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Cover: Rufous-headed Hornbill *Rhabdotorrhinus waldeni* © Philip Godfrey C. Jakosalem.

INTRODUCTION

Patterns of spatial distribution and fine-scale habitat-use by species are important aspects to understand their ecology and to initiate conservation measures to ensure population stability (Law & Dickman 1998; Phillips et al. 2004; Abrahms et al. 2016; Massara et al. 2018). Habitat components such as topography, canopy cover, water sources, prey species availability, proximity of habitat edges, and anthropogenic activities have significant roles in shaping the occurrence of a species (Durbin et al. 2004; Grassman et al. 2005; Jenks et al. 2012; Srivathsa et al. 2014; Aryal et al. 2015; Ferreguetti et al. 2016; Ferreguetti et al. 2017; Punjabi et al. 2017). Some species are habitat specialists with narrow niche requirements in specific habitats while others are habitat generalists occurring in a variety of habitats (Thorpe & Thorpe 2019). Within this behavioural diversity, it is hard to manage any species without information on its distribution and ecology (Aryal et al. 2015). Such information is a prerequisite for planning and developing species conservation strategies (Guisan & Zimmermann 2000; Halstead et al. 2010; Aryal et al. 2014, 2012; Lee et al. 2012).

The Dhole *Cuon alpinus* is a habitat generalist and a social carnivore that lives in packs of 3–20 adults (Valkenburgh 1991; Iyengar et al. 2005; Reddy et al. 2019). Dholes occur in a variety of habitats, occupying a wide distribution range across central Asia, southern Asia, and southeastern Asia (Lekagul & Mc Neely 1977; Johnsingh 1985; Srivathsa et al. 2014; Kamler et al. 2015). They are also found on the islands of Sumatra and Java (IUCN 2015). In Nepal, they are distributed from southern lowland protected areas of Bardia, Chitwan, and Parsa national parks (Thapa et al. 2013; Yadav et al. 2019) to the northern high mountain protected areas of Kanchanjunga Conservation Area, Makalu Barun National Park, and Dhorpatan Hunting Reserve (Jha 2003; Khatiwada 2011; Aryal et al. 2015). Despite their wide geographical distribution, they are endangered because of low population density and continued population decline caused by prey depletion, disease, habitat loss, and persecution (Kamler et al. 2015; Reddy et al. 2019). The Dhole is categorized as ‘Endangered’ in the IUCN Red List and placed in Appendix II of CITES (Kamler et al. 2015; CITES 2017). In spite of its endangered status, there have been relatively few quantitative studies throughout its range (Khatiwada 2011; Aryal et al. 2015) and very little is known about its distribution and ecology in Nepal (Thapa et al. 2013). Our study documents the influence of various ecological factors on the habitat-use patterns



Image 1. Camera trap photograph of Dholes *Cuon alpinus* in Parsa National Park (X:279520, Y:3015710). (© DNPWC/NTNC/ZSL Nepal/Panthera).

of dholes at a fine spatial scale in Parsa National Park Nepal. This study generates baseline information about dholes in Parsa with potential applications for improving dhole conservation efforts in Nepal.

MATERIALS AND METHODS

Study Area

The study was conducted between 2016 and 2017 in Parsa National Park (PNP) in south-central Nepal (27.25–27.55 N, 84.68–84.96 E) covering an area of 499 km² (area of PNP before extension). PNP was established in 1984 as a wildlife reserve, which was extended eastward to 627.37 km² in 2015 (Figure 1), and was upgraded to a national park in 2017. Parsa is the easternmost protected area of the trans-boundary Terai Arc Landscape (Lamichhane et al. 2018). The park was established primarily to preserve the unique sub-tropical dry ecosystem and to protect habitats of resident Asian Elephant *Elephas maximus* populations. However, it also provides good habitat for Dholes as they have been frequently recorded in camera-traps (PNP 2020) and directly sighted (Thapa et al. 2013). The reduced anthropogenic pressure, improved security and good prey base (Thapa et al. 2013; Thapa & Kelly 2016; Lamichhane et al. 2018) have made the landscape suitable for Dholes.

PNP has many carnivore species including the Tiger *Panthera tigris*, Leopard *Panthera pardus*, Striped Hyena *Hyaena hyaena*, Clouded Leopard *Neofelis nebulosa*, and Golden Jackal *Canis aureus*. The park also supports populations of a wide range of herbivore

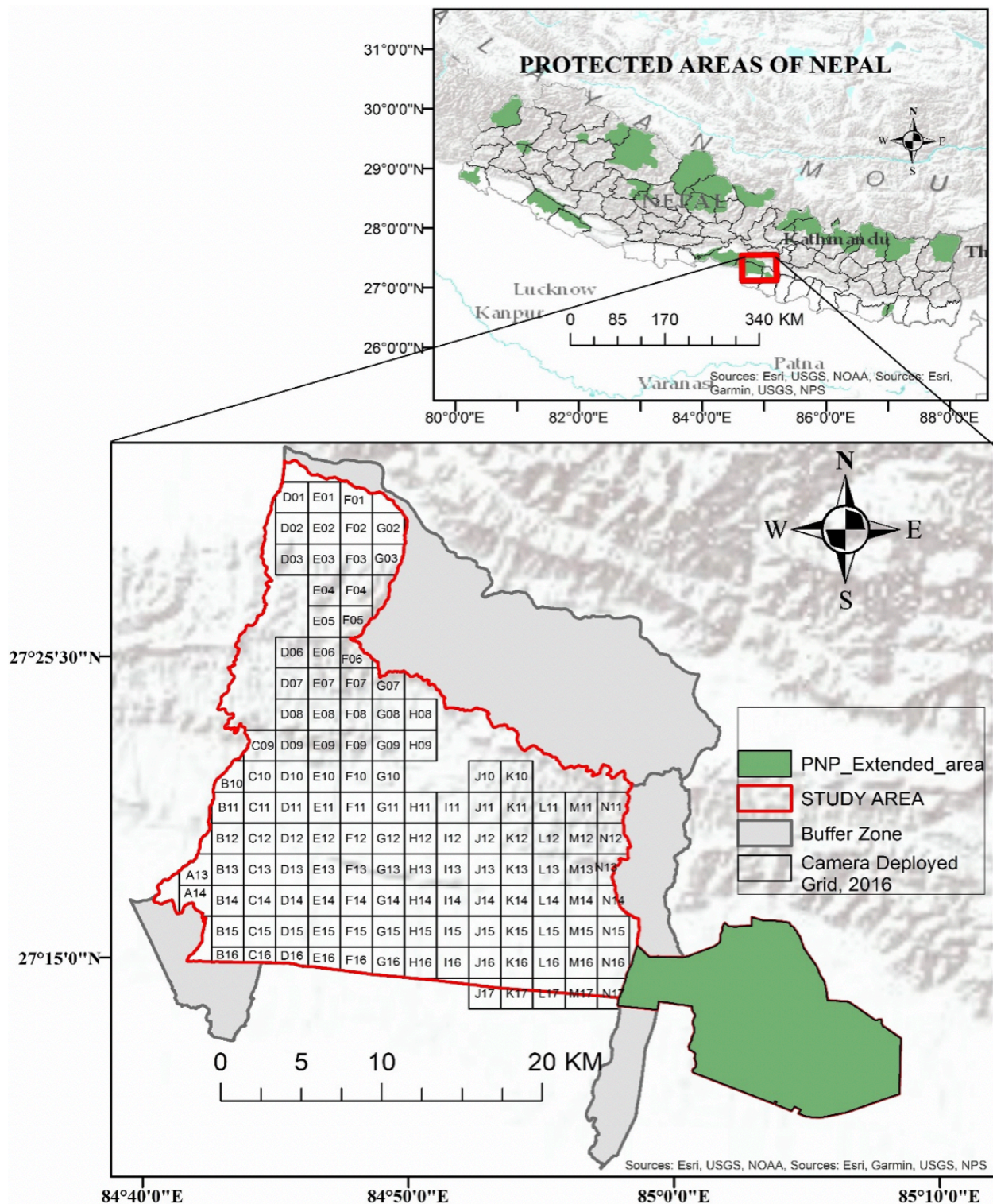


Figure 1. Map of the study area showing camera deployed grids in Parsa National Park, Nepal.

species such as Greater One-horned Rhinoceros *Rhinoceros unicornis*, Gaur *Bos gaurus*, Sambar *Rusa unicolor*, Nilgai *Boselaphus tragocamelus*, Spotted Deer *Axis axis*, Barking Deer *Muntiacus vaginalis*, and

Wild Pig *Sus scrofa* (Thapa et al. 2013). Parsa has a fragile geology and highly porous alluvial substrate. The streams running off the Churia Hills permeate the porous sediment and flow underground, reappearing

south of the park and restricting water availability in >70% of PNP throughout the dry months (Lamichhane et al. 2018). Besides its biodiversity conservation value, PNP also serves the vital needs of the large human population living south of the park by conserving water sources and reducing the soil erosion in the Siwalik Hills (Bhattarai et al. 2018). PNP includes mainly sub-tropical forests of the Siwalik and Bhabar physiographic regions of Parsa, Makwanpur, and Bara districts. The vegetation is mainly dominated by Sal *Shorea robusta* forest (90%). However, the forests are dominated by Khote salla *Pinus roxburghii* on the southern slope of the Siwalik Hills (60%). The riverbeds and flood plains are covered by riverine species including Khair *Acacia catechu*, Simal *Bombax ceiba*, Kans *Saccharum spontaneum*, and Cogon Grass *Imperata cylindrica* (Chhetri 2003; PNP 2020).

Field Survey

We overlaid 2 x 2 km² grid cells on 499 km² area of PNP and set up a pair of automatic motion sensor digital cameras (Panthera V4 and V5) in each grid cell selecting the best possible locations. The paired cameras were positioned 45 cm above ground, perpendicular to, and 5–7 m apart, on either side of game trails, grassland, forest roads and riverbeds with higher probability of detecting carnivores (Figure 1). The camera-traps were kept for 21 days within each grid cell. Camera-traps were installed in the field during the winter season (November–January) of 2016–17. Due to limited camera-traps availability, the entire area was divided into two blocks and surveyed sequentially. The camera-traps pictures were sorted species-wise, and all the Dhole photographs were obtained in a separate folder. Dhole photographs obtained from a location at 30 minutes apart were considered as independent detections (Silver et al. 2004; Di Bitetti et al. 2006; Thapa et al. 2013).

Data Analysis

The estimated home-range of dhole is ~85 km² (Srivathsa et al. 2017) which exceeded our sampling unit 4 km², so we described occupancy as a measure of 'habitat-use' instead of 'true occupancy' (Sunarto et al. 2012; Srivathsa et al. 2014; Thapa & Kelly 2016). We constructed the detection history of dholes in each grid. We considered 24 hours as a sampling occasion, so that each grid had 21 sampling occasions. We then grouped five consecutive sampling occasions to obtain four temporal replicates in each location (discarding first camera-trap day) to avoid redundancy in data transformations that might arise from zero counts (Kafley et al. 2016; Wolff et al. 2019). The final detection

history of Dholes in each grid therefore included four independent sampling occasions (replicates). We coded detection of Dholes in each replicate as '1' and non-detection as '0'. We estimated the detection probability and habitat-use following MacKenzie et al. (2002). We estimated the probability of detection, p based on the two possible outcomes for each survey occasion, namely, (1) the animal was detected, p , and (2) the animal was not detected, $1-p$. Consequently, the probability of habitat-use based on the detectability was translated as follows: (1) the site was occupied and the species was detected, ψxp ; (2) the species was present but not detected, $\psi x(1-p)$; or (3) the species was not present and, hence, not detected, $(1-\psi)$. We used single season single species occupancy models (MacKenzie et al. 2006) to estimate the relative effect of land cover (forest cover, grassland and streams/exposed surfaces), terrain ruggedness index, distance to the nearest settlement, and prey species covariates at a fine-scale on the probability of Dholes habitat-use and distribution. We used the prey species (Sambar) captured on the same camera-traps as sample covariate and others as site covariates (Karanth & Sunquist 1995; Andheria et al. 2007; Punjabi et al. 2017). Areas of different habitat types, i.e., forest cover, grassland, and stream/exposed surfaces were obtained from supervised classification of Landsat satellite images and were used as site covariates (Lillesand et al. 2004). Similarly, we calculated average terrain ruggedness index (TRI) values for each grid cell from the digital elevation model (DEM) of ASTER Global DEM at 30 m resolution by using a "DOCELL" command in ArcGIS 10.3. We calculated the distance of each grid from its center to the nearest settlements using ArcGIS 10.3 and used this as a surrogate of disturbance index. We assumed farther the distance from settlements, lower is the disturbance and higher is the occupancy and vice-versa. All predictor variables were standardized (z-transformations) so that the model coefficients could be directly interpreted as effect sizes. We tested auto-correlation between the predictor variables using Pearson's coefficients. We constructed covariate combinations such that highly correlated predictors (Pearson's $|r| > 0.70$) did not appear in the same model. For example, grassland and streams/exposed surfaces were not used together within the same model due to high correlation between the variables (Pearson's $|r| = 0.74$). We performed all analyses on program PRESENCE Version v2.12.32 and selected the best model based on minimum Akaike Information Criteria (Burnham & Anderson 2002). We estimated parameters in two steps. First, a general structure for habitat-use was

defined as a function of forest cover F_c , grassland G , streams/exposed surfaces SES , terrain ruggedness index TRI , distance to the nearest settlements D and prey species S i.e. $\psi(F_c+G+SES+TRI+D+S)$ as global model ψ (Global) and modeled detection probability (p) either as an intercept-only model or as a function of individual covariates and their combinations (Table 1). Second, the habitat-use probability (ψ) was modeled incorporating the top ranked model for probability of detection in the first step (Table 2). Influence of different covariates on habitat-use was again modeled either individually or additively combining covariates in different biologically plausible combinations. Models with ΔAIC of <2 were considered to be strongly supported by the data. We used estimated β -coefficients to assess the strength of association of each covariate with habitat-use probability. Model fit was assessed for over-dispersion in the global model by running 1,000 bootstrap iterations (Burnham & Anderson 2002). The global models with $c\text{-hat}>4$ were considered structurally inadequate (Burnham & Anderson 2002) and excluded from further analyses. A total of seven candidate models (Table 2) were run for determining factors influencing habitat-use by Dholes.

RESULTS

Distribution of Dholes

With a total survey effort of 2,520 trap-nights at 126 camera-traps locations, we obtained 63 independent pictures of Dholes in PNP. Dholes were photographed at least once in 27 different locations (21.43% of the surveyed grids) with the naïve occupancy estimate of 0.21. Dholes were recorded primarily in the Churia hill forest (59.26%) followed by the forest in plains (29.63%), grassland (7.41%), and stream/exposed area (3.70%). Most photo-captures were in the western and northwestern part of the park bordering Chitwan National Park with a few records on the southern border (Figure 2).

Detection probability of Dhole

Streams/exposed surfaces (SES), terrain ruggedness index (TRI), and Sambar (S) affected the detection probability (p) in the top ranked model (Table 1, Figure 3). The estimated detection probability (p) was found to be 0.24 ± 0.05 . The top model indicated that dhole detection probability was positive for prey species Sambar ($\beta_S = 2.44 \pm 1.02$) but was negative for streams/exposed surfaces ($\beta_{SES} = -0.99 \pm 0.32$) and terrain ruggedness index ($\beta_{TRI} = -0.09 \pm 0.23$) as shown in the Table 1.

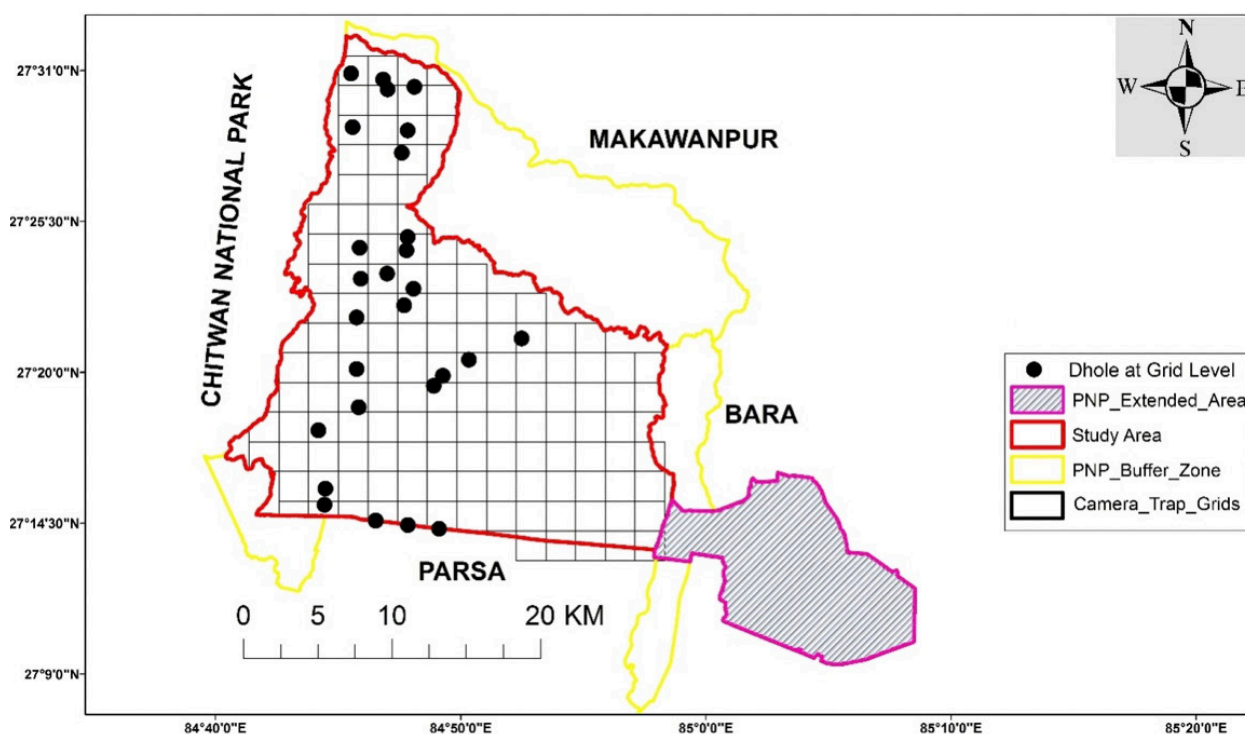


Figure 2. Photo-captured locations of Dhole in Parsa National Park.

Table 1. Summary of β -coefficient parameter estimates and associated standard errors (SE) of covariates from top models used to explain Dhole detection (p) in PNP. Given are intercept (Int.), stream/exposed surfaces (SES), terrain ruggedness index (TRI), Sambar presence (S), grassland availability (G), distance to the nearest settlements (D), Akaike Information Criteria (AIC), relative difference in AIC(Δ AIC), and AIC model weight (W).

Model (M)	$\beta_{\text{Int.}} \pm \text{SE}$	$\beta_{\text{SES}} \pm \text{SE}$	$\beta_{\text{TRI}} \pm \text{SE}$	$\beta_{\text{S}} \pm \text{SE}$	$\beta_{\text{G}} \pm \text{SE}$	$\beta_{\text{D}} \pm \text{SE}$	AIC	Δ AIC	W
ψ (Global), p(SSES+TRI+S)	-2.29 \pm 0.15	-0.99 \pm 0.32	-0.09 \pm 0.23	2.44 \pm 1.02	-	-	256.03	0	0.46
ψ (Global), p(TRI+S)	-1.29 \pm 0.11	-	-0.25 \pm 0.16	0.47 \pm 0.21	-	-	257.42	1.39	0.23
ψ (Global), p(S)	0.31 \pm 0.14	-	-	0.50 \pm 0.25	-	-	257.64	1.61	0.21
ψ (Global), p(SES)	0.51 \pm 0.78	-0.30 \pm 0.13	-	-	-	-	260.53	4.50	0.05
ψ (Global), p(G+S+TRI+D)	1.13 \pm 0.71	-	-0.22 \pm 0.17	0.41 \pm 0.11	-0.48 \pm 0.16	-0.19 \pm 0.13	261.23	5.20	0.03
ψ (Global), p(.)	2.13 \pm 1.45	-	-	-	-	-	262.20	6.17	0.02

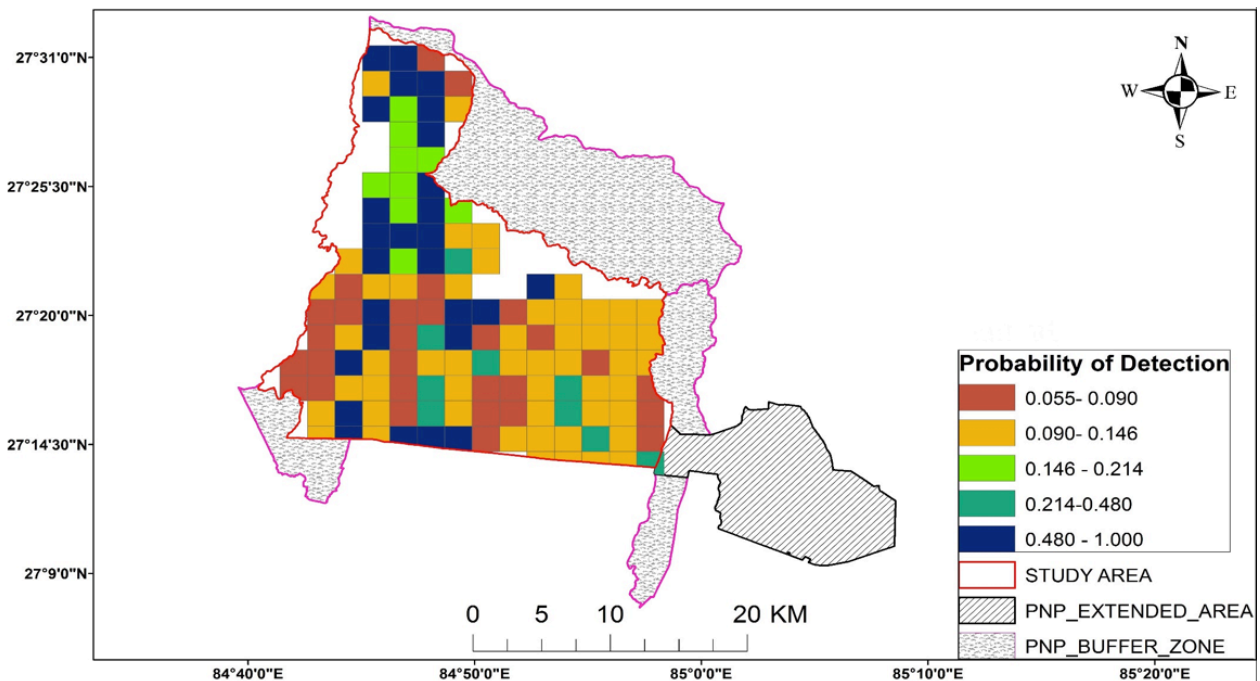


Figure 3. Detection probability of Dholes in Parsa National Park at grid level.

Table 2. Summary of β -coefficient parameter estimates and associated standard errors (SE) of covariates from top models used to explain dhole habitat use (ψ) in PNP. Given are intercept (Int.), grassland availability (G), terrain ruggedness index (TRI), Sambar presence (S), stream/exposed surfaces (SES), Akaike Information Criteria (AIC), relative difference in AIC(Δ AIC), and AIC model weight (W).

Model (M)	$\beta_{\text{Int.}} \pm \text{SE}$	$\beta_{\text{G}} \pm \text{SE}$	$\beta_{\text{TRI}} \pm \text{SE}$	$\beta_{\text{S}} \pm \text{SE}$	$\beta_{\text{SES}} \pm \text{SE}$	AIC	Δ AIC	W
ψ (G+TRI), p(SSES+TRI+S)	0.91 \pm 0.37	8.00 \pm 3.09	0.73 \pm 0.34	-	-	251.54	0.00	0.49
ψ (G+S), p(SSES+TRI+S)	-1.19 \pm 0.23	0.21 \pm 0.09	-	1.06 \pm 0.51	-	252.56	1.02	0.29
ψ (G), p(SSES+TRI+S)	0.63 \pm 0.09	0.29 \pm 0.16	-	-	-	254.86	3.32	0.09
ψ (Global), p(SSES+TRI+S)	-0.61 \pm 0.47	8.78 \pm 2.81	-3.70 \pm 1.15	2.31 \pm 1.20	-3.70 \pm 1.151	254.97	3.43	0.09
ψ (SES+S), p(SSES+TRI+S)	-1.26 \pm 0.24	-	-	0.39 \pm 0.51	-0.45 \pm 0.43	258.09	6.55	0.02
ψ (S), p(SSES+TRI+S)	-1.19 \pm 0.22	-	-	0.38 \pm 0.51	-	260.70	9.16	0.01
ψ (.), p(.)	0.29 \pm 0.16	-	-	-	-	262.20	10.66	0.00

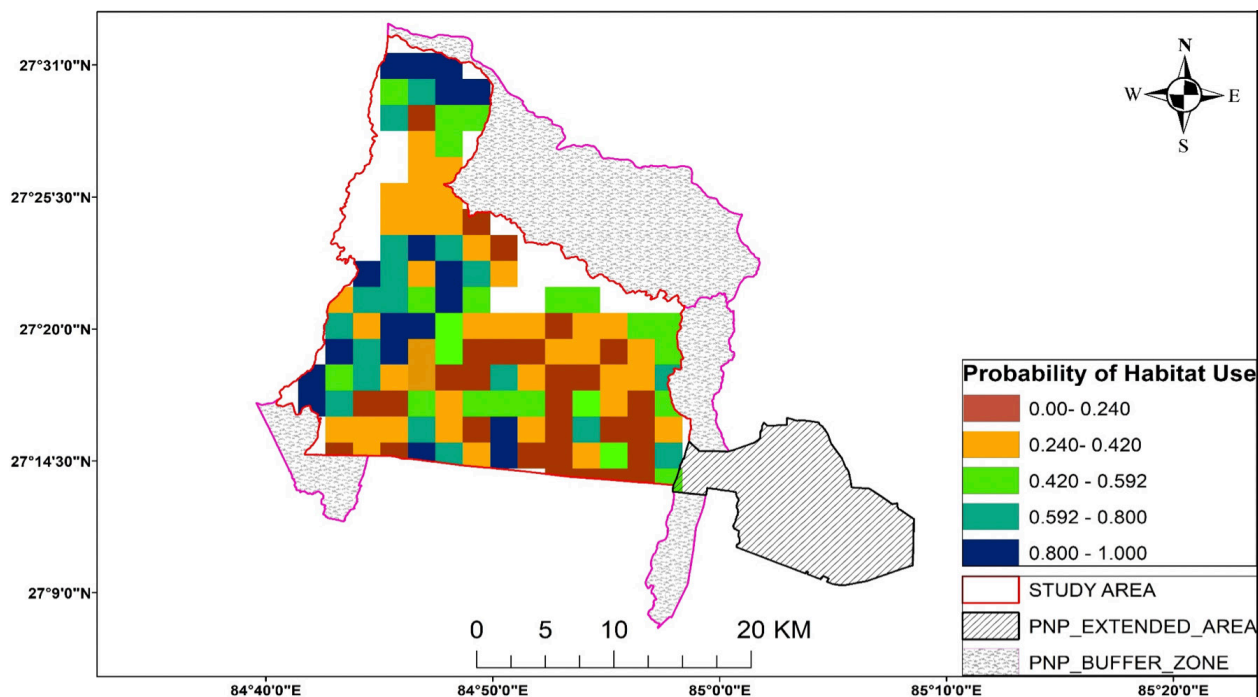


Figure 4. Map showing the probability of habitat-use by Dholes in Parsa National Park at grid level.

Probability of habitat-use

We used top ranked model for detectability, ψ (Global) p (SES+TRI+S) to model fine-scale habitat-use (ψ). Among a set of seven candidate occupancy models, the model with ψ as a function of grassland and terrain ruggedness index, ψ (G+TRI) and p as a function of stream/exposed surfaces, terrain ruggedness index and Sambar, p (SES+TRI+S) best fit the data. Our model estimate of the probability of habitat-use (ψ) was 0.47 ± 0.27 , more than double the naïve occupancy estimate. The model indicated that the habitat-use was strongly associated with grassland availability ($\beta_G = 8.00 \pm 3.09$), terrain ruggedness index ($\beta_{TRI} = 0.73 \pm 0.34$) and prey species (Sambar) presence ($\beta_S = 1.06 \pm 0.51$) but had strong negative association with streams/exposed surfaces ($\beta_{SES} = -0.45 \pm 0.43$) as shown in Table 2. We model averaged across a set of models for estimating probability of habitat-use (Figure 4).

DISCUSSION

Our study provides insights into the factors affecting spatial distribution and habitat-use by Dholes at a fine spatial scale in PNP, Nepal using camera-trap data. The survey was conducted primarily to monitor Tigers. Hence, probable bias in camera-traps placement towards Tigers cannot be denied. However, the camera-

traps also produced a good number of Dhole detections ($n = 63$), which were used in this study. It provides an opportunity to obtain information on Dhole but our results may have underestimated the probability of habitat-use and detection of Dholes in PNP due to the bias in the placement of camera traps. Positive association of Dholes with grassland can be explained by the availability of prey species in higher density and ease of predation in grasslands. Prey populations of large carnivores occur in a wide range of habitats including grasslands (Karanth et al. 2009; Wegge et al. 2000; Dinerstein 1980, 1979; Schaller 1967). Our findings are similar to those reported by Jenks et al. (2012) and Grassman et al. (2005) in Thailand. The inter-specific competition like tigers and leopards, both of which typically prefer lowland areas, may have pushed the dholes in rugged areas in Siwalik hills (Reddy et al. 2019; Dhakal et al. 2014; Venkataraman 1995; Johnsingh 1983; Wood 1929). Another reason may be due to year-round availability of their preferred prey species (Sambar) in these hills (Thapa & Kelly 2016; Shrestha 2004; McKay & Eisenberg 1974). Moreover, the rugged areas (Churia hills) of Parsa are generally distant from settlements and hence there is comparatively less disturbance. We also found strong positive association between Dhole habitat-use and Sambar presence similar to the findings of Jenks et al. (2012). This is probably because Sambar is one of the most preferred prey species of Dholes (Hayward et

al. 2014; Acharya et al. 2007). In Parsa, there are many streams flowing from the Siwalik hills towards south with large amount of sediments deposited in the streambeds. The streambeds are wide and remain dry most of the time (except flash floods during rainy season). Avoiding these streambeds and exposed surfaces by dholes can be linked to the low density of prey species and difficulty in predation as prey species can easily spot Dholes from a distance. Previous studies documented the Dhole habitat use increasing with an increasing distance from forest edge but we did not find the effect of distance to forest edge (Durbin et al. 2004; Punjabi et al. 2017; Aryal et al. 2015; Srivathsa et al. 2014; Khatiwada 2011). In a nutshell, our results show that dholes prefer rugged areas with grasslands and prey (Sambar). In addition to these findings, obtaining information on their population size and viabilities in the Terai Arc Landscape (that PNP is a part of) would be important from a conservation standpoint.

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