

Estimating tropical forest ungulate densities from sign surveys using abundance models of occupancy

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Abstract

Large ungulates critically influence forest structure and functioning besides being seriously threatened by anthropogenic pressures. For assessing their populations, surveys of ungulate sign encounters are widely used because of their practicality. However, these yield unreliable results because of their failure to address the problem of imperfect detection. Here, we present an innovative application to address this key weakness in traditional ungulate sign surveys. We describe the ecological process of ungulate sign deposition as well as the observation process of sign detection in our modelling. We simulate 183 ecological and sampling-related parameter values to first evaluate model performance. Simulation results demonstrate that we can achieve good estimates of animal density when the radius of the animal daily movement range is accounted for during survey design. We design and conduct a field survey of ungulate signs to estimate ungulate densities using both occupancy and distance sampling approaches. For five species of ungulates, the densities estimated from our sign survey (number of ungulate clusters km⁻²) were 1.46(0.68) chital *Axis axis*, 1.42(0.67) sambar *Rusa unicolor*, 1.01(0.44) gaur *Bos gaurus*, 0.74(0.39) wild pig *Sus scrofa* and 1.42(1.59) muntjac *Muntiacus muntjak*, and were similar to those generated from line transect sampling 2.16(0.76) chital, 2.47(0.56) sambar, 0.94(0.3) gaur, 1.09(0.37) wild pig and 4.03(0.83) muntjac, except for muntjac. The potential utility of this approach extends beyond sign surveys of forest ungulates to a wider range of animal monitoring contexts, including those based on scent-station surveys and camera trap surveys of elusive mammals.

Introduction

Most large mammal species are threatened globally by over-hunting and habitat destruction, consequent upon rapid human population growth and economic development (Ceballos *et al.*, 2005; Schipper *et al.*, 2008). Large ungulates (>15 kg body mass) are particularly vulnerable because of biological traits, such as their wide-ranging movements, tendency to forage on croplands and body size that attracts hunters (Macdonald, 2001; Madhusudan & Mishra, 2003). However, densities of most tropical forest ungulate species are now significantly depressed, and several species are threatened with extinction because of human impacts, potentially driving major changes in forest ecology. Several species impact agriculture or forestry, and many are harvested for food by local populations. Given their critical ecological role, reliable assessment of their populations assumes importance. Effective conservation, or even sus-

tained harvest of ungulate populations, requires reliable estimates of their population size (abundance) and densities (Katzner *et al.*, 2011).

In the face of imperfect detection, capture–recapture modelling (Williams, Nichols & Conroy, 2002) has been successfully used for estimating abundance of ungulate species that are individually identifiable from photographs (Goswami, Madhusudan & Karanth, 2007) or from fecal DNA (Eggert, Eggert & Woodruff, 2003). Photo captures require specialized camera trap surveys (O’Connell, Nichols & Karanth, 2010), whereas DNA captures demand sophisticated and costly laboratory support, thus limiting their application in the field. Although estimation methods based on photographic encounter rates have been proposed for individually unidentifiable species (Rowcliffe *et al.*, 2008), these require accurate data on animal movement rates that are often difficult to acquire in the field (Rovero & Marshall, 2009).

Line transect surveys (Buckland *et al.*, 2001) involve visual counts of either ungulates (Karanth & Sunquist, 1992; Jathanna, Karanth & Johnsingh, 2003) or their dung (Plumptre & Harris, 1995; Marques *et al.*, 2001), and are widely employed to estimate abundance. However, visual surveys are sometimes rendered impractical by low densities or extreme wariness of animals, dense vegetation or difficult terrain. Often, converting dung counts from line or point transect surveys (Buckland *et al.*, 2001) into estimates of ungulate density is also problematic because of difficulties in estimating species-specific rates for daily defecation and dung decay across seasons and habitats (Nchanji & Plumptre, 2001; Laing *et al.*, 2003). Furthermore, the amount of dung or tracks deposited by an individual ungulate is usually so large that establishing a reliable statistical relationship between such signs and actual animal densities is a futile exercise.

Consequently, there exists a need for reliable, accurate and a cost-effective method for monitoring forest ungulate populations in situations where transect surveys are not feasible – particularly when abundance is low. This is a more general abundance estimation problem in ecology and conservation that has received methodological focus in recent times (see Isaac *et al.*, 2011; Katzner *et al.*, 2011; Rowcliffe *et al.*, 2011; Archaux, Henry & Gimenez, 2012). For our specific problem with forest ungulates, and more broadly across a range of taxa, we believe that the conceptual framework offered by MacKenzie *et al.* (2006) and Royle & Dorazio (2008) is appropriate to address our specific need. We present here the outcome of a rigorous field study that develops and validates the use of such an approach that shows promise.

Study species and objectives

We develop a practical field sampling and density estimation protocol based on field counts of easily detectable signs (dung or tracks) for five species of Asian forest ungulates: gaur *Bos gaurus*, sambar *Rusa unicolor*, chital *Axis axis*, wild pig *Sus scrofa* and muntjac *Muntiacus muntjak*. These species exhibit a diverse range of body sizes (20–1000 kg), social behaviors (solitary territorial to solitary wide-ranging to social herding), diets (selective feeders to browsers to mixed feeders to grazers), habitat preferences (dense forests to open grasslands; Macdonald, 2001) and variations in population densities (0.89–50 animals km⁻²).

Our methodology rests on the application of an abundance model of occupancy (see Royle & Nichols, 2003) on designed sign survey data. Although this model is designed for temporally replicated samples, we explore its relevance for spatially replicated samples (hereafter called AOS model, for abundance–occupancy–spatial) through simulations. We validate properties of our estimates with density estimates derived from extensive computer simulations, and compare it with density estimates derived from line transect surveys using visual counts.

Study area

We conducted this study in Bhadra Tiger Reserve, Karnataka, India (Fig. 1; Longitude 75°29' E to 75°47' E and Latitude 13°22' to 13°47' N) from April to June 2007. The line transect survey was carried out between April and May, and the occupancy survey was conducted during the month of June when pre-monsoon showers begin. This 492 km² moist deciduous forest tract (Jathanna *et al.*, 2003) supports populations of the five forest ungulate species of interest. It also supports several large mammal species, such as Asian elephant *Elephas maximus*, sloth bear *Melursus ursinus*, dhole or Asiatic wild dog *Cuon alpinus*, leopard *Panthera pardus* and tiger *Panthera tigris*, and is considered to be an important conservation site within a global biodiversity hot spot (Das *et al.*, 2006). Most of these ungulate species currently occur well below their optimal densities here (Jathanna *et al.*, 2003; Karanth *et al.*, 2004) because the reserve is still in the process of recovering from past anthropogenic impacts (Karanth, 1982, 2007; Jathanna *et al.*, 2003). Within the Bhadra reserve, we chose a specific study area of 178 km² size in Muthodi (Fig. 1).

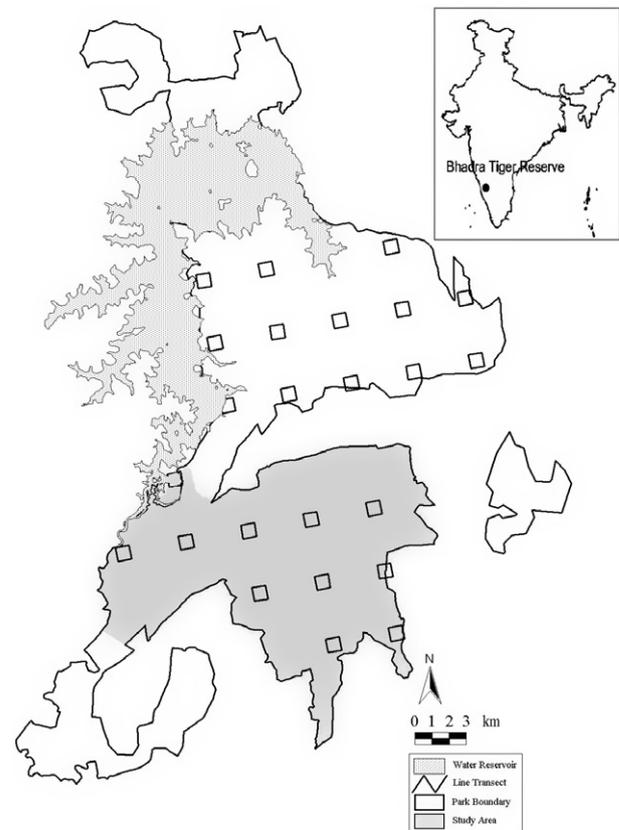


Figure 1 Map of Bhadra Tiger Reserve with a system of line transects (inset map shows the location of the park in India). The study area (Muthodi) is shaded grey.

Methods

Design of simulations

Model component for the spatial distribution of ungulates and their signs

Ungulates are assumed to be spatially distributed in the study area following a random poisson process (Pielou, 1969: 81–82). For the simulation exercises, we utilized a grid of $20 \times 20 = 400$ cells to overcome potential biases of small sample size on parameter estimates. Point locations of ungulate groups were generated using the software package R (R Development Core Team, 2009), with their x and y coordinates in a Cartesian plane. Locations were drawn from a uniform distribution so that a binomial process can describe the number of individual groups in each cell and be approximated as a poisson variate. Let $S = (S_x, S_y)$ represent points on the Cartesian plane and defined as a collection of activity range centres of all individual ungulate groups present within the grid (Fig. 2).

For a square grid composed of $Q (= 400)$ cells, S_x and S_y are modelled as follows:

$$S_x \sim \text{Uniform}(0, \sqrt{Q})$$

$$S_y \sim \text{Uniform}(0, \sqrt{Q})$$

We assume that signs (tracks or dung) generated by individual ungulate groups are deposited at a uniform rate over a pre-defined period within a circle of radius R (Fig. 2).

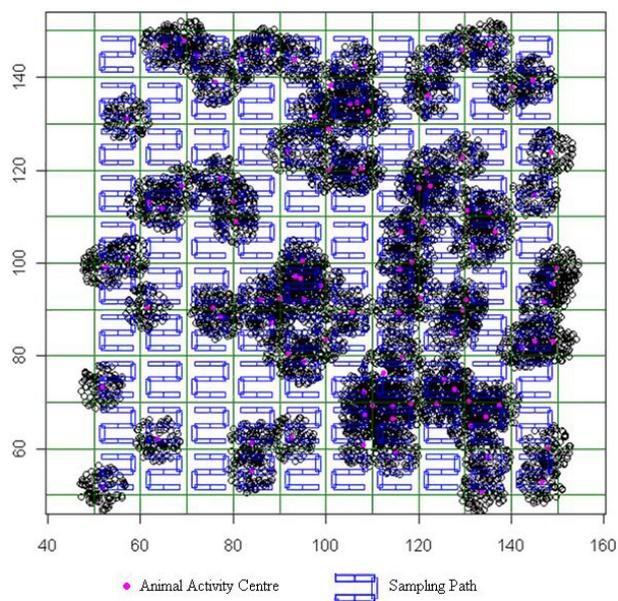


Figure 2 An example of a simulation output in R describing the ecological process of sign deposition (black circles) around animal group activity centres (pink dots), within 100 sampling grid cells.

Using the simulation approach described by Hlynka & Loach (2005), we define two additional random variables:

$$\alpha \sim \text{Uniform}(0, R)$$

$$\theta \sim \text{Uniform}(0, 2\pi)$$

For an individual ungulate group u , located at x_u, y_u represents one possible location of a sign.

Then the location (x_u, y_u) is generated by

$$x_u = S_{x(u)} + \sqrt{\alpha} \cos(\theta)$$

$$y_u = S_{y(u)} + \sqrt{\alpha} \sin(\theta)$$

The purpose of employing the Hlynka & Loach (2005) approach is to ensure that signs are ‘uniformly’ distributed within a circle of a fixed radius without clustering either at the centre or at the rim. We acknowledge that other distributions may also be relevant in the simulation, such as the bivariate normal distribution commonly employed in spatially explicit capture–recapture modelling nowadays (Borchers & Efford, 2008; Royle *et al.*, 2009).

Model component for the field survey sampling process

The survey was designed so that skilled field personnel record species presence by detecting signs (fresh tracks and dung), systematically along S-shaped predetermined survey routes within each grid cell (Fig. 3). For performing computer simulations, we treated sign detections as occurring over narrow detection strips on such trails. Each trail consists of eight segments, which form ‘spatial replicates’ (Hines *et al.*, 2010) within a cell (Fig. 3). Observers record detections or non-detections of signs of each ungulate species only once on each replicate.

We simulated two broad scenarios of detection conditions. The first assumed that if signs are present in a spatial replicate, observers detect species presence with certainty. In the second, a more realistic scenario, we permitted the probability that observers could miss some signs present on a replicate.

We modelled the probability of detecting ungulate group presence using the Royle & Nichols (2003) formulation

$$p_{\text{sign}(ij)} = 1 - (1 - r_{\text{sign}})^{N_{\text{sign}(ij)}}$$

where $p_{\text{sign}(ij)}$ = probability of detecting ungulate group presence if at least one sign is in the spatial replicate j given presence of ungulate group in the replicate of cell i ; r_{sign} = probability of detecting a sign of an individual present along a segment; $N_{\text{sign}(ij)}$ = total number of signs actually present at spatial replicate j of cell i . Hence, given presence

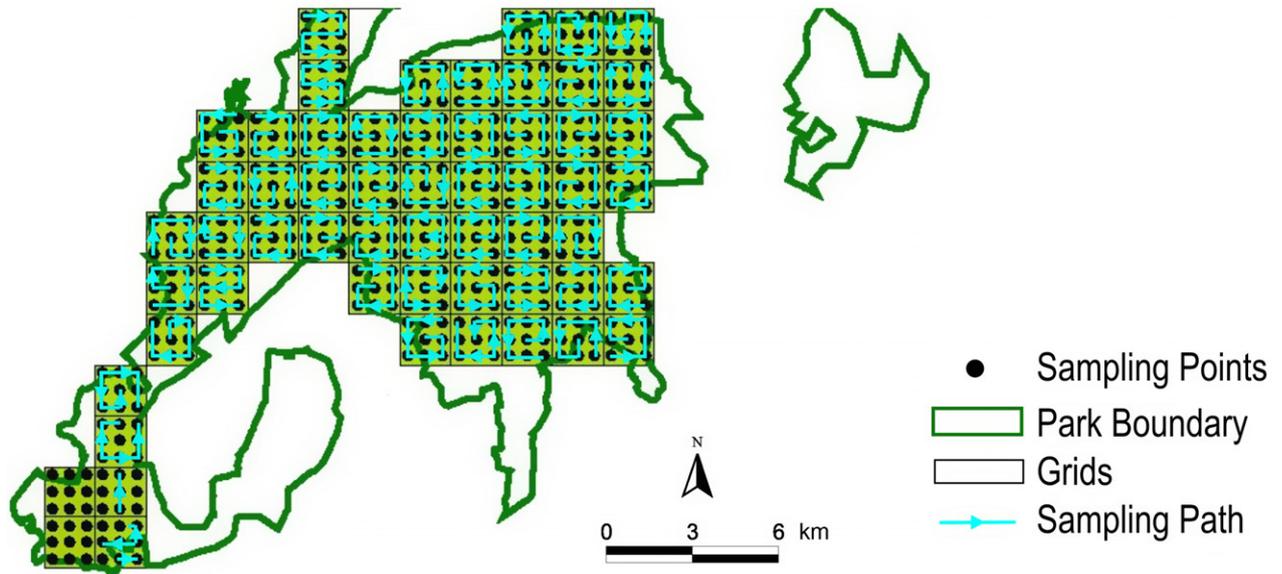


Figure 3 Ungulate sign survey conducted in 55 grid cells (each of size 3.24 km²) within Muthodi (Bhadra Tiger Reserve).

of ≥ 1 sign in the replicate, the detection of sign at replicate j of cell i , d_{ij} was simulated as a Bernoulli random deviate,

$$d_{ij} \sim \text{Bernoulli}(p_{\text{sign}(ij)})$$

In simulations, the following parameters were varied: (1) animal group density per grid cell via the total number of animal group activity centres N of the grid; (2) the number of signs deposited by each animal group N_{sign} ; (3) the radius of the circle that represents the daily movement range R of an individual animal group; and (4) the probability of detecting an individual animal groups sign, r_{sign} on a spatial replicate, although we did not assess for heterogeneity in r_{sign} between replicates. We expected, *a priori*, that the value of R will play a critical role in the estimates of abundance.

In addition to the initial large sample of 400 grid cells, simulations were also run to investigate model performance with fewer cells to cover a smaller area. We simulate 100 datasets based on 183 plausible scenarios to evaluate the performance of the AOS model. All simulations were coded and executed using software package R (R Development Core Team, 2009). The simulation and the estimation codes are available upon request.

Model validation using simulations

Counts of signs generated from the simulated data from spatial replicate j in cell i were stored in matrix form (number of grid cells [sites] \times number of segments [spatial replicates] in each cell). For example, in a survey for animal signs as in (Fig. 2) that consists of eight spatial replicates within a cell, the vector representing actual number of signs in a cell $N_{\text{sign}(i,j)}$ may look as follows.

$$N_{\text{sign}(i,j)} = \{23\ 24\ 0\ 2\ 4\ 68\ 23\ 5\}$$

By reducing this numerical vector into a binary detection and non-detection form,

$$w_i = \{11011111\}$$

Detection vector w_i will take this form if the value of $r_{\text{sign}} = 1$ because $p_{\text{sign}(ij)} = 1$.

However, if the value of r_{sign} takes any other value between 0 and 1 due to imperfect detections, for example if $r_{\text{sign}} = 0.5$, then one possible manifestation of w_i can be,

$$w_i = \{11001111\}$$

The extra zero that now appears in w_i in the fourth column is a chance consequence arising out of the fact that $p_{\text{sign}(i4)} = 1 - (1 - 0.5)^2 = 0.75$ (which is < 1). Applying the same logic at the cell level,

$$p_{\text{animal}(i)} = 1 - (1 - r_{\text{animal}})^{N_{\text{animal}(i)}}$$

where, $p_{\text{animal}(i)}$ is the probability of detecting at least one animal group in cell i in a replicate. r_{animal} is the probability of detecting an individual animal group in a replicate. $N_{\text{animal}(i)}$ is the number of animal groups in cell i .

In our sampling situation, the probability of detecting an individual animal group r_{animal} is the result of the product: $r_{\text{animal}} = (\text{probability of an individual group located in the vicinity of a replicate}) \times (\text{probability of detecting at least one sign of an individual group on replicate conditional on group located in the vicinity})$.

Our sampling situation and protocol does not provide sufficient information to estimate the earlier two probabilities describing r_{animal} separately. Further, the quantity r_{animal} can vary between replicates within a cell as a consequence of the earlier two probabilities. In reality, we would expect the second probability, that is the probability of detecting at least one sign of an individual group on replicate, to very rapidly approach unity because the quantum of signs usually deposited by an ungulate group is very high (usually in several thousands). So our main concern is the possibility of variation in the quantity r_{animal} as a result of the location of a spatial replicate relative to the location of ungulate groups because the AOS model that we apply is based on the assumption that r_{animal} will be a constant. Our objective is to investigate how the AOS model performs in spite of this assumption violation under varying conditions of these parameters in our simulations (Appendices S1, S2 and S3).

We considered the application of the poisson version of the likelihood (Royle & Nichols, 2003), which takes the form,

$$L(w_i | r_{animal}, \lambda) = \prod_{i=1}^M \sum_{k=0}^K \binom{T_i}{w_i} [1 - (1 - r_{animal})^k]^{w_i} \times [(1 - r_{animal})^k]^{T_i - w_i} \left[\frac{e^{-\lambda} \lambda^k}{k!} \right]$$

where w_i is the number of detections in cell i (i.e. the sum of the vector d_i). λ is the average number of animal groups in each cell. M is the total number of cells. T_i is the number of trials (sampled replicates) in cell i . K is the upper limit of the number of animal groups in a cell.

We assessed the quality of the earlier estimator for estimating λ against simulated data (see Appendices S1, S2 and S3) using the root mean squared error (RMSE; Casella & Berger, 1990):

$$RMSE(\hat{\lambda}) = \sqrt{Var(\hat{\lambda}) + [\hat{\lambda} - \lambda_{true}]^2}$$

where λ_{true} = true value of λ defined in the simulation. We also fit the over-dispersed version (Pielou, 1969, pages 94–95) of the earlier likelihood to the real data (Royle & Nichols, 2003) using the form

$$L(w_i | r_{animal}, \lambda) = \prod_{i=1}^M \sum_{k=0}^K \binom{T_i}{w_i} [1 - (1 - r_{animal})^k]^{w_i} \times [(1 - r_{animal})^k]^{T_i - w_i} \left[\frac{\Gamma(k + a)}{k! \Gamma(a)} \right] \times \left[\frac{(1/a) \mu}{1 + (1/a) \mu} \right]^k \left[\frac{1}{1 + (1/a) \mu} \right]^a$$

where, μ is the average number of animal groups in each cell and a is the over-dispersion parameter.

Throughout our formulation, we describe $N_{animal(i)}$ and λ or μ as the number of animal groups rather than number of animals, deviating from the original Royle & Nichols, (2003) formulation, because our study species occur in

groups of varying sizes (Karanth & Sunquist, 1992). Failure to recognize this behavioral trait will seriously distort our interpretation of the results because the AOS model assumes that the probability $1 - r_{animal}$ can be multiplied $N_{animal(i)}$ times, implying *independence*.

Field surveys

Choice of grid cell size

We choose a grid cell size of 3.24 km², which is sufficiently large to circumscribe expected daily movement of the study species based on home range size and movement rates reported in field studies. For sambar, see Schaller (1967), Dinerstein (1979), and Sankar & Acharya (2004); for gaur, see Conry (1989) and Sankar *et al.* (2000); for chital, see Schaller (1967), Mishra (1982), Mishra & Wemmer (1987), and Moe & Wegge (1997); for muntjac, see Barrette (1977, 1987), and Odden & Wegge (2007); and for wild pig, see Singer (1981), Baber & Coblentz (1986), and Caley (1997).

The study area in Muthodi (178 km²) is partitioned into 55 grid cells. Each cell contains nine equally spaced point locations called ‘sampling destinations’, and the distance between any two adjacent points is 600 m (Fig. 3). Each spatial replicate is visualized as a 300-m trail segment along the sampling route passing through these nine sampling destinations. Consequently, each grid cell contained 16 spatial replicates (Fig. 3).

Survey teams consisting of 2–3 skilled field personnel searched sampling routes in each cell to locate fresh (< 24 h old) tracks or dung of ungulates. Teams optimized sign detections by deviating from the survey route by < 50 m on either side to search logging roads, river banks, stream beds, water holes, mineral licks or wallows, all the while ensuring proximity to nine sampling destinations and uniform spatial coverage of the cell.

The survey was conducted after light showers when fresh signs were clearly visible and detectable. Thus, we could reasonably assume that the individual animal depositing a sign was present within the cell. Field teams surveyed each cell within < 8–10 h to limit potential biases induced by animal movements between cells (Fig. 3).

Line transect surveys of ungulates

To derive independent estimates of ungulate density, we also used the standard line transect sampling method (Buckland *et al.*, 2001) based on visual detections. This method has been effectively employed since 1988 (Karanth & Sunquist, 1992; Jathanna *et al.*, 2003; Karanth *et al.*, 2004), and this study followed field and analytical protocols described elsewhere (Karanth, Thomas & Kumar, 2002; Thomas & Karanth, 2002). We used a subset of 11 line transects used for long-term monitoring of ungulate populations (Karanth *et al.*, 2008). The survey generated using design options in the program DISTANCE 5.0 (Thomas *et al.*, 2010) employed systematic transect placements at 3-km spacing, with a random start (Fig. 1). Each 3.2-km long transect

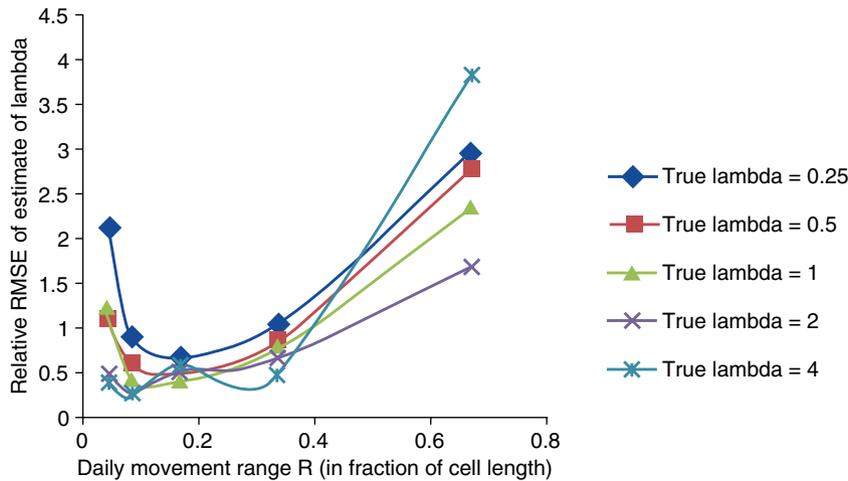


Figure 4 Effect of daily movement range R on the relative RMSE value of the estimate of $\hat{\lambda}$ from simulation exercises. Graph demonstrates that low or high values of R produces large relative RMSE values. RMSE, root mean squared error.

sampler is of a square geometry, with each side of 800 m in length. Each spatial replicate was sampled eight times – thus, a total walk effort of 272.8 km was invested.

Line transect data were analyzed using the program DISTANCE for each ungulate species. We fitted several plausible detection probability models generated under hazard-rate, half-normal and uniform detection functions to the observed distance data, to select the most appropriate models (see Buckland *et al.*, 2001). We generated estimates of detection probability, animal cluster densities, cluster size and animal densities (Thomas & Karanth, 2002).

Results

Simulations of occupancy models

Results of the various simulation runs are tabulated in Appendices S1, S2 and S3. We report only the key findings from these simulations. The RMSE values indicate that the model performed optimally (least relative RMSE value) when the number of animal groups per cell varied from 0.5 to 4 (Appendices S1 and S2). The RMSE values indicate (Appendices S1 and S2) that the model performance improved when the number of signs deposited by each animal group is increased. Similarly, in the face of imperfect detection of signs ($r_{sign} = 0.5$), the quality of the estimation drops, albeit only marginally. However, the number of signs deposited is usually so large that the effect of a decrease in r_{sign} is relatively negligible because p_{sign} would asymptote to a value very close to 1. We note here that p_{sign} is also influenced by the width of the strip considered in this simulation, which was maintained as a constant in our study.

We observe that the estimate of cell-specific abundance is most strongly influenced by the choice of R , the radius of the daily movement range, as indicated by a positive bias. We conclude that accuracy of the specification of R is critical for estimating animal abundance under the AOS model. We do note that the direction of the bias is consistent (Supporting Information Appendices S1 and S2). From the estimated

RMSE values, we observe that the model performs most optimally when the radius of the daily movement range of an animal group is set between 6 and 15% of the length of a grid cell (Fig. 4). Alternatively, if we have an accurate estimate of R , this bias can always be corrected.

We examined the effect of reduced sample sizes of grid cells because our field occupancy survey of large ungulates contain fewer than the 400 cells used in all other simulations. These results show that while the mean estimate of the parameter λ is positively biased by reduction in sample size, the median value of the estimate remains relatively unbiased. This is the classical small-sample size bias. These results confirm the desirability of having as many grid cells (say 200+) of the right size with > 8 replicates for reliable estimation of λ (also see Royle & Nichols, 2003). However, when the number of signs deposited is very large, the quality of the estimation improves drastically (see RMSE results in Supporting Information Appendix S3).

Estimates from field surveys

Influence of heterogeneity in detection probabilities on estimates of occupancy

The standard occupancy model (MacKenzie *et al.*, 2002) assumes that sign detection probabilities do not vary among cells even if animal abundance varies across them, whereas the AOS model permits such variation and attributes it to variation in cell-specific abundances. For four of the five study species (chital, sambar, gaur and wild pig), the occupancy models of AOS model fit the data better than the standard MacKenzie *et al.* (2002) model ($\Delta AIC = +36.43, +38.05, +59.38$ and $+5.80$ for chital, sambar, gaur and wild pig, respectively; Table 1). For muntjac, the smallest ungulate, the reverse was true ($\Delta AIC = -2.01$). These results indicate that heterogeneity in detection probabilities among cells, presumably due to varying cell-specific abundances, does exist for all ungulates except muntjac, although the wide standards errors weaken the inference.

Table 1 Comparison of performances of habitat occupancy models of MacKenzie *et al.* (2002) model and AOS model using data from sign surveys of ungulate species in Bhadra Tiger Reserve, India

Species	Number of spatial replicates per cell	AIC value from MacKenzie <i>et al.</i> (2002) model	AIC value from AOS model	ΔAIC
Chital	16	888.10	851.67	+36.43
Sambar	16	1147.01	1108.96	+38.05
Gaur	16	1187.56	1128.18	+59.38
Pig	16	765.26	759.46	+5.80
Muntjac	16	688.78	690.79	-2.01

AIC, Akaike's Information Criterion.

Table 2 Estimates of individual group-specific detection probability and cell-specific animal group abundance generated from AOS model using data from sign surveys of ungulate species in Bhadra Tiger Reserve, India. \hat{r} is the estimate of animal group-specific detection probability, $\hat{\lambda}$ or $\hat{\mu}$ is the estimate of average number of animal groups in a cell, \hat{a} is the over-dispersion parameter, $\hat{\rho}$ is the estimate of the correlation coefficient

Species	No. of spatial replicates	AOS poisson			AOS Over-dispersed poisson				ΔAIC
		$\hat{r}[\hat{SE}(\hat{r})]$	$\hat{\lambda}[\hat{SE}(\hat{\lambda})]$	$\hat{\rho}_{\lambda}$	$\hat{r}[\hat{SE}(\hat{r})]$	$\hat{\mu}[\hat{SE}(\hat{\mu})]$	$\hat{a}[\hat{SE}(\hat{a})]$	$\hat{\rho}_{\mu}$	
Chital	16	0.31 (0.07)	4.74 (1.23)	-0.96	0.30 (0.01)	4.98 (1.93)	71.6 (379.05)	-0.98	+2.03
Sambar	16	0.20 (0.05)	4.61 (1.21)	-0.96	0.08 (0.47)	12.13 (74.65)	6.12 (21.11)	-1.0	+2.07
Gaur	16	0.20 (0.04)	3.30 (0.80)	-0.93	0.03 (0.02)	23.71 (12.92)	3.04 (0.92)	-0.98	-1.43
Pig	16	0.08 (0.02)	2.41 (0.70)	-0.91	0.07 (0.025)	2.47 (0.875)	71.60 (525.49)	-0.94	+2.02
Muntjac	16	0.03 (0.02)	4.60 (2.86)	-0.99	0.03 (0.02)	4.84 (3.509)	71.59 (363.08)	-0.99	+2.04

AOS, abundance-occupancy-spatial.

Density estimates from AOS model

The parameter estimates, \hat{r}_{animal} and $\hat{\lambda}$, along with the computed correlation coefficient between the two parameters, are reported (Table 2), where $\hat{\lambda}$ refers to the average number of animal groups present within one grid cell of size 3.24 km² and \hat{r}_{animal} refers to group-specific detection probabilities for each species. Due to the relatively small sample size attained in the field survey (number of cells = 55 < 200 + suggested by the simulations), we obtained a correlation coefficient of less than -0.9 between the estimated parameters \hat{r}_{animal} and $\hat{\lambda}$ for all species surveyed. Hence, we view the estimate with some caution, although the median estimate of λ in our simulations (Supporting Information Appendix S3) for low sample sizes suggests these estimates are reliable. However, in the extreme case where the correlation coefficient between \hat{r}_{animal} and $\hat{\lambda}$ is as extreme as -0.98 (for muntjac data), and estimated r_{animal} is also very low (0.03), we are concerned with the estimate of λ in our survey. This is because we are not sure if r is indeed very low or whether it is an outcome due to high correlation with λ during estimation.

Our results also provide evidence that the study area was fairly homogenous, and consistent with our *a priori* assumption, because the over-dispersed version of the Royle & Nichols (2003) received considerably lower support ($\Delta AIC > 2$) relative to the poisson model for all species, except gaur ($\Delta AIC = 1.432$) (Table 2). However, the correlation coefficient between \hat{r}_{animal} and $\hat{\lambda}$ was very high ($\rho_{ru} = -0.98$) for the gaur analysis, indicating that the

Table 3 Results of density estimation for ungulate species using line transect sampling data at Bhadra Tiger Reserve

Species	Model	n	$\hat{\rho}$	$\hat{S}[\hat{SE}(\hat{S})]$	$\hat{D}_s[\hat{SE}(\hat{D}_s)]$	$\hat{D}[\hat{SE}(\hat{D})]$
Sambar	HN-cos	59	0.49	1.78 (0.12)	2.47 (0.56)	4.40 (1.03)
Chital	HN-cos	47	0.33	4.11 (0.81)	2.16 (0.76)	8.88 (3.58)
Muntjac	UN-cos	49	0.52	1.08 (0.04)	4.03 (0.83)	4.35 (0.91)
Gaur	UN-cos	21	0.59	4.10 (0.90)	0.94 (0.30)	3.86 (1.49)
Wild pig	UN-cos	29	0.61	2.24 (0.39)	1.10 (0.37)	2.46 (0.94)

Model choice (HN-cos = half-normal model with cosine adjustment terms; UN-cos = uniform model with cosine adjustment terms), number of sightings (n after right truncation of data), and estimates of detection probability ($\hat{\rho}$), cluster size (\hat{S}), cluster density (\hat{D}_s) and animal density (\hat{D}), along with their standard errors (se), are reported.

parameters r_{animal} and μ are virtually non-identifiable, causing concern in the parameter estimates with the over-dispersed model.

Density estimates from line transect surveys

The line transect surveys yielded 20–59 visual detections for chital, sambar, gaur and muntjac, enabling us to fit detection functions reasonably well and generate density estimates (Table 3). The number of detections for wild pigs ($n = 12$) was inadequate for reliable density estimation (Buckland *et al.*, 2001). Therefore, we borrowed density estimates derived from a larger set of 24 transects from an expanded area around the study site, and assumed pig densities to be uniform across the wider area. Our results show that despite a fairly high sampling effort (273 km), sample sizes from visual detections were very low.

Table 4 Comparison of sampling effort and density estimates for ungulate species in Bhadra Tiger Reserve generated from sign surveys using AOS model and from line transect surveys based on visual detections

Species	AOS approach		Distance sampling	
	Sampling effort (in km)	Density of animal groups ^a $\hat{D}_s [\hat{SE}(\hat{D}_s)]$	Sampling effort (in km)	Density of animal clusters ^a $\hat{D}_s [\hat{SE}(\hat{D}_s)]$
Chital	256.80	1.46 (0.68)	272.78	2.16 (0.76)
Sambar	256.80	1.42 (0.67)	272.78	2.47 (0.56)
Gaur	256.80	1.01 (0.44)	272.78	0.94 (0.30)
Wild Pig	256.80	0.74 (0.39)	523.68 ^b	1.09 (0.37) ^b
Muntjac	256.80	1.42 (1.59)	272.78	4.03 (0.83)

^aA group here is defined as a 'social group', while a cluster is defined as a momentary congregation of animals. Group size \geq cluster size. For the species we refer to here, group size \approx cluster size. ^bEstimates for wild pigs were derived from a larger study area.

Half-normal detection key function models, in combination with cosine adjustment of orders, produced the best fit for sambar and chital sighting data, while the uniform + cosine adjustment models fitted muntjac and gaur detection data best (Table 3). However, a combination of few spatial replicates ($n = 11$) and detection events ($n < 60$) produced wide standard errors. Comparisons (Table 4) between the two survey methods show that cluster density estimates, despite being derived from two different approaches, matched well for all species except muntjac.

Discussion

Understanding the processes influencing forest structure and dynamics by large ungulates requires reliable information on their densities. However, consequent upon anthropogenic pressures, large ungulate densities have declined drastically, reducing them to occur in very low numbers in most remaining forests. Additionally, logistical issues preclude the application of standard methods, such as distance sampling or capture–recapture sampling, to estimate their densities. Therefore, there is a premium in developing approaches that enable assessments of absolute or relative densities that directly address the issue of imperfect detections.

Our study provides one possible solution to this problem. We estimate densities of four large ungulate species from simple, cost-effective sign surveys using the AOS model in a region where ungulate densities are relatively low. It is important for investigators to incorporate biological knowledge of a target species in the design of such a sign survey. Of critical importance is the reasonably accurate specification of expected daily range sizes of animals to establish cell sizes, and consideration of the length of spatial replicates. However, simulation results show that, although underestimation or overestimation of values assumed for radius of activity R can bias estimates of density, the direction of this bias appears predictable. This consistency in direction of bias makes our approach a useful tool, at least as an 'index', for monitoring ungulate densities across space and time. On a related note, if accurate information on R , or the number of cells expected to be visited by each animal group, is based on prior knowledge (e.g. via radio-telemetry), this information can be profitably incorporated into the survey design. In our specific study, the specification of cell size was tar-

geted primarily for larger ungulate species, and turned out too large for muntjac, the smallest among five species considered. As a result, our survey data may have failed to capture the evidence of heterogeneity in detection probability among cells for muntjac because the cell-specific abundance value encountered (> 12 animal groups per cell) may have been too high. We emphasize that the AOS model approach works better when expected densities of ungulates are low, enabling the capturing of heterogeneous detection rates among cells that is critical for the model to work.

Our study is a preliminary step towards reliably estimating absolute abundance of large ungulate species from field counts of signs along trails using spatial replications. While our approach employs survey design and protocols based on species biology, and the approach is flexible to accommodate for varying group sizes, we recognize that supplementary information in the form of prior data on daily movement ranges, sizes of groups and other covariates influencing ungulate abundance and detection rates across space can all improve the reliability of this approach. At another large site in the same region, Rayar (2010) has also confirmed the reliability of this approach more recently using additional covariates to describe cell-specific λ . In addition to density, environmental factors (substrate type, moisture and local weather) may often be determinants of encounter rates of animal signs (tracks, dung) during surveys. These factors can vary widely across or within cells. However, our approach of aggregation of survey data into simple binary counts, combined with a systematic sampling regime, ensures that fluctuations in sign encounter rates do not unduly affect the estimation process. Further, if required, all these environmental factors can be incorporated in the modelling of r_{animal} directly (see Royle & Nichols, 2003) under this approach. Future research in this domain can focus on models that account for unmodelled heterogeneity in detection probability and spatial autocorrelation between spatial replicates, which are not accounted for in this study. From a practical standpoint, this approach is most justified when the aim is to find a cost-effective approach when animal abundance is low. Unlike in transect surveys, whereby 'pre-marking' of transect lines is sometimes essential (in our case, about 3 months in the field), the AOS method requires little preparation time, and is thus cost-effective.

This approach can also potentially be extended from sign surveys to other animal detection techniques, such as camera traps, scent stations and track-plates, which are currently used to assess populations of other animal taxa (e.g. Nag, 2008). It has recently been applied to assess better prevalence in wildlife disease (Lachish *et al.*, 2012). Therefore, the potential utility of our approach may extend to include a wide range of animal monitoring contexts. But, more immediately, we foresee our approach to be utilized for studies of ungulate species of high conservation priority, including the Sao La *Pseudooryx vukongensis*, Malay Tapir *Tapirus indicus* or the Sumatran Rhinoceros *Dicerorhinus sumatrensis*, which are very rare species and unlikely to be surveyed well with other methods.

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Supporting information

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

Appendix S1. Results of simulations for 90 scenarios run on 100 datasets assuming an underlying poisson distribution where sign-specific detection probability for the sign of an individual group was set at equal to 0.999. The simulations were run assuming different values for the radius of movement within which signs are deposited R (represented as a fraction of the length of a grid cell), the number of signs deposited by each animal groups (N_{sign}) and the total number of animal groups S in the grid. The width of the detection strip d is represented as the fraction of the length of a grid cell. See *Methods* for description of other parameters.

Appendix S2. Results of simulations for 90 different scenarios run on 100 datasets assuming an underlying poisson distribution where sign-specific detection probability for an individual animal group was set at equal to 0.5. The simulations were run assuming different values for the radius of movement within which signs are deposited R (represented as a fraction of the length of a grid cell), the number of signs deposited by each animal cluster (N_{sign}) and the total number of animal clusters S in the grid. The width of the detection strip d is represented as the fraction of the length of a grid cell. See *Methods* for description of other parameters.

Appendix S3. Results of simulations for three scenarios run on 100 datasets assuming an underlying poisson distribution. The radius of movement within which signs are deposited R , the number of signs deposited by each animal group (N_{sign}) and the cell-specific detection probability are kept constant. The simulation scenarios are run by varying the number of animal groups (S) and the number of grid cells (N_{cells}).

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