Copyright © 2017 by the IUCN/SSC Canid Specialist Group. ISSN 1478-2677

Research report

Distribution of the dhole in its northern range limits in the Western Ghats, India



Girish A. Punjabi^{1,2*}, Advait Edgaonkar³, Arjun Srivathsa^{2,4,5}, Shrikar Ashtaputre⁶ and M. K. Rao⁷

¹ Wildlife Research and Conservation Society, Flat No. 1A, Shriyog Society, 127/3 Sus Road, Pashan, Pune 411021, India. Email: <u>girisharjunpunjabi@gmail.com</u>.

² Researchers for Wildlife Conservation, National Centre for Biological Sciences, Tata Institute of Fundamental Research, GKVK, Bellary Road, Bengaluru 560065, India.

³ Indian Institute of Forest Management, PO Box 357, Nehru Nagar, Bhopal, Madhya Pradesh, India.

⁴School of Natural Resources and Environment, 103 Black Hall, University of Florida, Gainesville, Florida 32611, USA.

⁵ Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, University of Florida, Gainesville, Florida 32611, USA.

⁶E2, Lake Town, Bibwewadi. Pune 411037, India.

⁷ Office of the Additional Principal Chief Conservator of Forests (Wildlife West), Maharashtra Forest Department, Borivali (W) 400091, Maharashtra, India.

* Correspondence author

Keywords: Asian wild dog, camera-traps, Cuon alpinus, distribution, occupancy, Western Ghats.

Abstract

The dhole *Cuon alpinus* is an Endangered carnivore, whose population status is hitherto undetermined across most of its range. We update information on dhole distribution patterns in the northern Western Ghats, India, which forms the northern range limits for the species in the region. We use two sources of data: a landscape-scale (7000km²) habitat occupancy study (from 2010-11), and opportunistic camera-trap photographic records (2012-15) from the region. Estimated occupancy ($\hat{\Psi}$) was found to be 0.65 (± 0.18) in the surveyed landscape. Presence of protected areas, high percentage forest cover and availability of preferred prey (sambar *Rusa unicolor*, muntjac *Muntiacus muntjac*) were positive influences, while human disturbance showed a negative effect on dhole occupancy. The dhole was photo-captured in 14 camera-trap locations outside protected areas, of which 11 locations were outside the area surveyed in the occupancy study. The dhole has likely been extirpated from further north of our study landscape in the Western Ghats, indicating the need to corroborate range maps through renewed field assessments of this carnivore. Findings from this study can serve as a critical component in conservation of the dhole in one of their largest global populations.

Introduction

The dhole *Cuon alpinus* is a globally Endangered social carnivore distributed widely from Central Asia, India, to South-East Asia (Kamler et al. 2015). In the absence of reliable methods to determine their population sizes, expert opinion estimates suggest that the total population is 4,500-10,500, of which 949-2,215 mature individuals may currently survive in the wild, with the overall population declining across its geographic range (Kamler et al. 2015). Prey depletion and loss of habitat seem to be the most prominent threats to dholes, and persecution (retaliatory killing) may still be a threat in large parts of its range (Kamler et al. 2015). While intraguild predation and competition with tigers *Panthera tigris* may potentially suppress small, insular dhole

The following is the established format for referencing this article:

Punjabi, G.A., Edgaonkar, A., Srivathsa, A., Ashtaputre, S. and Rao, M.K. 2017. Distribution of the dhole in its northern range limits in the Western Ghats, India. *Canid Biology & Conservation* 20(3):7-13. URL: http://www.canids.org/CBC/20/dhole_in_western_ghats.pdf.

populations (Steinmetz et al. 2013), this may not hold true in other areas where prey densities are sufficiently high (Karanth and Sunquist 2000). Besides, dholes may continue to persist in areas where tigers are absent or their densities are low, given adequate habitat and prey availability.

Recognising the dhole's precarious state and concurrent threats, studies have examined the distribution (Jenks et al. 2012), patterns and determinants of occurrence (Srivathsa et al. 2014) and ecology (Acharya et al. 2010, Kamler et al. 2012, Steinmetz et al. 2013, Hayward et al. 2014) of this threatened carnivore. Recent assessments aimed at examining dhole distributions across large geographic areas (Karanth et al. 2009, Jenks et al. 2012) have relied on predictive modelling at coarse spatial scales. Although these are important in determining geographic range limits of the species, such assessments need to be complimented by landscape-scale studies so as to facilitate identification of meta-population structure, population sources and sinks, functional landscape connectivity and threats, all of which are immensely useful for conservation planning.

India appears to be a stronghold for dhole populations and the Western Ghats might hold the largest dhole meta-population globally (Kamler et al. 2015). Yet, information on the status, population and distribution of the species in certain parts of the Western Ghats is limited, especially the northern regions. This study aimed to update and understand distribution patterns of the dhole in its northern range limit in the Western Ghats. First, we used a landscape-scale (7,000km²) study conducted in 2010-11 to assess ecological and anthropogenic correlates of dhole habitat occupancy. Using predicted probability of occurrence values we created a habitat occupancy map of dholes for this region. Next, we identified areas of dhole presence outside this intensively surveyed (7,000km²) region using point locations obtained from opportunistic camera-trap surveys (2012-15). Given the precarious status of the dhole, we used both sources of data to create a distribution map of dholes in the northern Western Ghats landscape to update current information and highlight data gaps in the known distribution of this species.

Methods

Study area

The Western Ghats in India is a global biodiversity hotspot (Myers et al. 2000) and a priority landscape for large carnivore conservation (Karanth et al. 2011). The study landscape (c. 7,000km², Figure 1) in the State of Maharashtra is a linear mountain chain, which includes three protected areas (henceforth PAs). Koyna Wildlife Sanctuary and Chandoli National Park have been designated as the Sahyadri Tiger Reserve (1165.57km²), where levels of protection have been enhanced considerably since its declaration in the year 2010. The third, Radhanagari Wildlife Sanctuary (350km²), is located c. 60km south of the Sahyadri Tiger Reserve. The study area comprises of reasonably large forest regions, which are more or less structurally connected throughout the landscape. Regions beyond our study area to the West and East are severely fragmented forests or completely human-modified, thus holding little potential for either current presence or for future dhole population recovery. Human population densities vary from 200 people per km² to 460 people per km² across the study landscape.

Occupancy study

For assessing dhole occupancy at the landscape-level (2010-11), we followed the sampling design as described in Karanth et al. (2011) and Srivathsa et al. (2014), by overlaying square-shaped grid-cells, each measuring 188km² in area. Major forest trails and dirt roads were sampled continuously for fresh signs of dhole in 37 grid cells, since trails are used as travel routes, for marking territory and for defecation (Kamler et al. 2012, Srivathsa et al. 2014). Two teams, of two-three surveyors each, sampled trails on foot, searching for fresh carnivore signs; 890km were walked from May 2010 to February 2011. We refer the reader to Karanth et al. 2011 for more details on sampling design used in this landscape-scale study.



Figure 1. The study landscape in the northern Western Ghats indicating protected areas, array of 188km² grid cells sampled, and overall forest cover in the five districts of Maharashtra State, India.

Fresh signs were identified based on appearance, size and presence of secondary signs (Cohen et al. 1978). We used our discretion in recording signs which were relatively fresh and could be accurately identified. Signs such as footprints may be confused with sympatric species (e.g. domestic dog, golden jackal Canis aureus), therefore we only recorded signs when we were certain about dhole identity based on species behaviour (e.g. communal latrines). Each field team comprised of one trained field researcher, ensuring consistency in identification of animal signs. We also recorded detection/non-detection of ungulates or their signs at every 100m replicate segment of the sampling trail to be used as covariates, since they are principal prey of dholes (Karanth and Sunquist 1995, Andheria et al. 2007). Wild ungulates recorded were gaur Bos gaurus, sambar Rusa unicolor, Indian muntjac Muntiacus muntjac, wild pig Sus scrofa, and four-horned antelope Tetracerus quadricornis. Although elsewhere chital Axis axis is a preferred prey species of the dhole, in the Western Ghats (Srivathsa et al. 2014) we did not find their signs in our surveys, and it is unlikely that they occurred in substantial densities anywhere in the study area during the survey. Signs of domestic livestock (cattle, buffalo and goat) were also recorded at every 100m replicate segment on sampling trials.

We examined the influence of percentage forest cover, presence of protected area (PA), index of all wild prey abundance, index of preferred prey abundance (sambar and muntjac, from Kamler et al. 2012, Hayward et al. 2014), and index of livestock abundance (as a surrogate for human disturbance, from Srivathsa et al. 2014) on occupancy of dholes in the landscape. Index of livestock abundance, which we treated as a surrogate for human disturbance, was expected to have a negative effect on dhole occupancy, whereas all other covariates were expected to have a positive effect. Given limitations of sample size, we did not examine patterns of co-occurrence with sympatric large carnivores (tiger, leopard Panthera pardus) at this large scale. We calculated indices for all prey species, preferred prey and livestock abundance as a ratio of 1km replicates with signs, divided by the total effort (in km) in each grid cell. All continuous covariates were standardized to z-scores and used as site-specific covariates for species occupancy. Presence of PA was denoted as a binary (1/0) covariate to represent presence or absence of PA in a grid cell. Detection histories were formed by combining detections and non-detections of dhole signs for 1km spatial replicates of each grid cell. We used the Markovian model (Hines et al. 2010) to estimate probability of site-level occupancy ($\hat{\Psi}$), replicate-level detection probability given presence (\hat{p}_t), and other key parameters of interest, as surveys involved spatially dependent replicates. Details on model parameters, definitions and their estimation are in Hines et al. (2010) and Karanth et al. (2011).

Dhole in Western Ghats

We first performed Pearson's correlations among covariates, using the 'Hmisc' package (Harrell Jr. et al. 2013) in R (R Core Team 2013). This was important to avoid the effects of severe multicollinearity among covariates, which can affect estimation of model parameters when used together in the same model. Similar to Karanth et al. (2011), we first fixed a model structure for the detection probability component of the Markovian model. Due to limitations of sample size we only examined the effect of index of livestock abundance on detection probability, as the presence of livestock trampling and defecation on trails could potentially influence our detection of dhole signs. We used a global occupancy model and two alternative structures for detection probability, one with index of livestock abundance and the other with intercept-only (no covariate) to decide the structure for detection probability. Based on difference in Akaike's Information Criterion scores (Δ AIC) and Akaike weights (w_i), we chose the covariate structure for detection probability, which remained unchanged during further analysis of habitat occupancy.

Once the covariate structure for detection probability was fixed, we tested a set of 13 candidate models to examine the effect of ecological and anthropogenic correlates on dhole occupancy. We performed all analyses in Program PRESENCE (version 9.3, Hines 2006) using the single-season correlated detections model (Hines et al. 2010) and evaluated candidate models using the Akaike's Information Criterion (AIC) and model weights. $\hat{\beta}$ -coefficients of covariates from top models (cumulative $w_i > 0.90$) were used to determine the effect of important correlates on dhole occupancy. Goodness of fit for candidate models were not assessed as the feature is currently not available for this model. A map of dhole occupancy was generated in Quantum GIS v. 2.2.0 (QGIS Development Team 2014) using model-averaged $\hat{\Psi}$ values from the top models.

Camera-trap surveys

Camera-traps were opportunistically placed at multiple sites in the study landscape for four years (2012-15) to understand large carnivore presence outside protected areas. Camera-traps (Model: Deer Cam DC 300, USA) were deployed in 21 locations from December 2012 to March 2013, in 43 locations (Model: Moultrie M-880c, USA) during May and June 2014, and in 41 locations (Models: Moultrie M-880c, Cuddeback C2 (WI, USA), Bushnell Nature View HD Max (KS, USA)) from February to May 2015. Sites were selected based on a preliminary survey of trails and sign encounters in these areas. Cameras were either placed singly or in pairs, depending on the width of the trail and were kept active throughout the day, and each 24-hr period was considered as one camera day. An effort was made to deploy each camera for a minimum of one-week at a site. In some cases, this was not possible due to excessive livestock movement

which exhausted camera films (in 2012-13), or camera theft and malfunctioning (all years). Maps of camera-trap locations where dholes were photographed were created in Quantum GIS v. 2.2.0 (QGIS Development Team 2014).

Distribution map

Using Quantum GIS, a minimum convex hull or polygon (MCP) was created around dhole presence locations obtained from camera-traps. This MCP was overlaid with the dhole habitat occupancy map and the outermost boundaries of both layers were joined to delineate the distribution of the dhole in the region. This distribution was then compared with the coarse-scale distribution map available from the IUCN Red List species assessment for dhole (Kamler et al. 2015) to identify data gaps for the northern Western Ghats region.

Results

Of the two models used for detection probability (p_t) of signs, the null model received almost 70% of the Akaike weight ($w_i = 0.71$, Table 1). The model with index of livestock abundance for p_t ranked lower; but since the difference in AIC scores was small (Δ AIC < 2) we used index of livestock abundance as a covariate so as to account for any heterogeneity in detection probability.

A total of 13 *a priori* candidate models were used to assess the effect of ecological and anthropogenic covariates on dhole occupancy. Two models were removed from this candidate set during analysis due to convergence problems. Of the remaining 11 models, eight models gathered most support (>90% of w_i , Table 2).

 $\hat{\beta}$ -coefficient values indicated percentage forest cover, presence of PA and index of preferred prey to be positive influences (showing positive slopes) on dhole occupancy, while index of livestock abundance, used as a surrogate for human disturbance, showed a negative influence (negative slope) on dhole occupancy (Table 3). All coefficients showed high standard errors making them less reliable in explaining dhole occupancy at the landscape scale. However, the direction of the slope values was consistent with our expectations for these variables, indicating that these values are still ecologically meaningful. The influence of all prey species abundance on dhole occupancy was unreliable at this spatial scale, as the $\hat{\beta}$ -coefficient for the covariate showed probabilities of dhole occupancy across sampling units in the study landscape are shown in Figure 2.

Table 1. Alternate models in explaining detection probability for dhole in the northern Western Ghats, India, ranked using Akaike's Information Criterion (AIC), along with difference in Akaike scores (Δ AIC), Akaike weights (w_i) and number of parameters.

 ψ = probability of site-level occupancy; θ_0 = probability of presence on replicate, given absence on previous replicate, θ' = probability of presence on replicate, given presence on previous replicate; p_t = replicate-level detection probability, given presence; F.cov = percentage forest cover; PA = Presence of protected area; lvs = index of livestock abundance; pref_prey = index of preferred wild prey abundance.

S. No.	Model	AIC	ΔAIC	W i	К
1	$ψ$ (F.cov + PA + lvs + pref_prey), $θ_0$ (.), $θ'$ (.), p_t (.)	428.23	0	0.71	9
2	ψ (F.cov + PA + lvs + pref_prey), θ_0 (.), θ' (.), p_t (lvs)	430.06	1.83	0.29	10

Table 2: Most-supported models (in bold) used to assess the effect of environmental correlates on occupancy of the dhole in the northern Western Ghats, India, ranked using Akaike's Information Criterion (AIC), along with difference in Akaike scores (Δ AIC), Akaike weights (w_i) and number of parameters.

 ψ = probability of site-level occupancy; θ_0 = probability of presence on replicate, given absence on previous replicate, θ' = probability of presence on replicate, given presence on previous replicate; p_t = replicate-level detection probability, given presence; F.cov = percentage forest cover; PA = Presence of protected area; all_prey = index of all wild prey abundance; lvs = index of livestock abundance; pref_prey = index of preferred wild prey abundance.

S. No.	Model	AIC	ΔAIC	Wi	К
1	ψ (F.cov), θ ₀ (.), θ' (.), p _t (lvs)	432.89	0	0.29	7
2	ψ (PA), θ ₀ (.), θ' (.), p _t (lvs)	433.76	0.87	0.18	7
3	$ψ$ (F.cov + all_prey), $θ_0$ (.), $θ'$ (.), p_t (lvs)	434.69	1.8	0.12	8
4	ψ (F.cov + pref_prey), θ ₀ (.), θ' (.), <i>p</i> t (lvs)	434.89	2	0.10	8
5	$ψ$ (PA + pref_prey), $θ_0$ (.), $θ'$ (.), p_t (lvs)	435.75	2.86	0.07	8
6	ψ (lvs), θ ₀ (.), θ' (.), p _t (lvs)	435.81	2.92	0.07	7
7	ψ (.), θ ₀ (.), θ' (.), p _t (lvs)	436.17	3.28	0.06	6
8	$ψ$ (lvs + all_prey), $θ_0$ (.), $θ'$ (.), p_t (lvs)	436.61	3.72	0.04	8
9	ψ (lvs + pref_prey), θ_0 (.), θ' (.), p_t (lvs)	437.4	4.51	0.03	8
10	$ψ$ (pref_prey), $θ_0$ (.), $θ'$ (.), p_t (lvs)	438.08	5.19	0.02	7
11	ψ (all_prey), θ_0 (.), θ' (.), p_t (lvs)	438.16	5.27	0.02	7

Table 3. β -coefficient parameter estimates and associated standard errors (SE) of covariates from top models used to explain dhole occupancy in the northern Western Ghats, India.

int = Intercept; F.cov = percentage forest cover; PA = Presence of protected area; all_prey = index of all wild prey abundance; pref_prey = index of preferred wild prey abundance; lvs = index of livestock abundance.

Models	$\hat{\boldsymbol{\beta}}_{\text{int}}$ (SE)	$\widehat{\boldsymbol{\beta}}_{\text{F.cov}}$ (SE)	$\hat{\boldsymbol{\beta}}_{PA}$ (SE)	$\widehat{\boldsymbol{\beta}}_{\text{all_prey}}$ (SE)	$\hat{\boldsymbol{\beta}}_{\text{pref_prey}}$ (SE)	$\hat{\boldsymbol{\beta}}_{\text{lvs}}$ (SE)
Model 1	0.73 (0.67)	1.38 (0.76)				
Model 2	-0.03 (0.61)		2.38 (1.72)			
Model 3	0.66 (0.63)	1.34 (0.71)		0.24 (0.52)		
Model 4	0.72 (0.68)	1.38 (0.76)			0.01 (0.54)	
Model 5	-0.02 (0.63)		2.46 (2.24)		0.06 (0.72)	
Model 6	1.03 (1.13)					-1.12 (1.16)
Model 7	0.99 (0.72)					
Model 8	1.25 (1.03)			-0.84 (0.93)		-2 (1.42)



Figure 2: Estimated model-averaged dhole occupancy probability (2010-11) in the northern Western Ghats landscape in the State of Maharashtra, India. Occupancy probabilities have been divided into five classes to show variation in the landscape.

Mean $\widehat{\Psi}$ for dholes in the landscape was estimated to be 0.65 (± 0.18), while the naive occupancy estimate (without accounting for imperfect detection) was 0.54. Probability of presence on replicate given absence on previous replicate ($\widehat{\theta}_0$), probability of presence on replicate given presence on previous replicate ($\widehat{\theta}'$), and replicate-level detection probability given presence (\widehat{p}_i) were found to be 0.14 (± 0.07), 0.76 (± 0.26), and 0.27 (± 0.04) respectively.

A total effort of 1,699 camera days (105 locations) was invested from 2012 to 2015 outside protected areas (317 camera days, 521 camera days, and 861 camera days in 2012-13, 2014, and 2015 respectively). Eleven cameras were lost due to theft during this period. Dholes were captured in 14 locations (Figure 3), with observations of one to three adults/sub-adults in the photographs (Figure 4); one of adults with two pups indicating presence of breeding individuals (Figure 5). A pair of dholes with seven pups was taken using a hand-held camera in the study area (Figure 6). Eleven of the 14 camera-traps where dholes were photo-captured were outside the area surveyed in the occupancy study.

Dhole distribution is indicated in a coarse-scale IUCN Red List map, overlaid with the distribution map from the current field study in the northern Western Ghats (Figure 3. Google Earth map available at Figure 7).







Figure 4: Camera-trap photograph taken on 28 December 2012 at 17:28 shows two adult dholes with a sub-adult in the northern Western Ghats, India.



Figure 5. Camera-trap photograph of adult dholes with pups taken on 5 April 2015 at 18:25, indicating presence of breeding individuals in the northern Western Ghats, India.



Figure 6. Photograph showing two adult dholes and seven pups feeding on a sambar in the northern Western Ghats region, India. Taken using a hand-held camera on 12 March 2016 by Akshata Karnik.

Figure 7. Google Earth map of dhole distribution in the northern Western Ghats landscape in India; available at <u>https://drive.google.com/open?id=11a_5WcFuwfd0aXmQIB06iVwodzE&usp=sharing</u>

Discussion

Landscape-level field studies are important for understanding drivers of local extinctions, source-sink dynamics and persistence of species (Jones 2011). Our study estimated dhole occupancy to be moderately high (0.65 ± 0.18), with dholes occupying *c*. 2,720km² of the total forest habitat (4,183km²) in the surveyed region of the northern Western Ghats landscape. Together with earlier assessments in the adjacent State of Karnataka (Srivathsa et al. 2014), this accounts for *c*. 16,900km² of dhole-occupied habitats in the Western Ghats. Dholes were also photographed in 14 camera-trap stations outside of PAs, of which 11 stations were located beyond the surveyed area for the occupancy study. While this indicates the importance of conserving habitats outside PAs for the wide-ranging dhole, it also underscores the need for more assessments in potential habitats in the northern Western Ghats region, which stand the risk of being diverted for commercial use.

Our findings point to the positive role of PAs, forest cover and availability of preferred prey (sambar, muntjac) on dhole occupancy in the landscape. A positive effect of preferred prey also suggests that dholes likely select habitats with higher densities of sambar (Jenks et al. 2012, Kamler et al. 2012) and muntjac (Kamler et al. 2012). Chital is a preferred prey species of dhole (Karanth and Sunquist 1995, Andheria et al. 2007), but given their near absence in our study area, other dominant ungulates such as sambar and muntjac serve as primary prey species (as in south-east Asia, Kamler et al. 2012). Young gaur may be hunted by a pack of dholes, but adults are above the preferred prey weight range (130-190kg, Hayward et al. 2014).

We found that anthropogenic disturbance (indicated by index of livestock abundance as a surrogate) had a negative influence on dhole presence. Studies have examined the deleterious effects of freegrazing livestock and anthropogenic hunting on wild ungulate populations, which are important prey for dholes (Madhusudan 2004, Madhusudan and Karanth 2002). Dholes may also avoid potential interactions with humans in the day-time in areas where livestock is often accompanied by herders.

Habitats connecting Sahyadri Tiger Reserve and Radhanagari Wildlife Sanctuary in the State of Maharashtra to protected habitats in the States of Karnataka and Goa also support high occupancy of dhole (0.5-0.9). However, many forest habitats where the dhole occurs in the region have been earmarked for development projects such as wind farms, dams, hill stations, and mining. Such large-scale infrastructure projects and associated land-use changes would negatively impact this wide-ranging threatened carnivore due to further loss and fragmentation of intact forest habitats. Our study therefore presents useful information on dhole distribution in the northern Western Ghats. Presently, the Red List assessment (Kamler et al. 2015) shows a wide distribution range of the dhole in the northern Western Ghats, but it is likely that dholes only occupy smaller habitat patches within this plausible range. Results from our study could help prioritize specific areas for dholes, especially outside PAs.

It is important to corroborate coarse-scale geographic range-limits (Kamler et al. 2015) with field studies such as ours. The presence of dhole occurring in Bhimashankar (formerly Bhima Shancar, Sykes 1834) is a case in point. Bhimashankar is now a PA (130km²) located in the Western Ghats, c. 110km from the northernmost camera-trap location in Wai region in our study (see Figure 3). The recent IUCN assessment shows Bhimashankar as part of the distribution range of the dhole (Kamler et al. 2015). Presence of dholes was recorded in Bhimashankar almost two centuries ago, as Sykes (1834) noted that the tribal inhabitants in the region were "quite aware of the existence of troops of these Wild dogs"; however the species is now locally extinct (pers. obs.) and there are no recent confirmed records (published or verbal) of the dhole from the PA or neighbouring regions. Coupled with factors such as prey depletion and local hunting, we believe that isolation of Bhimashankar due to loss in forest connectivity (Panigrahy et al. 2010) is a plausible cause for dhole extinction in the Bhimashankar region. This underscores the need for periodic field assessments to address such data gaps and present a more realistic picture of dhole distribution throughout the species' known range.

Based on this study and similar assessments in the region, we emphasize the need for protecting remnant forest habitats against environmentally-detrimental development activities to conserve dhole populations. Hunting can deplete preferred ungulate prey such as sambar and muntjac (Madhusudan and Karanth 2002) and efforts should be directed by management agencies towards protecting these species in remnant habitats. Given their wide-ranging habits, dholes require larger zones than most other carnivores (Woodroffe and Ginsberg 1998, Kamler et al. 2012); therefore a long-term conservation strategy needs to include protected enclaves functionally-connected by habitats conducive for dhole persistence and dispersal.

Acknowledgements

We thank the Maharashtra State Forest Department for permissions and support. We are grateful to the Critical Ecosystem Partnership Fund (CEPF) and Ashoka Trust for Research in Ecology and the Environment (ATREE) for funding. The Centre for Wildlife Studies (Bengaluru) helped AE with planning the occupancy study and with permits. Project administration was supported by WRCS in 2013-14, and by V. Athreya, WCS India, CWS (Bengaluru), and Norwegian Institute for Nature Research (NINA), and its co-partners under the UN Program IPBES in 2012-13. AS was supported by Wildlife Conservation Society's Christensen Conservation Leaders Scholarship and Wildlife Conservation Network's Sidney Byers Fellowship. We thank D. Shinde, A. Kulkarni, S. Patil, R. Jhadhav, and many volunteers and local villagers who assisted us with fieldwork.

References

Acharya, B.B., Johnsingh, A.J.T. and Sankar, K. 2010. Dhole telemetry studies in Pench Tiger Reserve, Central India. *Telemetry in Wildlife Science* 13: 68–79.

Andheria, A.P., Karanth, K.U. and Kumar, N.S., 2007. Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *Journal of Zoology* 273: 169–175.

Cohen, J.A., Fox, M.W., Johnsingh, A.J.T. and Barnett, B.D. 1978. Food habits of the dhole in South India. *Journal of Wildlife Management* 42: 933–936.

Harrell Jr, F.E., Dupont, C. et al. 2013. Hmisc: Harrell Miscellaneous. R package version 3.13-0. http://CRAN.R-project.org/package=Hmisc.

Hayward, M.W., Lyngdoh, S. and Habib, B. 2014. Diet and prey preferences of dholes (*Cuon alpinus*): dietary competition within Asia's apex predator guild. *Journal of Zoology* 294: 255–266.

Hines, J.E. 2006. PRESENCE- Software to estimate patch occupancy and related parameters. USGS-PWRC. <u>http://www.mbr-pwrc.usgs.gov/software/presence.html</u>.

Hines, J.E., Nichols, J.D., Royle, J.A., MacKenzie, D.I., Gopalaswamy, A.M., Kumar, N.S. and Karanth, K.U. 2010. Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications* 20: 1456–1466.

Jenks, K.E., Kitamura, S., Lynam, A.J., Ngoprasert, D., Chutipong, W., Steinmetz, R., Sukmasuang, R., Grassman, L.I., Cutter, P., Tantipisanuh, N., Bhumpakphan, N., Gale, G.A., Reed, D.H., Leimgruber, P. and Songsasen, N. 2012. Mapping the distribution of dholes, *Cuon alpinus* (Canidae, Carnivora), in Thailand. *Mammalia* 76: 175-184.

Jones, J.P.G. 2011. Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology* 48: 9–13.

Kamler, J.F., Johnson, A., Vongkhamheng, C. and Bousa, A. 2012. The diet, prey selection, and activity of dholes (*Cuon alpinus*) in northern Laos. *Journal of Mammalogy* 93: 627–633.

Kamler, J. F., Songsasen, N., Jenks, K., Srivathsa, A., Li, Sheng and Kunkel, K. 2015. *Cuon alpinus*. The IUCN Red List of Threatened Species 2015: e.T5953A72477893. <u>http://dx.doi.org/10.2305/IUCN.UK.2015-</u> <u>4.RLTS.T5953A72477893.en</u>. Downloaded on 25 Jan 2017.

Karanth, K.U., Gopalaswamy, A.M., Kumar, N.S., Vaidyanathan, S., Nichols, J.D. and MacKenzie, D.I. 2011. Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys. *Journal of Applied Ecology* 48: 1048–1056.

Karanth, K.K., Nichols, J.D., Hines, J.E., Karanth, K.U. and Christensen, N.L. 2009. Patterns and determinants of mammal species occurrence in India. *Journal of Applied Ecology* 46: 1189–1200.

Karanth, K.U. and Sunquist, M.E. 1995. Prey selection by tiger, leopard and dhole in tropical forests. *Journal of Animal Ecology* 64: 439–450.

Karanth, K.U. and Sunquist, M.E. 2000. Behavioural correlates of tiger (*Panthera tigris*), leopard (*Panthera pardus*), and dhole (*Cuon alpinus*) in Nagarhole, India. *Journal of Zoology* 250: 255–265.

Madhusudan, M.D. 2004. Recovery of wild large herbivores following livestock decline in a tropical Indian wildlife reserve. *Journal of Applied Ecology* 41: 858–869.

Madhusudan, M.D. and Karanth, K.U. 2002. Local hunting and the conservation of large mammals in India. *Ambio* 31: 49–54.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–8.

Panigrahy, R.K., Kale, M.P., Dutta, U., Mishra, A., Banerjee, B. and Singh, S. 2010. Forest cover change detection of Western Ghats of Maharashtra using satellite remote sensing based visual interpretation technique. *Current Science* 98: 657–664. QGIS Development Team. 2014. QGIS Geographic Information System. Open Source Geospatial Foundation Project. <u>http://qgis.osgeo.org/</u>.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Srivathsa, A., Karanth, K.K., Jathanna, D., Kumar, N.S. and Karanth, K.U. 2014. On a dhole trail: examining ecological and anthropogenic correlates of dhole habitat occupancy in the Western Ghats of India. *PloS one* 9:e98803.

Steinmetz, R., Seuaturien, N. and Chutipong, W. 2013. Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation* 163: 66–78.

Sykes, W.H. 1834. Description of the wild dog of the Western Ghats. *Transactions of the Royal Asiatic Society of Great Britain and Ireland* 3: 405–411.

Woodroffe, R. and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280: 2126–2128.

Biographical sketch

Girish Punjabi is a conservation biologist, whose interests lie in landscape conservation, carnivore ecology and human-wildlife interactions.

Advait Edgaonkar is an Assistant Professor at the Indian Institute of Forest Management.

Arjun Srivathsa studies carnivores, with particular focus on wild canids, population ecology and intra-guild interactions in tropical forest systems.

Shrikar Ashtaputre is a software engineer by training, but passionate about wildlife research and conservation of the Western Ghats.

M.K. Rao is an Indian Forest Service officer with the Maharashtra Forest Department. He has a keen interest in large mammal conservation.