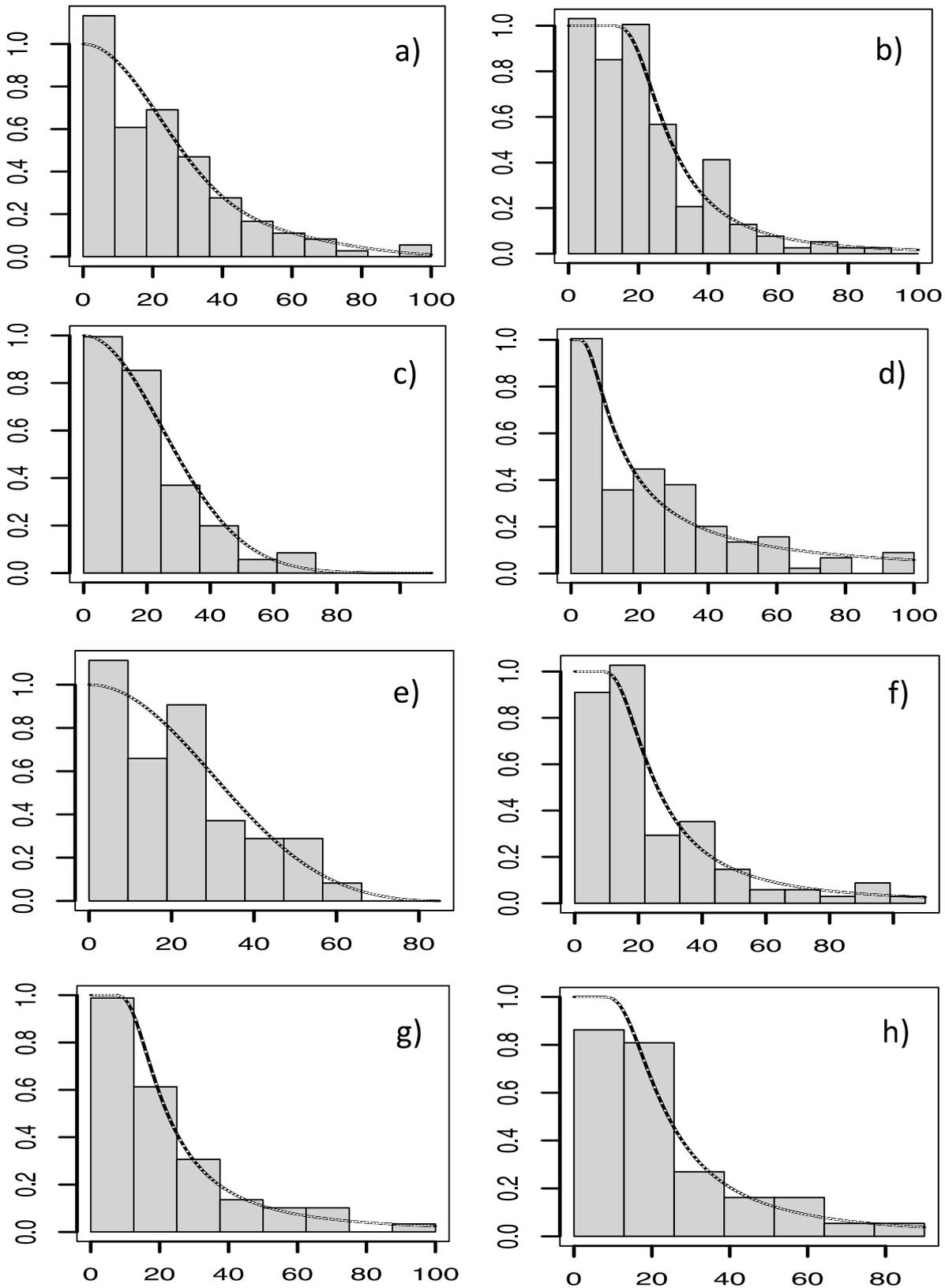
710Figure 2: Fitted detection function using Distance sampling method for all four species in both seasons;
711Sambar a) Summer, b) Winter; Nilgai c) Summer, d) Winter; Chital e) Summer, f) Winter; Wild pig g)
712Summer, h) Winter. x-axis shows detection probability and y-axis shows observed perpendicular distances.