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Determinants of dry season habitat use by Asian elephants in the Western Ghats of India

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Keywords

occupancy modelling; correlated detections; Bandipur; Nagarahole; Normalized Difference Vegetation Index; large herbivores; dry season.

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Abstract

Large herbivores respond to seasonal changes in resource availability through habitat selection. Understanding variations in habitat choice is crucial for targeting conservation efforts, particularly for endangered, wide-ranging species, such as the Asian elephant. We assessed patterns and determinants of elephant habitat use during the dry season, a period of resource limitation in tropical deciduous forests, in the Western Ghats of Karnataka, India. We collected detection/non-detection data on elephant signs under an occupancy sampling framework, using spatially replicated surveys on foot along forest trails to estimate probabilities of habitat use by elephants. Each of our 97 sites (sampling units) was a grid cell of 11.75 km² area. Data were analysed using an occupancy model, which estimated detection probabilities for signs, while explicitly addressing the potential spatial dependence between sign detections on adjacent replicates. Using covariates that are likely to influence resource use, we made ecological predictions about dry season habitat use by elephants across the study area of 1850 km². The site-level probabilities of habitat use by elephants ranged from $\hat{\psi}(SE[\hat{\psi}]) = 0.04(0.15)$ to $0.99(0.01)$. The estimated replicate level detection probability was $\hat{p}_r(SE[\hat{p}_r]) = 0.67(0.06)$. We found that distance to rivers was the best predictor of elephant habitat use, in dry season, demonstrating the overarching importance of riparian habitats in the landscape for the species. Artificial water holes established by wildlife managers do not appear to influence elephant habitat use, which is likely a result of abundant and near-uniform distribution of such water holes across the study area. The sign survey-based occupancy modelling approach provides a basis for reliable cost-effective assessment of spatial distribution and habitat use by elephants and other large herbivores. Such assessments are essential for effective conservation management of large herbivores.

Introduction

Large herbivores are dependent on vegetation which shows considerable seasonal flux in quality and availability across the world. Although more pronounced in the temperate regions (Moen, Andersen & Illius, 2006), seasonal fluxes in resource availability do occur even in tropical forests (Ahrestani *et al.*, 2012). Such seasonal variations in resources could potentially influence non-random spatial distribution patterns of large herbivores, which exhibit different strategies of habitat use (Moen *et al.*, 2006). Reliable predictions on seasonal distribution and patterns of habitat use by large herbivores are therefore a

pre-requisite for the conservation and effective management of such species. Such predictions enable habitat management for endangered species, such as the Asian elephant *Elephas maximus* that have large geographic ranges and undertake extensive annual movements within their home ranges (Desai & Baskaran, 1996).

Asian elephants are currently distributed across 13 countries. India harbours more than 50% of their extant populations distributed over 110 000 km² of highly heterogeneous habitats ranging from arid scrub to moist evergreen forests and human modified landscapes (Sukumar, 2003). A nation-wide assessment of elephants in India by Karanth *et al.* (2010) showed

that elephants face a high probability of local extinction. Currently, elephants persist in fragmented populations, largely confined to wildlife reserves (Karanth *et al.*, 2010).

In Africa, elephant–habitat relationships have been intensively researched, particularly for the savannah elephant *Loxodonta africana africana*. Many studies have examined factors influencing elephant distribution and habitat use (Redfern *et al.*, 2003; Chamailé-Jammes, Valeix & Fritz, 2007; Loarie, Van Aarde & Pimm, 2009). Insights from these studies have helped in management and conservation of the species in Africa. In contrast, management of elephants in India and elsewhere in Asia has been largely *ad hoc* rather than science based (Blake & Hedges, 2004). For example, although wildlife managers of Nagarhole and Bandipur National Parks in southwestern India allocate over 30% of their funds for habitat management schemes (Kumar, 2011), no study has examined how large herbivores like elephants and their habitats respond to such interventions.

Previous studies on Asian elephants have suggested that elephants respond to temporal and spatial availability of critical resources, such as forage and water (Sukumar, 1989), as well as varied levels of human impacts on their habitat (Desai & Baskaran, 1996). In tropical deciduous forests of India where elephants attain highest population density (Sukumar, 2003), forage and water required in large quantities for large herds may not always be available at the same location resulting in non-uniform patterns of space use (Sukumar, 1989). This is typical of the extended dry season from December to the pre-monsoon showers in April, during which primary production in forests is limited (Madhusudan, 2004). To understand variations in distribution patterns and space use of wild elephants in this resource-limiting period, rigorous field data modelled with ecologically meaningful predictor variables are needed.

Assessments of space use and habitat selection by elephants are largely based on telemetry studies (Desai & Baskaran, 1996; Fernando *et al.*, 2008) or visual re-sighting based records of identified individuals (Sukumar, 1989). In telemetry studies, the inferences are usually limited to few individuals in the case of bulls, or family units in case of the herds. Achieving sample sizes adequate to draw robust inference using these methods entail physical capture of many individuals, which is logistically challenging and expensive. Consequently, for population-level distribution and habitat use surveys, non-invasive survey methods that depend on detecting elephant signs are more often practical, especially in densely forested habitats (Goswami *et al.*, 2014)

Conventional methods based on animal sign surveys use the traditional ‘presence versus absence’ approach that does not

account for imperfect detection, an important source of bias in wildlife population studies (Williams, Nichols & Conroy, 2002). For elephants, Blake & Hedges (2004) suggest that official population estimates of elephants in India are highly unreliable, mainly because the survey methods employed tend to ignore the key problems of detectability and spatial sampling. In a recent paper, Jathanna *et al.* (2015a) recommend the use of visual detections of elephants along line transects to estimate abundance in key habitats under a distance sampling framework. To estimate elephant distribution and habitat use, however, occupancy sampling serves as a reliable and useful approach, as has been demonstrated in both Africa and Asia (Buij *et al.*, 2007; Jathanna *et al.*, 2015a,b).

We examined the relative influence of key ecological covariates identified based on our prior knowledge of elephant biology, as predictors of dry season habitat use of the Asian elephant. Our study area was a well-protected, high-density elephant population in the Western Ghats of India. We used rigorously collected sign-survey field data together with remotely sensed covariate data to develop models under an occupancy-modelling framework to predict probability of habitat use as a function of measured covariates. Our *a priori* expectations on influence of covariates on habitat use by elephants are summarized in Table 1.

Materials and methods

Study site

The Brahmagiri–Nilgiri–Eastern Ghats elephant landscape encompasses an area over 12 000 km² in the Western and the Eastern Ghats in southern India. This landscape supports the single largest population of Asian elephants in the world (Sukumar, 2003; Rangarajan *et al.*, 2010). Within this landscape, our survey was conducted in Bandipur National Park, Nagarhole National Park and Devmachi, Periyapatna and Maukal territorial forest areas abutting Nagarhole, covering an area of 1850 km² in the state of Karnataka (Fig. 1).

The altitudinal range in the study area is about 400–1450 m s.l. and the average annual rainfall decreases from 1500 mm in the west to 600 mm in the east (Karanth & Sunquist, 1992). The vegetation varies from tropical moist deciduous, through tropical dry deciduous, to tropical dry thorn forest. The moist deciduous forests are classified as *Lagerstroemia-Tectona-Dillenia* series and the dry-deciduous forests are of *Anogeissus-Tectona-Terminalia* series (Karanth & Sunquist, 1992). A reservoir built across perennial river Kabini attracts

Table 1 Covariates and *a priori* predictions about their influence on probability of habitat use by elephants during the dry season

Covariate	Measurement of the variable	Predictions for probability of use
ΔNDVI	Vegetation productivity. Percentage change in mean Normalized Difference Vegetation Index (NDVI) per grid cell between November 2013 and March 2014.	Elephants would select areas that maintain high NDVI values with less seasonal variability
Distance to River	Euclidean distance from the grid cell centroid to the nearest river was used as a covariate	Elephants would select areas closer to rivers
Stagnant water	The number of water holes in a grid cell and first-order neighbouring cells was used as a covariate	Elephants would select sites that have more water holes

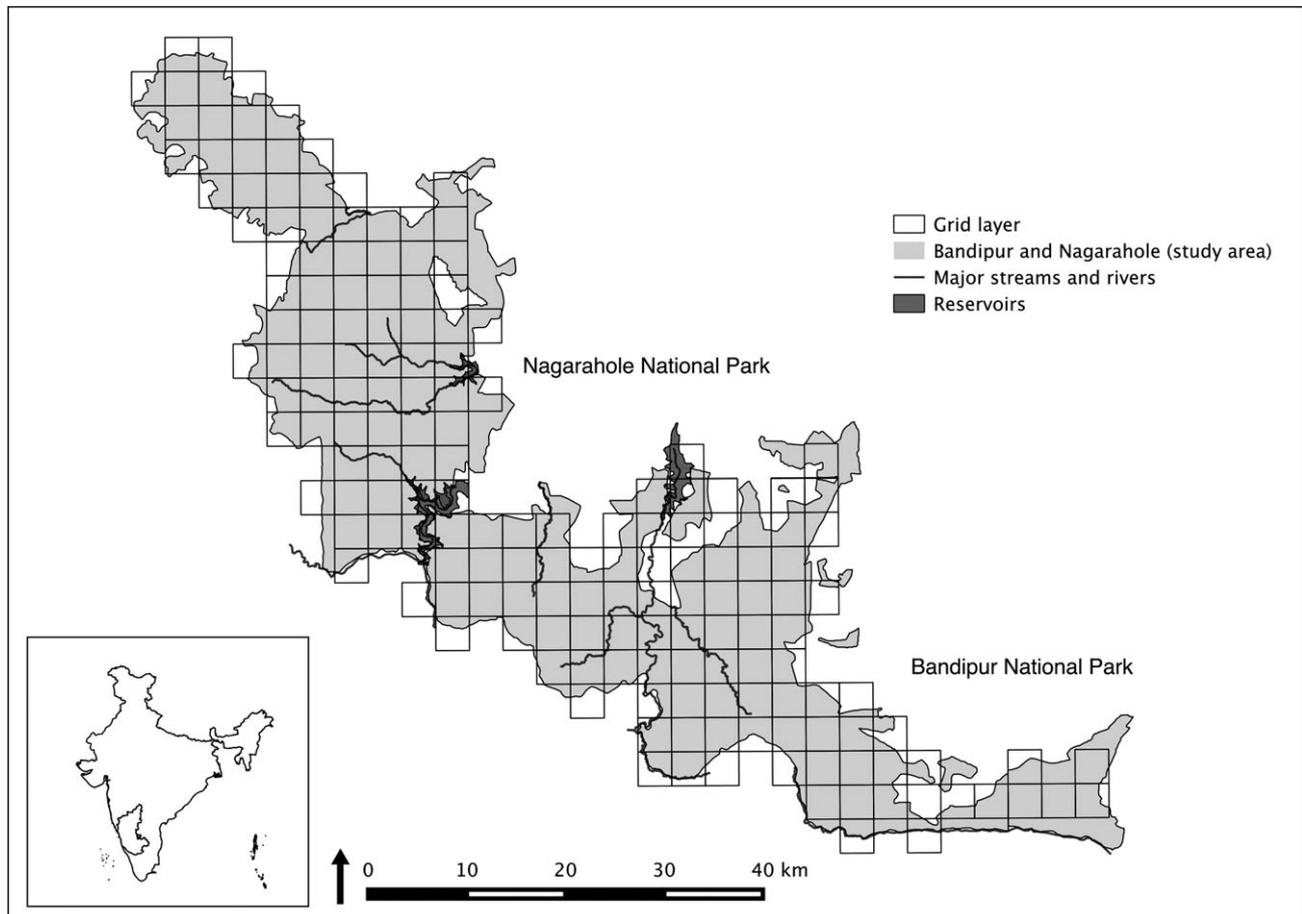


Figure 1 Study area and grid layer showing major rivers and reservoirs. Inset: India outline and Karnataka state in southwestern India where the study was conducted.

large summer aggregation of elephants on its highly productive pan when the water recedes (Madhusudan, 2004; Goswami, Madhusudan & Karanth, 2007). Nagarahole and Bandipur are protected areas with high elephant densities (Jathanna *et al.*, 2015a).

Survey design

We used a grid-based sampling approach to assess the key parameter of interest, probability of habitat use by elephants. This metric of ‘intensity of habitat use’ is measured at a scale smaller than the ‘true habitat occupancy’ metric, where the size of each sampled unit exceeds the maximum expected home-range size of the target species (MacKenzie *et al.*, 2006). Previous studies have estimated average home range of Asian elephants between 100 and 800 km², with considerable regional variation (see Fernando *et al.*, 2008).

For estimating intensity of habitat use, we used grid cells of size of 11.75 km² as a spatial sampling unit. We chose this grid cell size since it is sufficiently large to accommodate within-cell movement of elephant herds in search of their daily forage and water requirement. The estimated average daily

movement rate of Asian elephants is ≤ 3 km (Alfred *et al.*, 2012).

Occupancy surveys rely on either temporal or spatial replication to estimate detection probability. For logistical convenience, we preferred spatial replication and each replicate was sampled once (Kendall & White, 2009). In occupancy surveys, data collected from a fraction of sites within the sampling frame can be generalized for non-surveyed sites using covariate information (Mackenzie & Royle, 2005). We surveyed every alternate grid cell within the sampling frame (i.e. sampling fraction, $\alpha = 0.5$), and used relevant covariates (see Field sampling methods) to predict elephant habitat use to the non-surveyed grid cells.

Field sampling methods

The field survey of elephant signs was conducted during the dry months from December 2013 to March 2014. During this season, there is minimal rainfall induced variation in detectability of elephant dung. The relatively less dense undergrowth in the dry season also made it easier to visually detect elephant signs along the trails that we surveyed.

A field team comprising of three trained surveyors walked the forest trails and recorded presence of elephant signs and associated covariates at every 500 m interval, which we used as replicates for occupancy analyses. Each type of sign deposited by elephants was assigned '1' only once within 500 m segment when detected and non-detection of sign was recorded as '0'. Although we recorded elephant signs such as dung, tracks, and feeding signs for examining habitat use, we only used the dung detection data for occupancy analyses because of the ambiguity associated with assessing the freshness of other signs. In this manner, we avoided estimation biases arising from misclassification of signs. The dung boli encountered during the survey were classed by age following Karanth *et al.* (2012): Fresh dung, Reasonably Fresh and Old. Fresh ≤ 2 days in age was the easiest to classify unambiguously. We therefore used only fresh dung detection data for improving the accuracy and reliability of the analyses of habitat use prior to the survey.

Ecological determinants of habitat use

Distance to river

Many streams and small rivers drain the Nagarahole–Bandipur landscape. There are also three large perennial reservoirs. To create stream layer in the study area, we used 30-m resolution Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Digital Elevation Model (DEM). The DEM was processed in ArcGIS v10.2.1 using hydrology tools (Esri, California, USA). We retained stream orders 3–5, as they correspond to major streams that support riparian vegetation. Furthermore, using 1:50000 scale topographic maps, we corrected the stream layers extracted from the DEM. Additionally, the three large reservoirs in the study area were digitized and included in the river layer.

Since rivers are linear features sporadically located in the study area, we calculated the Euclidean distance from the centroid of each grid cell to the nearest river. The distance to river, thus measured, was used in the occupancy model as a plausible covariate influencing elephant habitat use.

Stagnant water

There are over 650 natural and man-made water holes in the study area. During field surveys, we mapped the water holes using a hand held GPS unit (GARMIN ETREX 20; Garmin International, Inc., Kansas, USA). Additionally, we located water holes from GoogleEarth Imagery in QGIS v 2.6.0. The density of water holes in the study area was high but variable (median = 3, range = 1–13 water holes/sampled grid cell). In view of the short length of our replicates in relation to potential elephant movement, we used the number of water holes as a covariate influencing habitat use by elephants. Furthermore, there is possibility of elephants accessing water holes in the adjoining grid cells as well. Therefore, we considered the first-order neighbouring grid cells (grid cells adjoining the focal grid cell) and obtained a sum of all the water holes within these grid cells for covariate modelling.

Vegetation characteristics

Studies of large herbivores often rely on remotely sensed vegetation indices as potential tools in investigating their distribution and other habitat relationships (Pettorelli *et al.*, 2011). We used vegetation productivity measured through Normalized Difference Vegetation Index (NDVI) as a coarse measure of forage availability for elephants. We used the Moderate Resolution Imaging Spectro-Radiometer datasets with a spatial resolution of 250 m and temporal resolution of 16 days. Drier habitats in our landscape have higher variability in NDVI in comparison to relatively stable moister habitats (Krishnaswamy, Kiran & Ganeshiah, 2004). Furthermore, higher NDVI values during dry season are indicative of moist forests. We expected that elephants would use areas that maintain high NDVI with minimal seasonal variability during the dry season. For each grid cell, we calculated the percentage change in green cover by comparing two images pertaining to November 2013 (maximum NDVI) and March 2014 (minimum NDVI), and extracted the mean NDVI as a covariate influencing habitat use by elephants.

Model structure and data analysis

Since we sampled continuous trails used by a highly mobile species, we could not assume complete independence of elephant signs between spatial replicates. Ignoring such potential dependence can seriously affect the precision of occupancy estimates (MacKenzie *et al.*, 2006). Therefore, we tested for possible spatial dependence of sign detections among the replicates using a model developed by Hines *et al.* (2010), which explicitly accounts for Markovian dependence between spatial replicates. Parameters in Hines *et al.* (2010) model that we estimated in the context of this study include:

ψ = probability of use of a sample unit by elephants

θ^0 = probability of elephant presence in the replicate given their absence in the previous segment

θ^1 = probability of elephant presence in the replicate given their presence in the previous segment

p_i = detection probability of a sign conditional on elephant presence in the replicate

The parameter estimates of θ^0 and θ^1 assess the degree of possible spatial dependence between replicates. If $\theta^0 \neq \theta^1$, there is evidence for spatial dependence between sign detections on replicates while $\theta^0 = \theta^1$ suggests lack of such dependence between spatial replicates. Our main interest was to examine the influence of selected covariates on elephant habitat use, ψ . We achieved this by modelling site-specific probabilities of elephant habitat use, ψ as a function of relevant ecological and management covariates. The covariates were scaled using z transformation to facilitate interpretation and comparison of relative influence of predictors (Schielzeth, 2010). We also examined autocorrelation between covariates using Pearson's correlation ($r > 0.5$), in the same candidate model.

We performed the occupancy analysis using software PRESENCE v 6.4 (Hines, 2006). We followed an information theoretic approach for model selection by comparing plausible

models with an intercept-only model (Burnham & Anderson, 2002). Covariate model comparisons were based on Akaike's Information Criterion (AIC) scores and corresponding AIC weights.

Results

Spatial independence between replicates

In the first step of our analysis, we compared the standard MacKenzie *et al.* (2002) model, which does not account for spatial dependence among spatial replicates, with the Hines *et al.* (2010) model. We found evidence for spatial dependence of sign detections using 500 m spatial replicates. The estimates of θ^0 and θ^1 , the dependence parameters of Hines *et al.* (2010) model demonstrated a high degree of spatial dependence between replicates (Supporting Information Table S2). Furthermore, the Hines *et al.* (2010) model had considerably higher model support (AIC weight = 1) than the standard occupancy model (Supporting Information Table S1). Therefore, we performed all further analyses using the Hines *et al.* (2010) model.

Model structure for detection probability (p_t)

Detection probabilities may vary across sampled sites due to both known (and recorded) and unknown factors. We note that the variation in detection probabilities needs to be examined and explicitly modelled to get unbiased estimates of the parameter of interest, ψ . We reasoned *a priori* that sign detection probabilities could be high in grid cells with more water holes, as opposed to grid cells with few water holes, as elephants frequent water holes regularly through well-used trails. Consequently, we constructed a global model, which included all the plausible covariates of ψ (see Table 1 for covariate details). We retained this global model structure for ψ , and compared a model with water holes/grid cell as a covariate for detection probability with another model where p_t was constant.

The global model (with covariate structure for ψ) without any covariates for detection probability performed better than the model with water holes/grid cell as a covariate for detection probability (Table 2). Therefore, we retained the model without any covariates for detection probability to model ψ . The best fit model yielded a high estimate of replicate-level detection probability at $\hat{p}_t(SE[\hat{p}_t]) = 0.67(0.06)$ even without any covariates. For estimating conditional sampling probability parameters θ^0 and θ^1 of Hines *et al.* (2010) model we did not use any covariates, as sign detection process in the field was fairly simple and straightforward along a narrow trail.

Table 2 Summary of model selection results to assess the effect of covariates on detection probability of elephant signs on 500 m long spatial replicates used in the field survey

Model	AIC	Δ AIC	AIC weight	Model likelihood	K	Deviance
ψ (global), $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_t(\cdot)$	1282.65	0	0.83	1	8	1266.65
$\psi(\cdot)$, $\theta^0(\cdot)$, $\theta^1(\cdot)$, $p_t(\cdot)$	1285.8	3.15	0.17	0.21	5	1275.8
ψ (global), $\theta^0(\cdot)$, $\theta^1(\cdot)$, p_t (water holes in a grid cell)	1293.19	10.54	0	0.01	8	1277.19

Covariates of ψ used in the global model are: R , distance to river; ΔN , Δ NDVI; WH, count of water holes in the focal grid cell and its first-order neighbouring grid cells.

Probability of habitat use and the influence of covariates

We detected fresh elephant dung in 72 out of the sampled 97 sites (grid cells), which yielded naïve occupancy estimate of 0.74. We chose seven plausible models and compared them with the basic intercept-only model. The candidate set of eight models with combinations of covariate structure for ψ and constant p_t is presented in Table 3. Models with Δ AIC < 2 lend substantial support from the data (Burnham & Anderson, 2002). In the candidate model set, top three models received similar support with Δ AIC < 1.83. However, the top models were all nested. Therefore, we used the top model in the candidate set of models to make inference on probability of habitat use by elephants.

Further, we examined the β coefficient estimates of selected covariates on elephant probability of habitat use, ψ . We used AIC weights to estimate the relative influence of the covariates. The AIC weights of individual covariates were obtained by summing the AIC weights of all the models in the candidate set in which the covariate appeared. Model-specific β coefficient estimates are provided in (Table 4).

The probability of habitat use by elephants in the study area ranged from $\hat{\psi}(SE[\hat{\psi}]) = 0.04(0.15)$ to $0.99(0.01)$. Distance to rivers (cumulative AIC weight = 0.87 for candidate models) and Δ NDVI (cumulative AIC weight = 0.66 for candidate models) best explained the variability in site-specific probability of habitat use, ψ . Distance to river had the strongest influence on elephant habitat use patterns, whereby the probability of habitat use decreased as the distance to rivers increased (Table 4). Similarly, elephant habitat use was negatively associated with Δ NDVI, whereby the probability of habitat use decreased as the percentage change in mean NDVI increased. Although β estimates are comparable, we note that the standard error of NDVI-based vegetation measure is high, suggesting more uncertainty. The third covariate, water holes in first-order neighbouring grid cells, did not receive adequate support (cumulative AIC weight = 0.28 for candidate models).

Estimates of ψ for non-sampled grid cells

We used covariate information to draw inference for the non-sampled grid cells using the inverse logit link function (MacKenzie *et al.*, 2006). The sign detection histories of non-sampled grid cells were treated as missing observations in this approach. The site-specific estimates of probability of habitat use by elephants, ψ for both the sampled and non-sampled grid cells based on the top model (Table 3) have been graphically presented for the study landscape (Fig. 2).

Table 3 Summary of model selection results to identify the influence of covariates on elephant probability of habitat use in Bandipur–Nagarahole landscape during dry season

Model	AIC	Δ AIC	AIC weight	Model likelihood	K	Deviance
$\psi (R + \Delta N), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1280.82	0	0.42	1	7	1266.82
$\psi (R), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1282.22	1.4	0.21	0.497	6	1270.22
$\psi (R + \Delta N + WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1282.65	1.83	0.17	0.401	8	1266.65
$\psi (R + WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1284.21	3.39	0.08	0.184	7	1270.21
$\psi (\Delta N), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1285.04	4.22	0.05	0.121	6	1273.04
$\psi (\cdot), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1285.8	4.98	0.04	0.083	5	1275.8
$\psi (\Delta N + WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1286.91	6.09	0.02	0.048	7	1272.91
$\psi (WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1287.78	6.96	0.013	0.031	6	1275.78

Covariates are: R , distance to river; ΔN , Δ NDVI; WH , count of water holes in the focal grid cell and its first-order neighbouring grid cells; NDVI, Normalized Difference Vegetation Index.

Table 4 Summary of model-specific β coefficient estimates for different covariates hypothesised to influence elephant habitat use during dry season, their relative AIC weights and the model averaged values

Model	Intercept $\hat{\beta}_0$ ($S\hat{E}$)	$\hat{\beta}_R$ ($S\hat{E}$)	$\hat{\beta}_{\Delta N}$ ($S\hat{E}$)	$\hat{\beta}_{WH}$ ($S\hat{E}$)	AIC weight
$\psi (R + \Delta N), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	2.45 (0.91)	−0.95 (0.39)	−1.28 (0.91)	–	0.42
$\psi (R), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1.89 (0.48)	−0.83 (0.34)	–	–	0.21
$\psi (R + \Delta N + WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	2.41 (0.90)	−0.95 (0.38)	−1.28 (0.89)	0.15 (0.37)	0.17
$\psi (R + WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1.88 (0.50)	−0.83 (0.33)	–	0.02 (0.40)	0.08
$\psi (\Delta N), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	2.45 (1.11)	–	−1.16 (1.02)	–	0.05
$\psi, \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$ NULL MODEL	1.97 (0.56)	–	–	–	0.04
$\psi (\Delta N + WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	2.48 (1.22)	–	−1.18 (1.07)	0.15 (0.46)	0.02
$\psi (WH), \theta^0(\cdot), \theta^1(\cdot), p_t(\cdot)$	1.97 (0.56)	–	–	0.07 (0.46)	0.01
Akaike weight of the covariates	–	0.87	0.66	0.28	–

Covariates are: R , distance to river; ΔN , Δ NDVI; WH , count of water holes in the focal grid cell and its first-order neighbouring grid cells; NDVI, Normalized Difference Vegetation Index.

Discussion

Overall, our results suggest that the elephant populations were not evenly distributed in the study area during the dry season. We found site-specific variation in probability of habitat use by elephants across the Bandipur–Nagarahole landscape. Distance to river was the best predictor of the observed variation in dry season habitat use patterns of elephants in our study area, whereby the probability of elephant habitat use declined as the distance to river increased. This finding is consistent with suggestions made by Sukumar (1989) that riparian zones in deciduous forests have high concentrations of elephants during the dry season. Individual elephants require large quantities of water every day (Sukumar, 2003), making proximity to large water bodies essential. We note, that intensive use of habitats close to rivers cannot solely be attributed for the availability of water. Riparian zones have browse plants and sedges that do not senesce much during dry season, and could act as potential foraging hotspots as well (Kumar, Mudappa & Raman, 2010). Furthermore, while some large streams may dry up during the dry season, it is plausible that elephants exploit the subsoil moisture in streambeds (Sukumar, 1989). Furthermore, in deciduous forests with open canopy during dry season, riparian habitats offer ample shade that could help elephants in better thermoregulation.

The number of artificial water holes per grid cell and first-order neighbouring grid cells, showed a positive but weak relationship with probability of habitat use. This was likely a result of the near-uniform distribution of such water holes established by managers across the sampling frame, whereby almost every grid cell had at least one water holes. We note that most previous studies on elephant–habitat relationships in Asia have not distinguished between rivers and artificial water holes as a source of surface water for elephants (e.g. Desai & Baskaran, 1996). We addressed this gap by modelling water holes and rivers separately in our analyses. Our results highlight the need to understand the relative influence of rivers and artificial water holes for better management of elephant habitats. Current management strategies to increase herbivore populations in Bandipur and Nagarahole include the creation of water holes and the artificial increasing of forage availability (Kumar, 2011). However, the need for such interventions has not been demonstrated by scientific evaluations, and do not appear to be supported by our results. Increasing water supply for large herbivores like elephants has been a contentious strategy in the African savannahs as well (Owen-Smith *et al.*, 2006). Research in Africa has examined over the years, the influence of artificial water-points and resultant long-term negative impact of elephants on vegetation neighbouring such water-points, with consequences for long-term elephant population dynamics (Redfern *et al.*, 2003; Chamaillé-Jammes *et al.*,

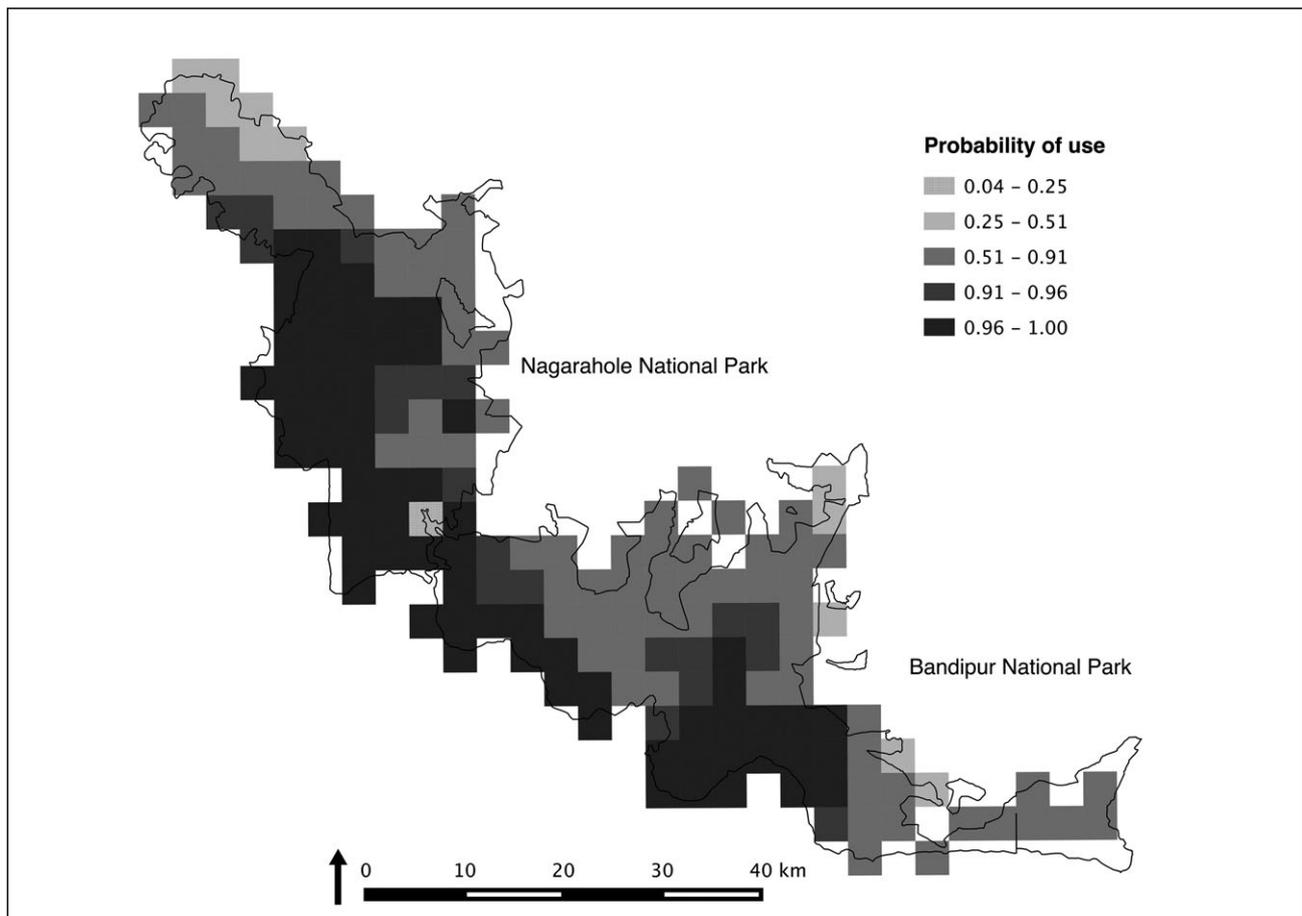


Figure 2 Predicted probability of habitat use by elephants during the dry season in Bandipur–Nagarahole landscape.

2007; Loarie *et al.*, 2009). Such an understanding has led to informed management of elephants in Africa (see Owen-Smith *et al.*, 2006). Our study provides preliminary insights into the effects of water distribution on Asian elephant habitat use, highlighting the overarching importance of natural water sources such as large streams and rivers as determinants of dry season habitat use patterns of elephants in tropical deciduous forests. In light of these results, we would urge caution that without deeper studies, intensification of water supply by managers in elephant habitats may be counterproductive for elephant conservation. This had been noted earlier as well (Sukumar, 2003; Rangarajan *et al.*, 2010).

We also assessed the role of vegetation in determining the probability of habitat use using remotely sensed NDVI. Our results show that Δ NDVI adds to the effects of distance to river, the best predictor, in influencing the probability of elephant habitat use in the dry season, whereby the probability of elephant habitat use declined as the percentage change in mean NDVI increased. While remotely sensed NDVI did prove to be a useful surrogate for green cover, it is pertinent to note its limitations. The invasive weed, *Lantana camara* forms dense undergrowth in the study area (Prasad, 2010), and it is inedible by elephants (Wilson *et al.*, 2013). Recent studies from similar

dry deciduous forests have shown that *L.camara* has a negative impact on habitat use (Wilson *et al.*, 2013). Therefore, a ground-based measure of vegetation, especially assessing the density of food plants of elephants would be critical to elucidate the influence of local habitat features on elephant habitat use patterns.

Conclusions

Large herbivores have to adapt to temporal and spatial variability in the essential resources that they depend on seasonally and annually. Consequently, the habitat use patterns of large herbivores in heterogeneous landscapes are not random, at least during resource-limiting periods (Moen *et al.*, 2006). Our findings lend further support to this hypothesis. In the Western Ghats region where our study area is located, monsoon has a profound quantitative effect on water availability and therefore, a more uniform distribution of elephants could be expected during the wet season. However, elephants might still select areas where forage quality and quantity are optimized.

Assessments of habitat use patterns, when repeated over time, can elucidate important aspects of behaviour, life history

tactics and population dynamics of large herbivores (Moen *et al.*, 2006). Furthermore, apart from environmental influences, large herbivores also respond to various management interventions in their habitats (Loarie *et al.*, 2009). Major management interventions on large herbivore habitats in Indian wildlife reserves include the establishment of physical barriers for the mitigation of human–wildlife conflict, the creation of water and fodder reserves, and the eradication of invasive weeds. All these interventions have potential to modify spatial distribution patterns of large herbivores, and, also entail substantial recurring annual investments. Therefore, periodic scientific assessment of large herbivore–habitat relationships is required as habitat management entails understanding of species' needs. Since the scale of such assessments can span hundreds of square kilometres, it is essential to develop survey protocols that are efficient, but at the same time do not require highly trained field personnel or advanced equipment. Furthermore, modelling frameworks used to handle such field data should be statistically rigorous without compromising on detectability or spatial sampling, while being flexible.

We demonstrate that data collected through spatially replicated sign surveys, when modelled under an occupancy framework using biologically meaningful *a priori* predictors, allow reliable yet cost-effective assessments of elephant habitat use even in large landscapes. Furthermore, the predictive capacity of our modelling approach permits the evaluation of management interventions across space and time. We believe such an investigation is a pre-requisite for wise allocation of resources for large herbivore management and conservation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Comparison between standard occupancy model and the model that uses spatial replicates with potential spatial dependence of sign detections among them.

Table S2. Parameter estimates of θ^0 and θ^1 demonstrating the degree of spatial dependence of sign detections.