RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Substituting space for time: Empirical evaluation of spatial replication as a surrogate for temporal replication in occupancy modelling

Arjun Srivathsa[1,2,3,4] | Mahi Puri[1,2,4] | Narayanarao Samba Kumar[1,2] | Devcharan Jathanna[1] | Kota Ullas Karanth[1,2,5,6]

[1]Wildlife Conservation Society, India Program, Bengaluru, India; [2]Centre for Wildlife Studies, Bengaluru, India; [3]School of Natural Resources and Environment, University of Florida, Gainesville, FL, USA; [4]Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA; [5]Wildlife Conservation Society, Global Conservation Program, New York, NY, USA and [6]National Centre for Biological Sciences, Bengaluru, India

Correspondence
Arjun Srivathsa
Email: arjuns.cws@gmail.com

Handling Editor: Ralph Mac Nally

Abstract

1. Occupancy models that account for detection probability are important analytical tools in conservation monitoring. Traditionally, occupancy models relied on detection/non-detection data generated from temporal replicates for estimating detectability. Due to logistical challenges and financial costs involved, many large-scale field studies instead use spatial replication as a surrogate. The efficacy of the two approaches and their statistical validity has generally sought support from simulation-based inferences rather than empirical data.

2. Using the sloth bear *Melursus ursinus* as an example, we compared estimates of occupancy and detection probabilities obtained from temporal and spatial sampling designs. We carried out temporally replicated camera trap surveys and spatially replicated sign surveys across a 754-km^2 area around Bhadra Tiger Reserve in the Western Ghats of India.

3. We sampled along forest/coffee plantation roads in 58 grid cells of 13 km^2 each, treating these cells as independent sites. We used the standard single-season model for the camera trap survey data, and the single-season correlated detections model (with Markovian dependence) for the sign survey data, and incorporated ecological covariates that likely influenced occupancy and detection probabilities.

4. Occupancy estimates from the two surveys and corresponding modelling approaches were similar [$\hat{\psi}^c(\widehat{SE})$ = 0.58 (0.03) for camera trap surveys; $\hat{\psi}^s(\widehat{SE})$ = 0.56 (0.03) for sign surveys]. In both cases, the influence of covariates corroborated our *a priori* predictions. Site-level estimates of occupancy from the two methods were highly correlated (*r* = .78). We generated a combined estimate of sloth bear occupancy in the region as an inverse-variance weighted average of the two estimates [$\hat{\psi}(\widehat{SE})$ = 0.57 (0.02)].

5. *Synthesis and applications*. Studies that aim to evaluate occupancy models should account for spatial variation in occupancy/detection probabilities, particularly when making inferences on species–habitat relationships. We show that spatial

replication can serve as a good surrogate for temporal replication in occupancy studies, which may be useful for distribution assessments of species when field resources are limited or logistical challenges preclude traditional survey approaches that yield temporally replicated data. Our results therefore provide a basis for efficient targeting of funds and field resources, particularly for practitioners involved in monitoring species at large landscape scales.

1 | INTRODUCTION

Species distribution models are useful for elucidating factors driving patterns of species occurrence and examining species–habitat relationships (Elith & Leathwick, 2009). Despite their widespread use, most commonly used distribution modelling approaches (based on either presence/absence data, or presence-only data) do not address issues related to observation processes such as unequal survey effort and uncertainties arising due to false absences. Inferences and predictions from such studies are often seriously vitiated by the confounding of spatial patterns in occurrence with patterns in sampling and detection (see Guillera-Arroita et al., 2015). Occupancy modelling methods that explicitly account for imperfect and variable detectability, variable probability of occurrence across sampling sites, and variable sampling effort across sites have therefore superseded methods that rely on presence-only or presence–absence data to model species distributions (Guillera-Arroita, 2017; MacKenzie et al., 2002, 2006; Yackulic et al., 2013). The strength of these models arises from their ability to disentangle true absence from non-detection within a probabilistic framework by exploiting information from replicated surveys (MacKenzie et al., 2006).

Studies that employ occupancy modelling methods use detection/non-detection data with replication at each site, or data on times to detection within a survey visit, to allow the estimation of detectability. The single-season single species occupancy modelling approach described by MacKenzie et al. (2002) uses data from temporal replicates (repeated surveys of each site), with the assumption that true occupancy state of a site remains constant, or changes randomly among visits (MacKenzie et al., 2006). However, many large-scale field studies rely on sampling using spatial replicates (sampling multiple spatial subunits of each site) as a logistically feasible surrogate. Substituting spatial for temporal replication introduces new problems because the model described by MacKenzie et al. (2002) no longer describes the field sampling reality; it is not possible to assume that site-level occupancy implies occupancy of all spatial replicates in that site, and this local occupancy is likely to be auto-correlated in space.

In reviewing the application of spatial replication in occupancy surveys, Kendall and White (2009) proposed random sampling with replacement of replicates to induce randomness in non-closure of occupancy state among spatial replicates within a site. However, this is not feasible for large-scale surveys in difficult terrain. Guillera-Arroita (2011) showed that sampling of replicates without replacement is more appropriate if occupancy in a spatial subunit is independent of occupancy in other subunits within a site. Hines et al. (2010) developed a model that explicitly accounts for Markovian dependence in local occupancy at the level of spatial replicates for scenarios where sampling is restricted to linear features in a landscape (e.g. successive segments along a forest trail), and Guillera-Arroita, Morgan, Ridout, and Linkie (2011), Guillera-Arroita, Ridout, Morgan, and Linkie (2012) developed a modelling approach that treats detection as a continuous point process, eliminating the need to divide sampled trails into discrete segments.

Much of the work on applicability of temporal or spatial replication in occupancy surveys has focused on assessments of estimator bias and precision using simulated data (Guillera-Arroita, 2011; Hines et al., 2010; Kendall & White, 2009). To our knowledge, there has been no assessment of the congruence of the two approaches applied to the same field system. In this study, we carried out occupancy surveys for sloth bears (*Melursus ursinus*) using both temporal (camera trap surveys) and spatial (indirect sign surveys) replication, in and around Bhadra Tiger Reserve, India. We based our comparison on (1) the similarity between the estimates of overall occupancy (proportion of area occupied, PAO) derived using the two approaches; (2) the estimated relative importance of ecological drivers of occupancy; and (3) the estimated responses of probability of occupancy to ecological covariates, and the site-specific model predictions based on these estimated responses. Last, we combine predictions based on the two approaches to derive a single estimate of sloth bear occupancy in the region.

2 | MATERIALS AND METHODS

2.1 | Study area and species

Bhadra Tiger Reserve is a protected wildlife reserve in the Western Ghats of Karnataka, India, covering an area of 492 km². The terrain is undulating (670–1,900-m elevation) and the reserve receives annual rainfall ranging from 1,200 to 2,540 mm. The vegetation is a heterogeneous mix of moist deciduous and wet evergreen forests in

the south, and dry deciduous forests towards the north, with both the understorey as well as the upper canopy dominated by bamboo (*Dendrocalamus strictus* and *Bambusa arundinacea* respectively). Prior to 2002, the lower valleys of the reserve consisted of swampy grasslands occupied by village settlements and paddy fields. Following voluntary resettlement of a large number of villages from the protected area in 2002 (Karanth, 2007), large mammal populations have been gradually increasing (Karanth, Nichols, Kumar, Link, & Hines, 2004), although these are still below optimal densities (Gopalaswamy, Karanth, Kumar, & Macdonald, 2012; Jathanna, Karanth, & Johnsingh, 2003). The protected area is surrounded by reserve forests and large tracts of coffee plantations (Bali, Kumar, & Krishnaswamy, 2007; Figure 1). The region has a wide network of forest and plantation dirt roads (Figure 2).

The sloth bear *M. ursinus* is endemic to the Indian subcontinent. It inhabits tropical and sub-tropical habitats across India, Nepal, Bhutan and Sri Lanka. Despite its extensive range across the Indian subcontinent, there are no reliable estimates of sloth bear population size (Dharaiya, Bargali, & Sharp, 2016). Sloth bears are listed as "vulnerable" under the IUCN Red List and under Schedule I of the Indian Wildlife (Protection) Act of 1972. In cases where absolute abundance of animals cannot be estimated from reliable methods, habitat occupancy metrics serve as useful surrogates for understanding their population status (MacKenzie & Nichols, 2004; Srivathsa, Karanth, Jathanna, Kumar, & Karanth, 2014; Wong & Linkie, 2013). We chose the sloth bear as our focal species for three reasons: (1) their indirect signs can be unambiguously identified on field, (2) sampling along forest roads (using either camera traps or sign surveys) usually yields adequate detections, since bears use roads and trails extensively, and (3) their home-range sizes within resource-rich habitats are small enough (*c.* 10 km^2; Ratnayeke, van Manen, & Padmalal, 2007; Yoganand, 2005) for making assessments of true occupancy at the spatial scale of a single reserve.

2.2 | Field surveys and design

In several field surveys of species' occupancy, the focus has increasingly shifted towards collection of data from non-invasive methods such as indirect sign surveys (Karanth et al., 2011; Thorn, Green, Bateman, Waite, & Scott, 2011), camera trap surveys (Burton, Sam, Balangtaa, & Brashares, 2012; Linkie, Dinata, Nugroho, & Haidir, 2007), interview surveys of experts or local informants (Pillay, Johnsingh, Raghunath, & Madhusudan, 2011) and field sampling for analysis of faecal DNA (Long, Donovan, MacKay, Zielinski, & Buzas, 2011). We chose camera trap surveys and indirect sign surveys for our study because both methods involved sampling along forest roads/
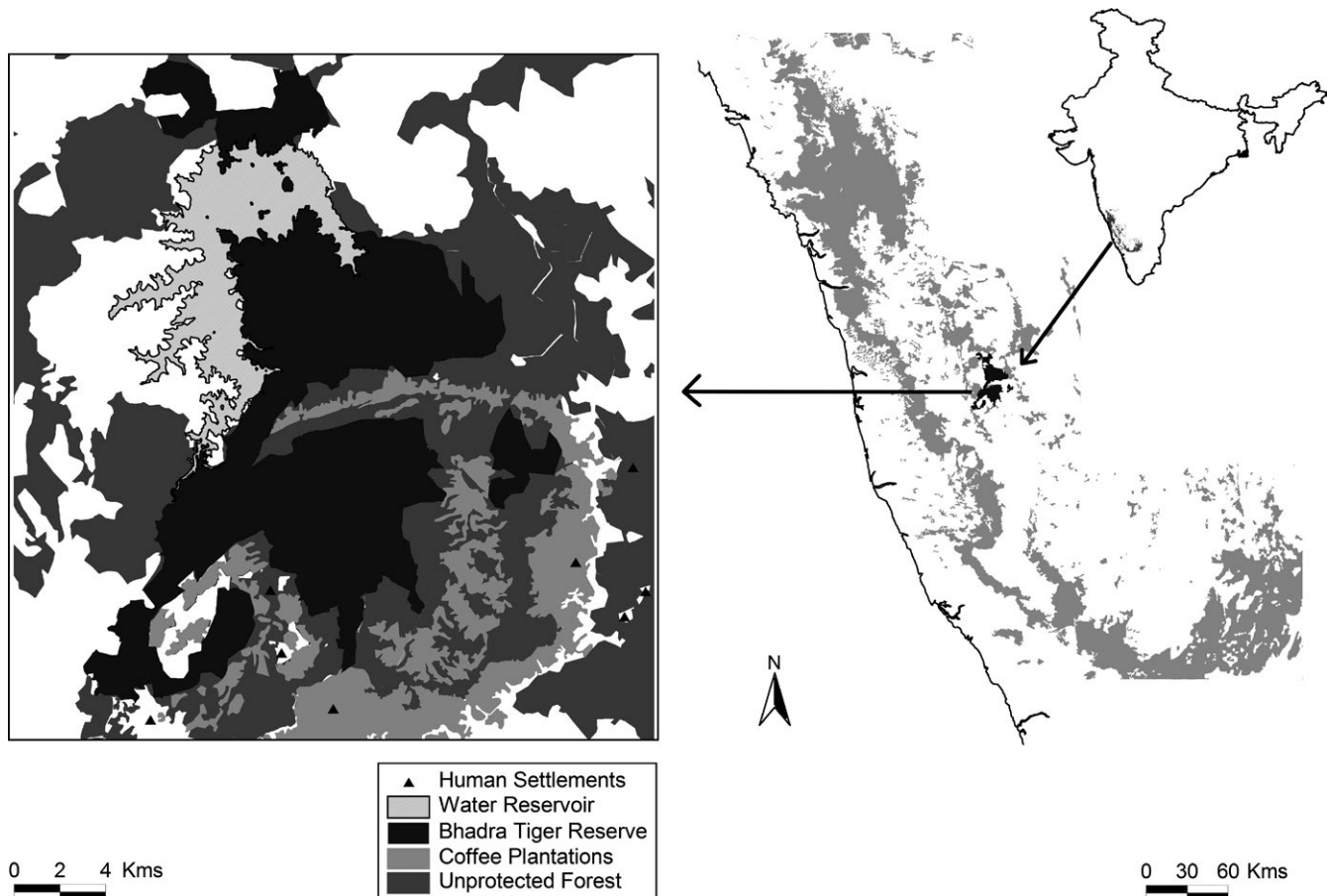
FIGURE 1 Location of Bhadra Tiger Reserve and surrounding land-cover matrix in the Western Ghats landscape, India. White areas represent open agriculture or urban/semi-urban areas

trails, which are known to be used extensively by sloth bears (Puri, Srivathsa, Karanth, Kumar, & Karanth, 2015). For our surveys, we defined sites as 13-km² grid cells, large enough to encompass sloth bear home ranges. Although sloth bear home-range sizes may extend to 85 km², they are generally much smaller within protected wildlife reserves (c. 10 km²; Garshelis, Joshi, & Smith, 1999; Ratnayeke, Van Manen, & Padmalal, 2007; Yoganand, 2005). The grid array consisted of 81 such 13-km² cells (henceforth, "sites"). Individual sites contained a variable number of camera trap stations, which was explicitly accounted for in our analyses (see below). Similarly, for sign surveys we expended variable search effort (in terms of total trail length surveyed) across sites, which were also explicitly accounted for by the analytical framework used, as described below.
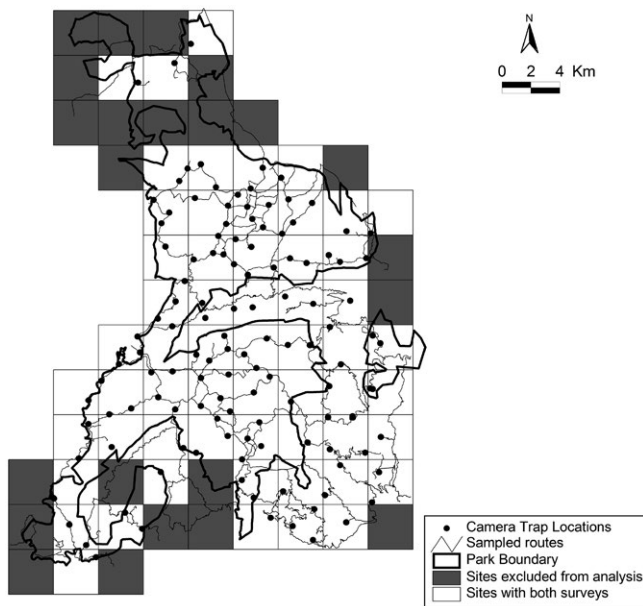
2.2.1 | Camera trap surveys

We carried out camera trap surveys during the dry season from 29 January to 28 February 2013. Camera trap stations were set up at 101 locations within the reserve, and at 21 locations in adjacent coffee plantations and non-protected forests. Camera trap locations, spaced 2–3 km apart, were chosen so as to obtain adequate and uniform geographical coverage of the area (Figure 2). To increase the probability of photo-capturing sloth bears, we set up camera traps along forest and coffee plantation roads. We placed two automated digital *PantherCam v4* camera trap units (Olliff et al., 2014) at each trap station, at a height of 45 cm from the ground and c. 3.5 m from the centre of the road. Each photo-capture of a sloth bear was referenced by the date and time of encounter, and the camera trap location. A detection (1) was defined as photo-encounter(s) of bears in one or more camera trap locations within each grid, during a replicate (conversely,

non-detection [0] implied no photo-encounter of the species at any of the camera trap locations within a grid cell, during a replicate). Pooling detection data across camera traps within each grid cell allowed us to assess occupancy at the same spatial grain as with spatially replicated sign survey data. We treated each day as a separate replicate (30 temporal replicates).

2.2.2 | Sign surveys

We conducted sign encounter surveys during the dry season, from December 2012 to April 2013 (with a break between 29 January and 28 February 2013). We surveyed along forest and plantation roads, and intensively searched for indirect signs of sloth bears that included fresh scats (<7 days) and tracks. Only fresh signs were considered for analysis so as to avoid biases that may arise from decay of signs (Rhodes, Lunney, Moon, Matthews, & McAlpine, 2011). We excluded other signs such as dug-out termite mounds and claw marks on trees that could potentially be misclassified or misidentified (Miller et al., 2011). Sampling along roads maximized detectability and the total number of signs recorded. The presence of signs was recorded in every 100-m segment of forest roads and the data were later pooled as either detected (1) or non-detected (0) in each 1-km replicate.

Given that our objective was to compare estimates derived from two data sources and corresponding modelling approaches, data from 58 sites (of the total 81 sites) where the two surveys overlapped were used in the analyses (Figure 2). The number of camera trap stations in the sites varied from 1 to 5. These surveys yielded temporally replicated detection/non-detection data over 30 daily temporal replicates. Effort for sign surveys in each site varied from 2 to 29 1-km spatial replicates, with a total walk effort of 553 km.

2.3 | Covariates for detectability and occurrence

We predicted that the total number of camera trap stations in a site (for camera trap surveys) would positively influence site-level detection probabilities. We also modelled the proportion of each site that was within the reserve boundary, predicting that detectability at a site would be higher within the reserve (for both camera trap and sign surveys) due to higher abundance of sloth bears. The variable number of spatial replicates in the sign surveys was fully accounted for as missing replicates in the occupancy modelling framework (see MacKenzie et al., 2002, 2006).

We chose ecological factors that were likely to influence sloth bear occurrence based on previous assessments (Dharaiya et al., 2016) and field studies (Puri et al., 2015). We predicted that the extent of forest cover and terrain heterogeneity would positively influence bear occurrence, while vegetation productivity would have a strong negative influence. Extent of forest cover was measured from remotely sensed data, and expressed as the proportion of area under forest cover within each grid cell. Terrain heterogeneity was calculated as the index of ruggedness described by Riley, DeGloria, and Elliot (1999), using the Terrain Analysis tool in QGIS

FIGURE 2 Schematic of the sampling design, showing camera trap locations, sign survey routes and the grid cells (sites) where the two surveys overlap

(version 2.2.0). We used the coefficient of variation in ruggedness across pixels in each site, as this measure better represented the heterogeneity in terrain (Puri et al., 2015). We used the mean value of Normalized Difference Vegetation Index (NDVI) in each site as an index of primary productivity of vegetation; lower values of mean NDVI indicating drier areas with lower canopy cover, which would positively influence sloth bear occurrence. We used these three as covariates of occurrence (ψ) for both camera trap survey data and sign survey data. All covariates were first checked for collinearity, and then scaled and normalized prior to analysis to have μ = 0 and σ = 1, so that estimated β-coefficients represented changes in logit(ψ) for a 1σ change in the covariate.

2.4 | Occupancy modelling

Camera trap surveys generated temporally replicated data, so we used the standard single-season habitat occupancy model described by MacKenzie et al. (2002) for analysis. Sign surveys generated data from spatial replicates, collected along contiguous forest or plantation roads. Sloth bears walk along such linear clearings, so replicate-level presence of the species would likely be described by a first-order Markov process. Therefore, we tested an extension of the single-season occupancy model for auto-correlated replicate-level presence, developed by Hines et al. (2010). This model estimates two additional parameters for replicate-level probability of presence, conditional on signs being absent or present in the previous surveyed replicate, respectively. The notation used and parameter definitions are:

1. ψ^c—probability of bear occurrence in a site, estimated from camera trap data.
2. p^c—probability of detecting bears in a replicate using camera trap data, given presence at the site.
3. ψ^s—probability of bear occurrence in a site, estimated from sign survey data.
4. θ^0 and θ'—probability of bear presence in a spatial replicate, conditional on the absence or presence in the previous surveyed replicate respectively (replicates are 1-km road segments).
5. p_t^s—probability of detecting bear signs in a spatial replicate from sign survey data, given presence in the site and replicate.

We first tested for spatially dependent non-closure for sign surveys by fitting the data to: (1) the standard single-season model (MacKenzie et al., 2002; which assumes that species' presence in a site implies species presence in all replicates); and (2) the single-season correlated detections model (Hines et al., 2010; allowing spatially dependent non-closure of occupancy among replicates), and assessed support for these models based on Akaike Information Criterion values (AIC; Burnham & Anderson, 2002). For both data sources, we followed a two-step process to estimate probability of detection (p^c and p_t^s) and probability of bear occurrence (ψ^c and ψ^s). First, we fixed a global covariate structure for ψ which included all three ecological covariates that could influence probability of

occurrence. We modelled different combinations of the detectability covariates with this covariate combination for ψ and selected the best model based on AIC. In the second step, we modelled probability of occupancy (ψ^c and ψ^s) after fixing covariates for detection probability based on the top-ranked model in the previous step (see Doherty, White, & Burnham, 2012 for a discussion of such two-step analyses). We conducted all analyses using a maximum likelihood-based approach implemented in program PRESENCE version 11.6 (Hines, 2006). Model fit was assessed using the parametric bootstrap procedure implemented within program PRESENCE (MacKenzie & Bailey, 2004).

2.5 | Combined estimate of occupancy

We derived a single combined estimate of overall occupancy from the two methods. While combining estimates from multiple sources, estimates from methods that offer more reliable information should receive higher weights. In such cases, an inverse-variance weighted mean (rather than just the arithmetic mean) serves to minimize the variance of the combined estimate (Hartung, Knapp, & Sinha, 2011). For the two methods presented above, we calculated the combined occupancy probability as the mean of the two estimates, weighted by the inverse of their respective variances:

$$\hat{\overline{\psi}} = \frac{\hat{\psi}^c/\text{vâr}(\hat{\psi}^c) + \hat{\psi}^s/\text{vâr}(\hat{\psi}^s)}{1/\text{vâr}(\hat{\psi}^c) + 1/\text{vâr}(\hat{\psi}^s)}$$

The variance of the combined estimate of sloth bear occupancy was computed as:

$$\text{vâr}(\hat{\overline{\psi}}) = \frac{1}{1/\text{vâr}(\hat{\psi}^c) + 1/\text{vâr}(\hat{\psi}^s)}$$

3 | RESULTS

The presence–absence estimates (i.e. assuming detectability = 1) indicated that bears occupied 26 of 58 sites (naïve occupancy = 0.45) based on 79 photo-encounters from camera trap surveys, and 20 of 58 sites (naïve occupancy = 0.34) based on 50 sign detections from sign surveys. These naïve estimates suggested that camera traps were more likely to detect the species, given its presence in a site, compared to sign surveys.

3.1 | Camera trap surveys

Comparing support for different covariate structures for detectability (p^c) indicated that site-level detection probability was positively influenced by the number of camera trap stations per site $[\hat{\beta}_{cams}(\widehat{SE}) = 0.54 \ (0.13)]$ (Table 1). Our assessment of the drivers of occupancy probability (ψ^c) included eight models: an intercept-only model and seven models with covariate combinations. Based on AIC values and corresponding model weights, no single model received unequivocal support from the data (Table 2); rather, all candidate models had some level of support. We therefore model-averaged

TABLE 1 Comparison of different covariate combinations for probability of detecting sloth bears from temporally replicated camera trap surveys in the Bhadra region, using a fixed, global model for bear occurrence

Model	AIC	ΔAIC	AIC weight	Model likelihood	K	Deviance
ψ^c(fcov+rugg+ndvi), p^c(cams)	528.52	0	0.9988	1	6	516.52
ψ^c(fcov+rugg+ndvi), p^c(.)	542.58	14.06	0.0009	0.0009	5	532.58
ψ^c(fcov+rugg+ndvi), p^c(resv)	544.58	16.06	0.003	0.003	6	532.58

fcov, proportion of forest cover; rugg, ruggedness; ndvi, Normalized Difference Vegetation Index; resv, proportion of site within reserve boundary; cams, number of camera trap stations. "cams" and "resv" were not used in the same model since they were highly correlated.
K = number of parameters.

TABLE 2 Model comparisons to identify ecological covariates influencing sloth bear occurrence from temporally replicated camera trap surveys in the Bhadra region

Model	AIC	ΔAIC	AIC weight	Model likelihood	K	Deviance
ψ^c(fcov+rugg), p^c(cams)	526.93	0	0.3465	1	5	516.93
ψ^c(fcov+ndvi), p^c(cams)	527.61	0.68	0.2466	0.7118	5	517.61
ψ^c(fcov), p^c(cams)	527.87	0.94	0.2166	0.625	4	519.87
ψ^c(fcov+rugg+ndvi), p^c(cams)	528.52	1.59	0.1565	0.4516	6	516.52
ψ^c(ndvi), p^c(cams)	532.68	5.75	0.0195	0.0564	4	524.68
ψ^c(rugg+ndvi), p^c(cams)	533.78	6.85	0.0113	0.0325	5	523.78
ψ^c(rugg), p^c(cams)	537.03	10.1	0.0022	0.0064	4	529.03

fcov, proportion of forest cover; rugg, ruggedness; ndvi, Normalized Difference Vegetation Index; resv, proportion of site within reserve boundary; cams, number of camera trap stations.
K = number of parameters.

predicted occupancy values (but not β-coefficients; Cade, 2015) for sites across all models (Burnham & Anderson, 2002). Although the χ^2 statistic observed when testing fit of the top model was unusually large (p = .04), it was smaller than the average of the simulated test statistics ($\hat{c}$ = 0.24), consistent with no overdispersion in the data.

Sloth bear distribution in the Bhadra region was positively associated with the extent of forest cover and terrain heterogeneity. The β-coefficients for NDVI indicated that vegetation productivity had a negative influence, with bears preferring drier, more open habitats. Model-specific β-coefficient estimates for the individual covariates are in Table 3. Site- and replicate-level detectability ranged from 0.03 (sites with one camera trap) to 0.17 (sites with five camera traps). We calculated overall detectability across all sampling occasions as p^* = 1 − ($(1 − p^c)^K$), where K is the number of temporal replicates, estimated at $\hat{p}^*(\widehat{SE})$ = 0.77 (0.02) from the top-ranked model, and model-averaged probability of occupancy of sloth bears in the landscape was $\hat{\psi}^c(\widehat{SE})$ = 0.58 (0.03).

3.2 | Sign surveys

We first confirmed that the correlated detections model (Hines et al., 2010) fitted the sign survey data better than the standard single-season occupancy model (ΔAIC = 2.79). Thereafter, we used the correlated detections model for subsequent analyses of sign survey data. The difference between estimates of replicate-level

presence provided further evidence for autocorrelation among spatial replicates: $\hat{\theta}^0(\widehat{SE})$ = 0.20 (0.08) and $\hat{\theta}^1(\widehat{SE})$ = 0.86 (0.22), conditional on sloth bear absence and presence in the previous replicate respectively (see Hines et al., 2010 for detailed parameter definitions). For replicate-level detectability, the intercept-only model p_t^s (.) fitted the data better than the model with "proportion of reserve" within the site [p_t^s (resv); ΔAIC = 1.79]. We assessed eight candidate models for effects on occupancy, with the same covariate combinations as with the camera trap surveys. No single model received unequivocal support from the sign survey data (Table 4). We estimated detectability [$\hat{p}_t^s(\widehat{SE})$ = 0.39 (0.07)] from the top-ranked model and model-averaged across all models to estimate probability of sloth bear occupancy at $\hat{\psi}^s(\widehat{SE})$ = 0.56 (0.03). The untransformed β-coefficient estimates from all models somewhat corroborated our predictions, and were similar to those estimated from camera trap survey data (Table 5).

3.3 | Temporal and spatial replication

The two approaches described above resulted in two distribution maps for sloth bears in the Bhadra region (Figure 3). The estimates of ψ(.) from the two intercept-only models were similar [ψ(SE) = 0.48 (0.07) from camera trap surveys; ψ(SE) = 0.52 (0.12) from sign surveys], but the estimate from sign survey data had lower precision. The estimates of overall occupancy derived from covariate models for the two methods were also similar $\hat{\psi}^c(\widehat{SE})$ = 0.58 (0.03) and $\hat{\psi}^s(\widehat{SE})$ = 0.56 (0.03)], and

TABLE 3 Estimates of β-coefficient values (SE errors in parentheses) for covariates influencing sloth bear occupancy in the Bhadra region, based on temporally replicated camera trap surveys

Model	$\hat{\beta}_{int}(\widehat{SE})$	$\hat{\beta}_{fcov}(\widehat{SE})$	$\hat{\beta}_{rugg}(\widehat{SE})$	$\hat{\beta}_{ndvi}(\widehat{SE})$
ψ^c(fcov+rugg), p^c(cams)	0.40 (0.56)	1.56 (0.57)	0.71 (0.47)	—
ψ^c(fcov+ndvi), p^c(cams)	0.31 (0.51)	1.30 (0.53)	—	−0.7 (0.52)
ψ^c(fcov), p^c(cams)	0.52 (0.62)	1.62 (0.62)	—	—
ψ^c(fcov+rugg+ndvi), p^c(cams)	0.29 (0.53)	1.38 (0.58)	0.49 (0.52)	−0.40 (0.62)
ψ^c(ndvi), p^c(cams)	0.85 (0.60)	—	—	−1.65 (0.79)
ψ^c(rugg+ndvi), p^c(cams)	0.88 (0.60)	—	0.43 (0.48)	−1.48 (0.80)
ψ^c(rugg), p^c(cams)	0.78 (0.65)	—	0.89 (0.58)	—

int, intercept; fcov, proportion of forest cover; rugg, ruggedness; ndvi, Normalized Difference Vegetation Index; resv, proportion of site within reserve boundary; cams, number of camera trap stations.

TABLE 4 Model comparisons to identify ecological covariates influencing sloth bear occurrence from spatially replicated sign surveys in the Bhadra region

Model	AIC	ΔAIC	AIC weight	Model likelihood	K	Deviance
ψ^s(ndvi), θ^0(.), θ^1(.), p_t^s(.)	294.96	0	0.305	1	6	282.96
ψ^s(rugg+ndvi), θ^0(.), θ^1(.), p_t^s(.)	295.86	0.9	0.1945	0.6376	7	281.86
ψ^s(fcov+ndvi), θ^0(.), θ^1(.), p_t^s(.)	296.05	1.09	0.1769	0.5798	7	282.05
ψ^s(fcov), θ^0(.), θ^1(.), p_t^s(.)	296.94	1.98	0.1133	0.3716	6	284.94
ψ^s(fcov+rugg), θ^0(.), θ^1(.), p_t^s(.)	297.56	2.6	0.0831	0.2725	7	283.56
ψ^s(fcov+rugg+ndvi), θ^0(.), θ^1(.), p_t^s(.)	297.6	2.64	0.0815	0.2671	8	281.6
ψ^s(rugg), θ^0(.), b θ^1(.), p_t^s(.)	299.42	4.46	0.0328	0.1075	6	287.42

fcov, proportion of forest cover; rugg, ruggedness; ndvi, Normalized Difference Vegetation Index.
K = number of parameters.

TABLE 5 Estimates of β-coefficient values (SEs in parentheses) for covariates influencing sloth bear occupancy in the Bhadra region, based on spatially replicated sign surveys

| Model	$\hat{\beta}_{int}(\widehat{SE})$	$\hat{\beta}_{fcov}(\widehat{SE})$	$\hat{\beta}_{rugg}(\widehat{SE})$	$\hat{\beta}_{ndvi}(\widehat{SE})$
ψ^s(ndvi), θ^0(.), θ^1(.), p_t^s(.)	0.70 (0.84)	—	—	−1.85 (1.01)
ψ^s(rugg+ndvi), θ^0(.), θ^1(.), p_t^s(.)	1.0 (0.91)	—	0.74 (0.74)	−1.86 (1.07)
ψ^s(fcov+ndvi), θ^0(.), θ^1(.), p_t^s(.)	0.26 (0.74)	0.52 (0.51)	—	−1.10 (0.94)
ψ^s(fcov), θ^0(.), θ^1(.), p_t^s(.)	−0.01 (0.50)	0.92 (0.40)	—	—
ψ^s(fcov+rugg), θ^0(.), θ^1(.), p_t^s(.)	0.09 (0.58)	0.79 (0.41)	0.56 (0.58)	—
ψ^s(fcov+rugg+ndvi), θ^0(.), θ^1(.), p_t^s(.)	0.45 (1.31)	0.38 (0.75)	0.45 (0.88)	−0.46 (0.30)
ψ^s(rugg), θ^0(.), b θ^1(.), p_t^s(.)	0.77 (1.02)	—	1.27 (0.93)	—

int, intercept; fcov, proportion of forest cover; rugg, ruggedness; ndvi, Normalized Difference Vegetation Index.

were more precise compared to estimates from the intercept-only models.

Examining differences in site-wise estimates of ψ_i from the two methods, we found that the occupancy estimates were strongly correlated (Pearson's correlation $r = .78$; $p < .001$). The relationship between site-specific ψ estimates from the two methods and their corresponding variances is presented in Figure 4. We estimated the combined overall probability of occurrence of sloth bears in the Bhadra region at $\hat{\psi}(\widehat{SE}) = 0.57$ (0.02). The same approach was used to compute combined site-specific probabilities of occupancy $\hat{\psi}_i$ and the respective $\widehat{SE}_i$. The combined site-specific occupancy probabilities in the Bhadra region are mapped in Figure 5.

4 | DISCUSSION

To our knowledge, only two studies so far have directly compared estimates of occupancy and detection from temporal vs. spatial replicates using empirical data: Charbonnel et al. (2014) with Pyrenean desmans *Galemys pyrenaicus*, and Whittington, Heuer, Hunt, Hebblewhite, and Lukacs (2015) with a large mammal assemblage in Canada. While Charbonnel et al. (2014) compare a suite of sampling schemes and corresponding models incorporating either spatial, temporal or both types of replication, Whittington et al. (2015) focus on a hierarchical approach, combining spatially and temporally replicated detection/non-detection data. Although novel in their respective

(a)

(b)
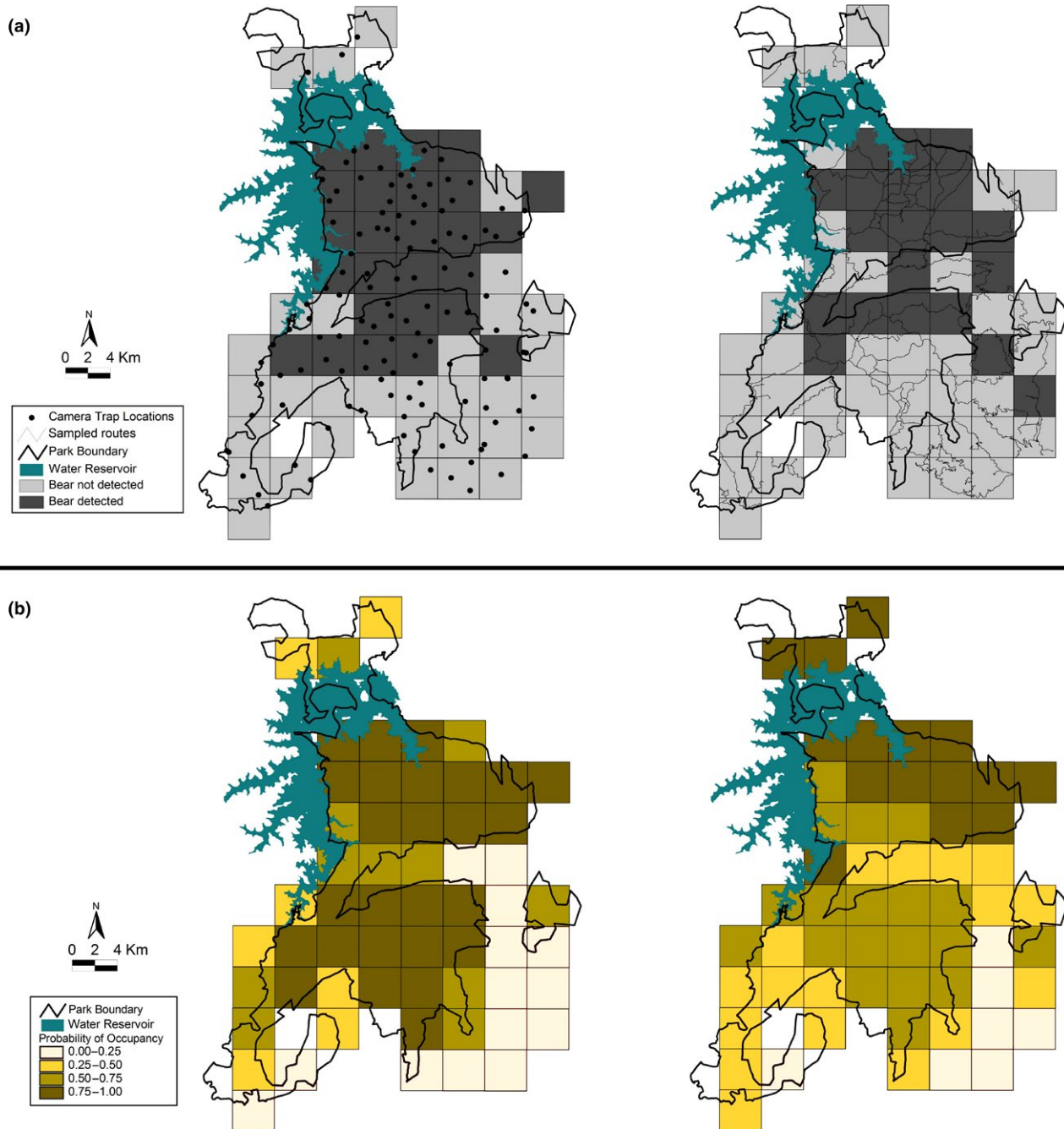
FIGURE 3 (a) Naïve occupancy of sloth bears in Bhadra region, based on camera trap surveys (left) and sign surveys (right). (b) Estimated probabilities of occupancy for sloth bears in Bhadra region, based on camera trap surveys (left) and sign surveys (right)

approaches, both studies relied on a single data type (indirect signs of their focal species) to provide detection/non-detection data for spatial and temporal analyses. Our comparisons, on the other hand, are from two distinct data sources from the same system. We use independent modelling approaches, as appropriate for the type of data and the scheme of sampling (Kéry, Royle, & Schmid, 2008), to derive estimates of patterns in occupancy and examine differences in the estimated patterns. The inferences on detectability and occupancy made by Charbonnel et al. are also limited by small sample sizes and estimates of occupancy close to a boundary (1). Moreover,

the two studies do not address the underlying spatial variation in occupancy and detection by including habitat-related or anthropogenic covariates.

In our study, estimates of ψ from the intercept-only models were $\psi(SE) = 0.48$ (0.07) and $\psi(SE) = 0.52$ (0.12) for camera trap surveys and sign surveys respectively. In contrast, the final estimates based on covariate models were substantially higher, at $\hat{\psi}^c(\widehat{SE}) = 0.58$ (0.03) and $\hat{\psi}^s(\widehat{SE}) = 0.56$ (0.03). Unmodelled heterogeneity in detectability is known to negatively bias estimated occupancy, while unmodelled heterogeneity in probability of occupancy is known to inflate estimated

FIGURE 4 Relationship between site-level estimates of occupancy ψ_i from camera trap surveys and sign surveys. The dots represent mean estimates and the corresponding ellipses represent standard errors along the respective axes. The filled dots were randomly sampled (with stratification) for representation
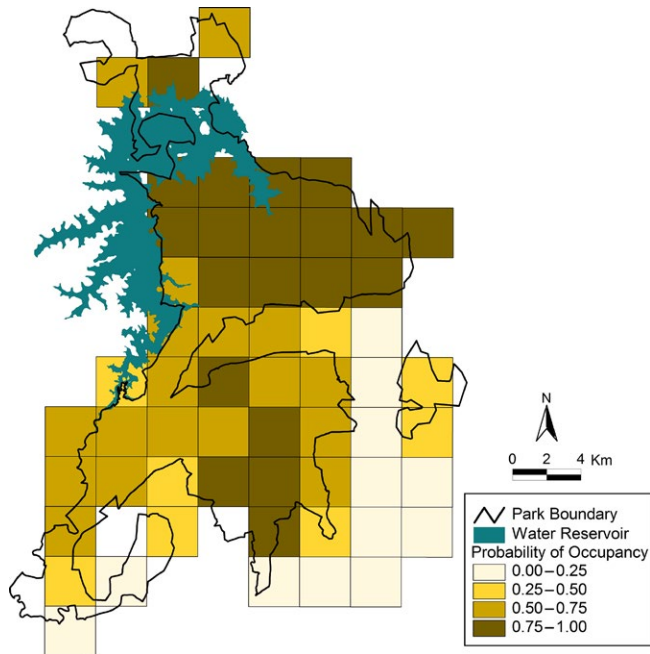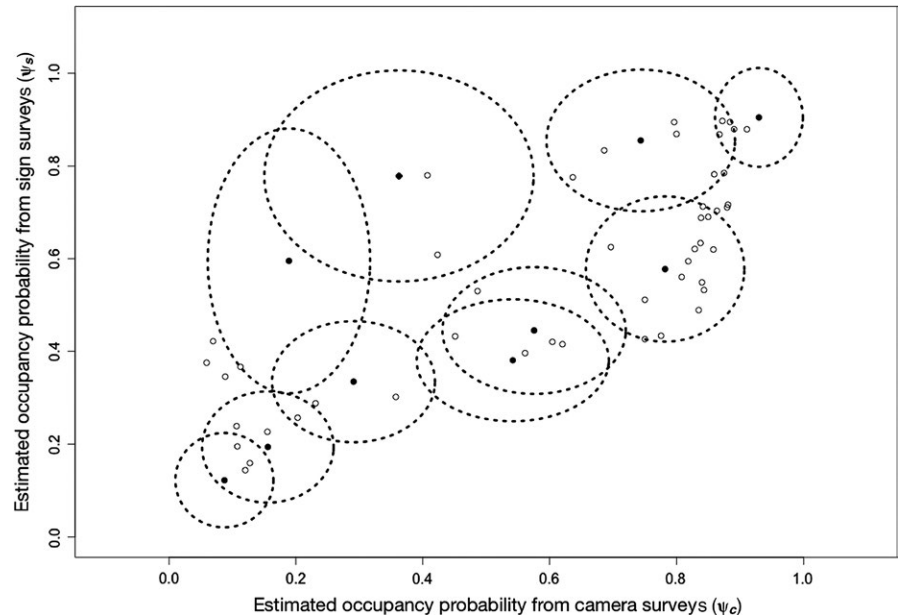
FIGURE 5 Combined estimates of sloth bear occupancy probabilities in the Bhadra region, calculated as a mean of estimates from camera trap surveys and sign surveys, weighted by the inverse of their respective variances

variance of occupancy (MacKenzie et al., 2006); our results are consistent in both respects. We note that detection probabilities from the two methods are not directly comparable; detectability from camera trap surveys (p^c) refers to probability of detecting the species in a site given its presence in the site, whereas detectability from sign surveys (p_t^s) refers to probability of detecting the species (from indirect signs) in a spatial replicate, given its presence in the site as well as its presence in the replicate.

For the camera trap data, we assessed model fit using the parametric bootstrap procedure (MacKenzie & Bailey, 2004) implemented within program PRESENCE. We were unable to assess fit of the correlated detections models to the sign survey data (Wright, Irvine, & Rodhouse, 2016) as sites had variable numbers of spatial replicates, requiring assessment of fit separately by cohort (a set of sites with the same pattern of missing observations). Of the 18 cohorts among 58 sites, most contained very few sites (e.g. six cohorts each contained a single site, two contained two sites, etc.). Nonetheless, we did assess fit of the MacKenzie et al. (2002) model, and also found that the Hines et al. (2010) model fit the sign survey data better (ΔAIC = 2.79), which affirms adequacy of fit for the sign survey data.

One of the primary aims of our study was to evaluate the ability of the two methods to identify ecological drivers of species occupancy. Our choice of covariates was based on previous ecological assessments of sloth bears across their geographical range (Dharaiya et al., 2016; Joshi, Garshelis, & Smith, 1995; Ratnayeke, van Manen, Pieris, & Pragash, 2007; Yoganand, Rice, Johnsingh, & Seidensticker, 2006). The predictors we used follow those reported by Puri et al. (2015), for sloth bears in the Western Ghats landscape. While our study area included coffee plantations on the periphery of the reserve, estimated β-coefficients from the camera trap analysis provided evidence for greater use of forested habitats by bears. We expected that areas with rugged terrain, which provide important resting and denning refuge (Ratnayeke, van Manen, Pieris, et al., 2007), would show higher probabilities of bear occupancy. We had also predicted that bears would preferentially occupy drier, more open habitats. However, statistical support for the magnitude of influence of these covariates was weak (95% confidence intervals straddled 0). We suspect that the weak covariate support might be due to the spatial scale at which our assessments were made, and the potential role of other unmeasured covariates inducing variation in probability of occupancy. It is likely that fine-scale factors such as the presence/abundance of fruiting trees

and distribution of termite mounds (which we were unable to measure during this study), would better explain patterns of sloth bear occupancy at this spatial scale.

4.1 | Implications for management

The importance of accounting for imperfect detection in assessing species distributions has been demonstrated in numerous studies, particularly for threatened or elusive species, where obtaining occurrence data from direct sightings or physical capture poses logistical difficulties (Karanth et al., 2011; Linkie et al., 2007; Olea & Mateo-Tomás, 2011; Sunarto et al., 2012). Several studies of large mammals, many of which are of conservation importance, have used indirect signs as the primary source of occurrence data (e.g. Gopalaswamy et al., 2012; Karanth et al., 2011; Kendall, Metzgar, Patterson, & Steele, 1992; Stephens, Zaumyslova, Miquelle, Myslenkov, & Hayward, 2006). Obtaining temporal replicates in such cases (while maintaining independence of detections) can be labour intensive, and methods such as camera trap surveys (which generate temporally replicated data) can also entail huge resource investments (Srbek-Araujo & Chiarello, 2005).

A multitude of reasons, such as difficult terrain, access, hostile field conditions and the need for independence of sign detections across replicates, restrict most sign-based surveys to rely on data from spatial replication. While ecologists have correctly cautioned that space-for-time substitutions may underestimate effects of predictors on ecological patterns (e.g. see França et al., 2016 for human impacts on biodiversity), our findings provide substantial support for using spatial replication as a surrogate for temporal replication in occupancy estimation, provided that the subsequent modelling explicitly accounts for the particular sampling processes brought in by substituting space for time.

We selected the sloth bear as an example for comparing overall estimates and spatial patterns of habitat occupancy from temporally and spatially replicated data. Our choice of study species offered clear advantages in ensuring no false positive detections because photo-captures of sloth bears from camera trap surveys and indirect signs of the species are unmistakable. The geographical location of the study was chosen to provide adequate sample sizes for drawing these inferences. However, for species that occur across much larger landscapes at lower local densities, these types of surveys may still yield very sparse data (see Steinmetz, Seuaturien, & Chutipong, 2013). Field survey methods employing one approach or the other may yield parameter estimates that are biased or too imprecise to effectively inform management. In such cases, a formal integration of the two approaches may provide the required gain in precision. Although there have been some attempts in this direction (Blanc, Marboutin, Gatti, Zimmermann, & Gimenez, 2014; Mordecai, Mattsson, Tzilkowski, & Cooper, 2011; Nichols et al., 2008), we anticipate the development of fully integrated hierarchical occupancy models that can combine estimates derived from data generated from multiple field methods (each with its corresponding model of the observation process), to obtain more reliable and more precise estimates of the state variables of interest.

AUTHORS' CONTRIBUTIONS

A.S., M.P. and K.U.K. conceived the study; A.S., N.S.K. and K.U.K. collected the data; A.S., M.P. and D.J. analysed the data; A.S., M.P., N.S.K., D.J. and K.U.K. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

The data used in this study include geo-spatial locations of a threatened species, restricting us from making them publicly available. Some parts of the data may be made available to individuals or institutions upon specific request. Data requests can be directed to the corresponding author.

ORCID

Arjun Srivathsa   iD   http://orcid.org/0000-0003-2935-3857

REFERENCES

Bali, A., Kumar, A., & Krishnaswamy, J. (2007). The mammalian communities in coffee plantations around a protected area in the Western Ghats, India. *Biological Conservation*, *139*, 93–102.

Blanc, L., Marboutin, E., Gatti, S., Zimmermann, F., & Gimenez, O. (2014). Improving abundance estimation by combining capture–recapture and occupancy data: Example with a large carnivore. *Journal of Applied Ecology*, *51*, 1733–1739.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer-Verlag.

Burton, A. C., Sam, M. K., Balangtaa, C., & Brashares, J. S. (2012). Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. *PLoS ONE*, *7*, e38007.

Cade, B. S. (2015). Model averaging and muddled multimodel inferences. *Ecology*, *96*, 2370–2382.

Charbonnel, A., D'Amico, F., Besnard, A., Blanc, F., Buisson, L., Némoz, M., & Laffaille, P. (2014). Spatial replicates as an alternative to temporal

replicates for occupancy modelling when surveys are based on linear features of the landscape. *Journal of Applied Ecology*, 51, 1425–1433.

Dharaiya, N., Bargali, H. S., & Sharp, T. (2016). *Melursus ursinus*. The IUCN Red List of Threatened Species 2016: e.T13143A45033815.

Doherty, P. F., White, G. C., & Burnham, K. P. (2012). Comparison of model building and selection strategies. *Journal of Ornithology*, 152, 317–323.

Elith, J., & Leathwick, J. R. (2009). Species distribution models: Ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, 40, 677–697.

França, F., Louzada, J., Korasaki, V., Griffiths, H., Silveira, J. M., & Barlow, J. (2016). Do space-for-time assessments underestimate the impacts of logging on tropical biodiversity? An Amazonian case study using dung beetles. *Journal of Applied Ecology*, 53, 1098–1105.

Garshelis, D. L., Joshi, A. R., & Smith, J. L. D. (1999). Estimating density and relative abundance of sloth bears. *Ursus*, 11, 87–98.

Gopalaswamy, A. M., Karanth, K. U., Kumar, N. S., & Macdonald, D. W. (2012). Estimating tropical forest ungulate densities from sign surveys using abundance models of occupancy. *Animal Conservation*, 15, 669–679.

Guillera-Arroita, G. (2011). Impact of sampling with replacement in occupancy studies with spatial replication. *Methods in Ecology and Evolution*, 2, 401–406.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: Advances, challenges and opportunities. *Ecography*, 40, 281–295.

Guillera-Arroita, G., Lahoz-Monfort, J. J., Elith, J., Gordon, A., Kujala, H., Lentini, P. E., … Wintle, B. A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*, 24, 276–292.

Guillera-Arroita, G., Morgan, B. J., Ridout, M. S., & Linkie, M. (2011). Species occupancy modeling for detection data collected along a transect. *Journal of Agricultural, Biological, and Environmental Statistics*, 16, 301–317.

Guillera-Arroita, G., Ridout, M. S., Morgan, B. J., & Linkie, M. (2012). Models for species-detection data collected along transects in the presence of abundance-induced heterogeneity and clustering in the detection process. *Methods in Ecology and Evolution*, 3, 358–367.

Hartung, J., Knapp, G., & Sinha, B. K. (2011). *Statistical meta-analysis with applications* (vol. 738, pp. 35–42). Hoboken, NJ: John Wiley & Sons.

Hines, J. E. (2006). *PRESENCE – Software to estimate patch occupancy and related parameters. Version 5.7. USGS-PWRC*. Retrieved from http://www.mbr-pwrc.usgs.gov/software/presence.html

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

Jathanna, D., Karanth, K. U., & Johnsingh, A. J. T. (2003). Estimation of large herbivore densities in the tropical forests of southern India using distance sampling. *Journal of Zoology*, 261, 285–290.

Joshi, A. R., Garshelis, D. L., & Smith, J. L. D. (1995). Home ranges of sloth bears in Nepal: Implications for conservation. *The Journal of Wildlife Management*, 59, 204–214.

Karanth, K. K. (2007). Making resettlement work: The case of India's Bhadra Wildlife Sanctuary. *Biological Conservation*, 139, 315–324.

Karanth, K. U., Gopalaswamy, A. M., Kumar, S. N., Vaidyanathan, S., Nichols, J. D., & 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. U., Nichols, J. D., Kumar, N. S., Link, W. A., & Hines, J. E. (2004). Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the United States of America*, 101, 4854–4858.

Kendall, K. C., Metzgar, L. H., Patterson, D. A., & Steele, B. M. (1992). Power of sign surveys to monitor population trends. *Ecological Applications*, 2, 422–430.

Kendall, W. L., & White, G. C. (2009). A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *Journal of Applied Ecology*, 46, 1182–1188.

Kéry, M., Royle, J. A., & Schmid, H. (2008). Importance of sampling design and analysis in animal population studies: A comment on Sergio et al. *Journal of Applied Ecology*, 45, 981–986.

Linkie, M., Dinata, Y., Nugroho, A., & Haidir, I. A. (2007). Estimating occupancy of a data deficient mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region, Sumatra. *Biological Conservation*, 137, 20–27.

Long, R. A., Donovan, T. M., MacKay, P., Zielinski, W. J., & Buzas, J. S. (2011). Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape Ecology*, 26, 327–340.

MacKenzie, D. I., & Bailey, L. L. (2004). Assessing the fit of site-occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics*, 9, 300–318.

MacKenzie, D. I., & Nichols, J. D. (2004). Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation*, 27, 461–467.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.

MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Hines, J. E., & Bailey, L. L. (2006). *Occupancy estimation and modeling: Inferring patterns and dynamics of species occurrence*. San Diego, CA: Elsevier.

Miller, D. A., Nichols, J. D., McClintock, B. T., Grant, E. H. C., Bailey, L. L., & Weir, L. A. (2011). Improving occupancy estimation when two types of observational error occur: Non-detection and species misidentification. *Ecology*, 92, 1422–1428.

Mordecai, R. S., Mattsson, B. J., Tzilkowski, C. J., & Cooper, R. J. (2011). Addressing challenges when studying mobile or episodic species: Hierarchical Bayes estimation of occupancy and use. *Journal of Applied Ecology*, 48, 56–66.

Nichols, J. D., Bailey, L. L., O'Connell, A. F. Jr, Talancy, N. W., Grant, E. H. C., Gilbert, A. T., … Thomas, P. (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, 45, 1321–1329.

Olea, P. P., & Mateo-Tomás, P. (2011). Spatially explicit estimation of occupancy, detection probability and survey effort needed to inform conservation planning. *Diversity and Distributions*, 17, 714–724.

Olliff, E. R. R., Cline, C. W., Bruen, D. C., Yarmchuk, E. J., Pickles, R. S. A., & Hunter, R. T. B. (2014). The Panthercam – A camera trap optimized for monitoring wild felids. *The Wild Felid Research and Management Association*, 7, 3–8.

Pillay, R., Johnsingh, A. J. T., Raghunath, R., & Madhusudan, M. D. (2011). Patterns of spatiotemporal change in large mammal distribution and abundance in the southern Western Ghats, India. *Biological Conservation*, 144, 1567–1576.

Puri, M., Srivathsa, A., Karanth, K. K., Kumar, N. S., & Karanth, K. U. (2015). Multiscale distribution models for conserving widespread species: The case of sloth bear *Melursus ursinus* in India. *Diversity and Distributions*, 21, 1087–1100.

Ratnayeke, S., van Manen, F. T., & Padmalal, U. K. G. K. (2007). Home ranges and habitat use of sloth bears *Melursus ursinus inornatus* in Wasgomuwa National Park, Sri Lanka. *Wildlife Biology*, 13, 272–284.

Ratnayeke, S., van Manen, F. T., Pieris, R., & Pragash, V. S. J. (2007). Landscape characteristics of sloth bear range in Sri Lanka. *Ursus*, 18, 189–202.

Rhodes, J. R., Lunney, D., Moon, C., Matthews, A., & McAlpine, C. A. (2011). The consequences of using indirect signs that decay to determine species' occupancy. *Ecography*, 34, 141–150.

Riley, S. J., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantifies topographic heterogeneity. *Intermountain Journal of Sciences*, 5, 23–27.

Srbek-Araujo, A. C., & Chiarello, A. G. (2005). Is camera-trapping an efficient method for surveying mammals in Neotropical forests? A

case study in south-eastern Brazil. *Journal of Tropical Ecology*, *21*, 121–125.

Srivathsa, A., Karanth, K. K., Jathanna, D., Kumar, S. N., & 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., & Chutipong, W. (2013). Tigers, leopards, and dholes in a half-empty forest: Assessing species interactions in a guild of threatened carnivores. *Biological Conservation*, *163*, 68–78.

Stephens, P. A., Zaumyslova, O. Y., Miquelle, D. G., Myslenkov, A. I., & Hayward, G. D. (2006). Estimating population density from indirect sign: Track counts and the Formozov–Malyshev–Pereleshin formula. *Animal Conservation*, *9*, 339–348.

Sunarto, S., Kelly, M. J., Parakkasi, K., Klenzendorf, S., Septayuda, E., & Kurniawan, H. (2012). Tigers need cover: Multi-scale occupancy study of the big cat in Sumatran forest and plantation landscapes. *PLoS ONE*, *7*, e30859.

Thorn, M., Green, M., Bateman, P. W., Waite, S., & Scott, D. M. (2011). Brown hyaenas on roads: Estimating carnivore occupancy and abundance using spatially auto-correlated sign survey replicates. *Biological Conservation*, *144*, 1799–1807.

Whittington, J., Heuer, K., Hunt, B., Hebblewhite, M., & Lukacs, P. M. (2015). Estimating occupancy using spatially and temporally replicated snow surveys. *Animal Conservation*, *18*, 92–101.

Wong, W. M., & Linkie, M. (2013). Managing sun bears in a changing tropical landscape. *Diversity and Distributions*, *19*, 700–709.

Wright, W. J., Irvine, K. M., & Rodhouse, T. J. (2016). A goodness-of-fit test for occupancy models with correlated within-season revisits. *Ecology and Evolution*, *6*, 5404–5415.

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, J. A., Nichols, J. D., Campbell Grant, E. H., & Veran, S. (2013). Presence-only modelling using MAXENT: When can we trust the inferences? *Methods in Ecology and Evolution*, *4*, 236–243.

Yoganand, K. (2005). *Behavioural ecology of sloth bear (Melursus ursinus) in Panna National Park, Central India*. PhD Thesis, Saurashtra University, India.

Yoganand, K., Rice, C. G., Johnsingh, A. J. T., & Seidensticker, J. (2006). Is the Sloth bear in India Secure? A preliminary report on distribution, threats and conservation requirements. *Journal of the Bombay Natural History Society*, *103*, 172–181.