

Monitoring carnivore populations at the landscape scale: occupancy modelling of tigers from sign surveys

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Summary

1. Assessing spatial distributions of threatened large carnivores at landscape scales poses formidable challenges because of their rarity and elusiveness. As a consequence of logistical constraints, investigators typically rely on sign surveys. Most survey methods, however, do not explicitly address the central problem of imperfect detections of animal signs in the field, leading to underestimates of true habitat occupancy and distribution.
2. We assessed habitat occupancy for a tiger *Panthera tigris* metapopulation across a c. 38 000-km² landscape in India, employing a spatially replicated survey to explicitly address imperfect detections. Ecological predictions about tiger presence were confronted with sign detection data generated from occupancy sampling of 205 sites, each of 188 km².
3. A recent occupancy model that considers Markovian dependency among sign detections on spatial replicates performed better than the standard occupancy model ($\Delta\text{AIC} = 184.9$). A formulation of this model that fitted the data best showed that density of ungulate prey and levels of human disturbance were key determinants of local tiger presence. Model averaging resulted in a replicate-level detection probability $\hat{p}_i(\text{SE}[\hat{p}_i]) = 0.17 (0.17)$ for signs and a tiger habitat occupancy estimate of $\hat{\psi}(\text{SE}[\hat{\psi}]) = 0.665 (0.0857)$ or 14 076 (1814) km² of potential habitat of 21 167 km². In contrast, a traditional presence-versus-absence approach underestimated occupancy by 47%. Maps of probabilities of local site occupancy clearly identified tiger source populations at higher densities and matched observed tiger density variations, suggesting their potential utility for population assessments at landscape scales.
4. *Synthesis and applications.* Landscape-scale sign surveys can efficiently assess large carnivore spatial distributions and elucidate the factors governing their local presence, provided ecological and observation processes are both explicitly modelled. Occupancy sampling using spatial replicates can be used to reliably and efficiently identify tiger population sources and help monitor metapopulations. Our results reinforce earlier findings that prey depletion and human disturbance are key drivers of local tiger extinctions and tigers can persist even in human-dominated landscapes through effective protection of source populations. Our approach facilitates efficient targeting of tiger conservation interventions and, more generally, provides a basis for the reliable integration of large carnivore monitoring data between local and landscape scales.

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Introduction

Large carnivores are among the most threatened mammals in the world (Ceballos *et al.* 2005). The decline of the tiger *Panthera tigris* Linnaeus, 1758, typifies the challenges of recovering large carnivore populations. Driven by synergistic impacts of habitat fragmentation, prey depletion and direct hunting (Karanth *et al.* 2004; Walston *et al.* 2010), tigers have suffered a range contraction of *c.* 93% in the past two centuries (Dinerstein *et al.* 2006). Global species recovery now depends on effective management of the remaining *c.* 40 'tiger source populations' (see Walston *et al.* 2010 for details) that occur as interconnected clusters within larger landscapes (Dinerstein *et al.* 2006; Ranganathan *et al.* 2008). Therefore, rigorous assessments of tiger populations are required at two spatial scales: protected reserves of a few hundred square kilometres each and wider landscapes of several thousand square kilometres.

Within reserves, tiger demographic parameters can be assessed reliably using intensive capture–recapture sampling of photographs or faecal DNA from individuals (Karanth *et al.* 2004, 2006; Mondol *et al.* 2009). Such intensive methods explicitly deal with the central problem of imperfect detections: that a proportion of animals in the surveyed area go undetected (Williams, Nichols & Conroy 2002). However, because of logistical constraints, landscape-scale surveys typically cannot employ intensive methods and depend on detecting tiger signs such as tracks and scats (Miquelle *et al.* 1999; Smith *et al.* 1999a,b; Johnsingh *et al.* 2004; Carroll & Miquelle 2006; Barlow *et al.* 2008; Jhala, Gopal & Qureshi 2008; Jhala, Qureshi & Gopal 2011). However, these 'presence-versus-absence' surveys do not discriminate between nondetection of sign and true absence of tigers, leading to underestimates of spatial distribution (MacKenzie *et al.* 2002). In past tiger surveys, environmental covariates have been incorporated into analyses in attempts to address this problem (Smith *et al.* 1999a,b; Miquelle *et al.* 2005; Barlow *et al.* 2008; Jhala, Gopal & Qureshi 2008; Jhala, Qureshi & Gopal 2011). Such results are, however, difficult to interpret because the covariates used may influence detection probability or occupancy or even both these quantities. More generally, investigators have used habitat suitability models (Engler, Guisan & Rechsteiner 2004) of various kinds, including regressions (Tyre, Possingham & Lindenmayer 2001; Gu & Swihart 2004), resource-selection functions (Boyce & McDonald 1999), ecological niche factor analysis (Hirzel *et al.* 2002) and simulations (Manley *et al.* 2004) for the analyses of animal presence/absence data. Even these approaches, however, do not explicitly model or estimate detection probabilities.

On the other hand, habitat occupancy models (MacKenzie *et al.* 2002, 2006; Royle & Dorazio 2008) do explicitly deal with imperfect detections and are increasingly being favoured (e.g.

Magoun *et al.* 2007 for wolverines *Gulo gulo* Linnaeus, 1758). If carefully designed, they can meet conservation needs (MacKenzie & Royle 2005) by explicitly confronting ecological or management predictions with sign survey data without ignoring imperfect detections. In practice, 'replications' necessary for estimating occupancy probabilities can be either 'temporal' or 'spatial' (Kendall & White 2009).

In this study, we confronted predictions incorporating *a priori* ecological and management hypotheses about local (site-level) tiger presence with data from a carefully designed, spatially replicated survey of tiger signs across a *c.* 38 000-km² landscape. This landscape currently harbours one of the largest wild tiger populations globally (Walston *et al.* 2010) holding an estimated 20% of India's wild tigers (Jhala, Gopal & Qureshi 2008). Using simple sign survey data, we modelled the ecological process of interest to us (tiger distribution and local presence) as well as the observation process (survey method), within a single inferential framework (MacKenzie *et al.* 2006; Royle & Dorazio 2008).

Based on prior knowledge of tiger ecology in the landscape (Karanth & Sunquist 2000; Karanth *et al.* 2004, 2006), we hypothesized that tiger 'source populations' that reproduce above replacement levels (Walston *et al.* 2010) would be confined to a few well-protected reserves and that tigers would occur at very low densities or be absent elsewhere. We further hypothesized that abundance of large ungulate prey species and protection from human disturbance (Karanth *et al.* 2004) would be the key determinants of local tiger presence. Our specific objectives were two-fold: First, to design a practical, landscape-scale, spatially replicated sign survey method to generate reliable estimates of tiger distribution that explicitly deals with imperfect detection of signs. Secondly, to measure local tiger habitat occupancy rates in the landscape and assess which key ecological variables (e.g. prey abundance) and management factors (e.g. human disturbances) influence these occupancy patterns. We present a practical application of a new occupancy model developed by Hines *et al.* (2010) specifically for spatially replicated sign surveys. These results have wider utility for monitoring of many other species of large carnivores (and mammals in general) at landscape scales.

Materials and methods

THE STUDY AREA, ECOLOGY AND HUMAN IMPACTS

The Western Ghats region of India (see Das *et al.* 2006 for a description; Fig. 1) is globally important for tigers (Dinerstein *et al.* 2006; Walston *et al.* 2010). Our survey was conducted in the central part of this region, known as the Malenad–Mysore Tiger Landscape (MMTL) in Karnataka State. The land cover is a matrix of natural moist-evergreen, moist-deciduous and dry-deciduous forests, interspersed with horticultural, agricultural and forestry crops covering 38 350 km² (Krishnaswamy, Kiran & Davande 2003). In this matrix,

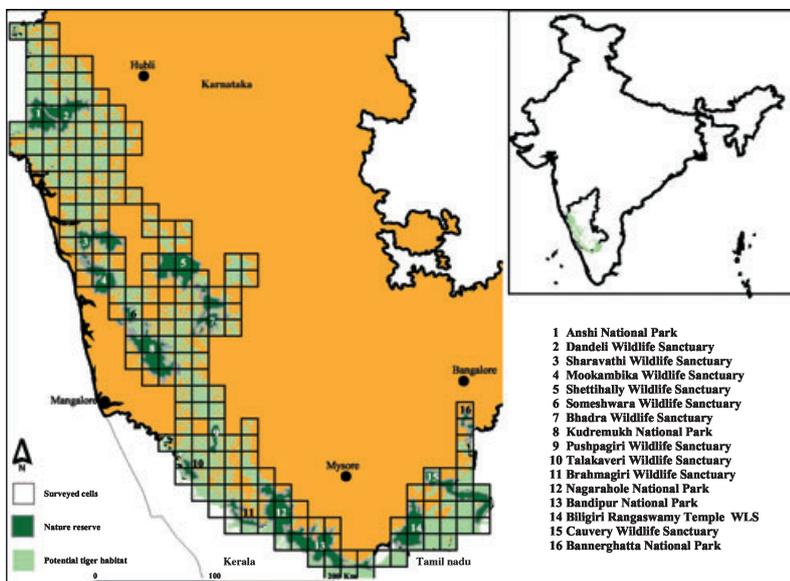


Fig. 1. Potential tiger habitat in Karnataka, India. Inset map: Location of the study area referred to as Malenad–Mysore Tiger Landscape (MMTL) in India.

potential tiger habitat consists of a forested area of 21 167 km² (Fig. 1) that includes 14 wildlife reserves (5 500 km²). This landscape, however, also supports ≈ 10.5 million people (Directorate of Census Operation 2004) and is characterized by pressures from illegal hunting, forest product collection, livestock grazing and rapid economic growth. Despite these pressures, tiger populations in better protected reserves are at higher densities and reproducing above replacement levels, facilitating dispersals through the wider landscape (Karanth *et al.* 2004; K. U. Karanth unpublished data). The forest connectivity appears to be sufficient (Das *et al.* 2006) for the tiger metapopulation to persist.

The principal ungulate prey of tigers (as well as of leopards *Panthera pardus* Linnaeus, 1758 and dholes *Cuon alpinus* Pallas, 1811) in this landscape are as follows: gaur *Bos frontalis* Lambert, 1804; sambar *Rusa unicolor* Kerr, 1792; chital *Axis axis* Erxleben, 1777; wild pig *Sus scrofa* Linnaeus, 1758; and muntjac *Muntiacus muntjak* Zimmermann, 1780. Based on tiger: prey density ratios established by Karanth *et al.* (2004), we expected the densities of wild ungulates to be an important covariate of local tiger presence. The effectiveness of

official wildlife protection varies across MMTL, being high in Bandipur, Nagarahole, Bhadra reserves, moderate in BR Temple, Kudremukh and Dandeli-Anshi reserves and somewhat poor at other locations (Fig. 1). Free grazing by livestock is widespread, often accompanied by illegal hunting and depletion of wild prey (Madhusudan & Mishra 2003; Rayar 2010). Because officials try to prevent intrusions by humans and livestock in nature reserves, and herders typically tend to stay within *c.* 10 km from their settlements, we assumed that encounter rate with signs of livestock is an easily detected surrogate for the intensity of negative human impacts (and for lack of effective protection) at the site level.

FIELD SURVEY PROTOCOLS

Survey design

The proportion of habitat in MMTL occupied by tigers, occupancy, ψ , was a key parameter of interest. Our 15-month-long survey (February 2006–May 2006 and December 2006–May 2007), with each sample

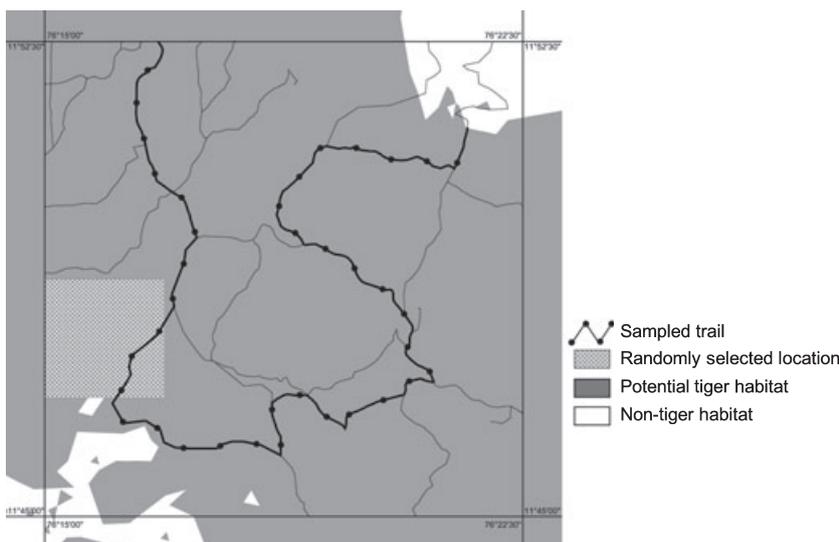


Fig. 2. Diagram of a sampled site (grid cell) depicting sequential coverage of a 1-km-long spatial replicates.

unit being surveyed within < 12–36 h, reasonably met the assumption of ‘closure’ (MacKenzie *et al.* 2006). The total survey effort was 2021 man-days, involving 4 174 km of walks along trails, and lead to the detection of 403 tiger signs (223 scat deposits and 180 sets of tracks).

The sample units consisted of a grid of square cells (sites) superimposed on the land-cover matrix in MMTL (Fig. 1). Because our goal was to measure true occupancy (proportion of area occupied) rather than intensity of habitat use by tigers (MacKenzie & Royle 2005; MacKenzie *et al.* 2006), the cell size chosen was, on average, larger than the maximum expected tiger home range size. Because nonresident male tigers have the largest home ranges (*c.* 80–90 km²; Karanth & Sunquist 2000), we used the cells of 188 km² size, whose boundaries coincided with graticules on our field maps (Fig. 2). Such ‘large’ grid cells also enabled us to logistically deploy survey teams more efficiently.

Occupancy studies typically survey only a subsample of cells (MacKenzie & Royle 2005; MacKenzie *et al.* 2006) and thereafter try to extend inference to the unsurveyed cells using covariate data from surveyed cells. However, we surveyed all the cells in MMTL because a key objective was to map tiger distribution to identify ‘source populations’ at higher densities and sufficient manpower was available.

We opted for spatial replication over temporal (Kendall & White 2009) primarily for logistical reasons (Hines *et al.* 2010). The survey effort/cell was a compromise that considered sufficiency of sign detections, replications and spatial coverage achieved. Thus, we fixed the total sampling effort (distance walked) in a cell with 100% habitat at 40 km, reducing the effort in decreasing proportion to habitat available. Cells with < 10% tiger habitat (20 km²) and forest fragments of < 10 km² size were excluded because tigers were unlikely to occupy these. Advance planning ensured adequate spatial coverage of cells (Kendall & White 2009) and field teams passed through one randomly chosen location in each cell (Fig. 2).

Field protocol based on tiger behaviour and environmental factors

The survey was conducted in dry seasons (October–May) to minimize variations in animal sign detection probabilities induced by rainfall. Because surveys targeted tracks/dung deposited along trails, variations in forest cover type did not influence sign detections.

Typically, tigers move *c.* 1–20 km day⁻¹ along forest trails to hunt or to locate, avoid or deter conspecifics (Karanth & Sunquist 2000). Their passage is marked by tracks and occasional scat deposits (Sunquist 1981; Smith, McDougal & Miquelle 1989). Fresh signs of tigers, leopards, dholes and major ungulate prey species in MMTL could be identified by our trained observers. Only unambiguously identified signs were recorded. Overall, the number of spatial replicates in a cell (sampling effort) varied from 4 to 40, depending on the extent of potential habitat in the cell.

Survey teams comprising of 2–3 skilled trackers walked the trails from morning to dusk (Fig. 2). They photographed, georeferenced and recorded signs of tigers, leopards, dholes and ungulate prey species, as well as signs of livestock presence. Each type of sign detection was assigned only once to each 100-m trail segment, thus yielding the standard ‘1’ (detection) or ‘0’ (nondetection) histories required for occupancy analyses (MacKenzie *et al.* 2006; Hines *et al.* 2010). These sign detection data were aggregated at 1 km length to form ‘spatial replicates’. At this replicate length, we were reasonably sure to detect the signs of prey as well as of human disturbances if present. Furthermore, as these metrics were being used only as covariates influencing tiger presence in our models, obtaining measures of their absolute density using intensive methods addressing imperfect detection was unnecessary as well as impractical at this spatial scale.

MODELLING AND ANALYSIS OF DATA

We used a recent refinement of the standard occupancy model (MacKenzie *et al.* 2002) developed by Hines *et al.* (2010), which explicitly deals with Markovian dependence of animal sign detection events on spatial replicates. General model notations are provided elsewhere and additional notations are provided under specific model descriptions. Analyses were performed using the program PRESENCE (Hines 2006).

Model structure and spatial dependency

The standard occupancy model is based on two key parameters:

ψ is the probability that a cell is occupied by tigers.

p is the probability of detecting tiger presence in a replicate, given that the cell is occupied by tigers.

The likelihood formulation for this model has been presented elsewhere (see MacKenzie *et al.* 2002 for details). However, occupancy models of MacKenzie *et al.* (2002) assume that replicate surveys can be modelled as statistically independent Bernoulli trials. Our replicates were aggregations of 100-m trail segments at 1 km. Because tigers might walk longer than 1 km along trails (Smith, McDougal & Miquelle 1989; Karanth & Sunquist 2000), we assumed that sign detection events on successive spatial replicates could potentially lack the statistical independence required by the occupancy models of MacKenzie *et al.* (2002). Therefore, we also considered the model developed by Hines *et al.* (2010), which explicitly accounts for such potential dependency using a first-order Markov process (Gillespie 1992). Of the two variants of the Hines *et al.*'s (2010) model implemented in program PRESENCE, we chose the variant that assumes that surveys can begin on any randomly chosen replicate (Fig. 2). In < 10% of the cells surveyed, when teams encountered unsuitable habitat along the trail (e.g. human settlements, large reservoirs) the resulting disjointed trail segments were combined sequentially (Fig. 2). The general computing expressions adapted from Hines *et al.* (2010) for probabilities associated with such sign detection histories are given in Appendix S1, Supporting Information.

The global model and ecological determinants of tiger presence

We first compared the models of MacKenzie *et al.* (2002) and Hines *et al.* (2010) without additional covariates, to choose the appropriate model type for conducting further analyses. All model comparisons were based on Akaike Information Criterion (AIC) values (Burnham & Anderson 2002), because sample size of cells was adequate (> 200, with 4–40 spatial replicates per cell).

We used program PRESENCE (Hines 2006) to estimate the overall occupancy rate, ψ , with the inference applying to the entire landscape matrix of 38 350 km² framed by the 205 surveyed cells (Fig. 1) including potential tiger habitat of 21 167 km². To estimate overall tiger habitat occupancy within MMTL, the cell-specific occupancy parameter, ψ , was weighted by the area of potential tiger habitat in each cell (Bevington & Robinson 2003; see detailed computations in Appendix S2, Supporting Information).

Based on earlier work (Karanth *et al.* 2004), which demonstrates a tiger: prey density ratio of *c.* 1 : 500, we hypothesized that local tiger presence would be positively influenced by the density of wild ungulate prey. We further wanted to test whether prey in certain body size classes influenced tiger presence. These ‘prey-density covariates’ for each cell were proportions of 1-km-long replicates that contained signs of each prey species. We thus considered 12 plausible alternative

occupancy models, incorporating the following covariates: density of all prey species combined and density of only larger ungulate species. To assess whether tiger presence is influenced by human disturbance, the proportion of replicates with livestock sign was used as an additional covariate in our models. Further, we also incorporated proportion of tiger habitat/cell (or sampling effort) as a covariate (Appendix S2, Supporting Information).

Model selection and parameter estimation

The ecological process parameter of interest was the cell-level tiger habitat occupancy rate ψ . We were also interested in the important covariates that influenced this site-level tiger presence. The sampling process parameters of interest were the replicate-level occupancy parameters θ and θ' that demonstrate the degree of dependence between replicated samples. However, we expected that some of the covariates influencing tiger presence may also contribute to variation in tiger abundance and thereby influence sign detection probability p_t (Royle & Nichols 2003). We also expected that other unknown factors could also influence the detectability of tiger signs. Thus, the nuisance parameter p_t had to be explicitly accounted for in our modelling process. Consequently, our model selection process initially focused on determining a suitable covariate model structure for p_t and subsequently on using this model structure to estimate cell-level occupancy ψ .

We defined a global occupancy model based on the recommendations of Burnham & Anderson (2002) and MacKenzie *et al.* (2006) and formulated 12 alternative plausible models to identify a covariate structure for the replicate-level detectability p_t , using the Hines *et al.*'s (2010) model structure. No covariates were included for replicate-level occupancy parameters θ and θ' in the global model described below:

ψ (all prey + livestock + proportion of habitat), θ (.), θ' (.), p_t (all prey + livestock + proportion of habitat).

Using program PRESENCE (Hines 2006), we selected the highest ranked 12 alternative models based on AIC values, to fix the model structure for p_t (Table 1). Thereafter, we kept this model structure component unchanged and ran further occupancy analyses for comparing models involving different covariate structures for ψ . We computed the final estimates of cell-specific occupancy rate $\hat{\psi}_i$, the total fraction of area occupied $\hat{\psi}$ and the replicate-level occupancy parameters $\hat{\theta}$ and $\hat{\theta}'$ and other parameters by model averaging using the top 10 models, all of which had similar support ($\Delta\text{AIC} < 2$ units; Burn-

ham & Anderson 2002). We note that the current version of PRESENCE (Hines 2006) does not facilitate any goodness-of-fit test for the spatial dependence model (Hines *et al.* 2010).

Results

MODEL SELECTION

In the first step of model selection, we compared the standard occupancy model of MacKenzie *et al.* (2002) which assumed statistical independence among tiger sign detections made on 1-km-long spatial replicates, with the Hines *et al.* (2010) model that provides for a first-order Markovian dependence among detections (See Materials and methods). These comparisons very clearly showed a lack of independence in sign detections on 1-km-long replicates. The Hines *et al.* (2010) model performed significantly better ($\Delta\text{AIC} = 184.9$) in comparisons with the standard model (MacKenzie *et al.* 2002). Therefore, all further occupancy analyses were performed using Hines *et al.* (2010) modelling approach implemented in program PRESENCE.

In the second step, we compared the adequacy of 12 plausible alternative occupancy models, which describe the expected influence of different combinations of covariates (see Materials and methods) on tiger occupancy as well as on detection probability parameters at the replicate as well as cell levels (Table 1). In these comparisons, a general model structure for the covariates likely to influence ψ remains fixed, whereas the covariates associated with replicate-level detection probability p_t are varied. Based on these comparisons, a model that incorporates the influence of combined abundance of larger prey (gaur, sambar, chital and wild pig), human disturbance (via relative abundance of livestock signs) and proportion of habitat surveyed (sampling effort) on replicate-level detection probability p_t emerged as the top-ranked model (AIC weight = 0.309). We note that the covariate structure for the detection probability in the top-ranked model is the most parameterized, thus limiting bias on occupancy estimates. Therefore, in all subsequent occupancy analyses, this basic

Table 1. Model selection results; role of covariates in determining probability of detecting tiger sign p_t on 1-km-long replicates, based on covariates for probability of tiger occupancy from the global model (see Materials and methods), using the Hines *et al.*'s (2010) model. Number of sites = 205. Covariates considered all prey (AP), large prey (LP), livestock (LVS) and proportion of available habitat (PH)

Model	AIC	ΔAIC	AIC weight	Model likelihood	Number of parameters	Deviance
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1446.84	0	0.309	1	10	1426.84
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (AP + LVS + PH)	1447.43	0.59	0.230	0.745	10	1427.43
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LP + LVS)	1447.66	0.82	0.205	0.664	9	1429.66
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (AP + LVS)	1447.89	1.05	0.183	0.592	9	1429.89
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LP + PH)	1452.37	5.53	0.019	0.063	9	1434.37
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LP)	1452.44	5.6	0.019	0.061	8	1436.44
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (AP)	1452.47	5.63	0.019	0.060	8	1436.47
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (AP + PH)	1452.78	5.94	0.016	0.051	9	1434.78
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LVS + PH)	1466.35	19.51	0	0	9	1448.35
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LVS)	1468.51	21.67	0	0	8	1452.51
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (.)	1497.79	50.95	0	0	7	1483.79
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (PH)	1498.81	51.97	0	0	8	1482.81

Table 2. Model selection results; role of covariates in determining probability of tiger occupancy ψ in Malenad–Mysore Tiger Landscape, based on modelling probability of detecting tiger sign p_t on 1-km-long replicates using the Hines *et al.* (2010). Covariate structure for p_t is obtained from the top model in Table 1 (see Materials and Methods). Number of sites = 205. Covariates considered all prey (AP), large prey (LP), livestock (LVS) and proportion of available habitat (PH)

Model	AIC	Δ AIC	AIC weight	Model likelihood	Number of parameters	Deviance
ψ (AP + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1445.77	0	0.158	1	9	1427.77
ψ (LP + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1445.99	0.22	0.142	0.896	9	1427.99
ψ (LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1445.99	0.22	0.142	0.896	9	1427.99
ψ (PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1446.71	0.94	0.099	0.625	8	1430.71
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1446.84	1.07	0.093	0.586	10	1426.84
ψ (LP + LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	1446.99	1.22	0.086	0.543	10	1426.99
ψ (.), θ (.), θ' (.), p_t (LP + LVS + PH)	1447.34	1.57	0.072	0.456	7	1433.34
ψ (AP), θ (.), θ' (.), p_t (LP + LVS + PH)	1447.35	1.58	0.072	0.454	8	1431.35
ψ (LVS), θ (.), θ' (.), p_t (LP + LVS + PH)	1447.44	1.67	0.069	0.434	8	1431.44
ψ (LP), θ (.), θ' (.), p_t (LP + LVS + PH)	1447.46	1.69	0.067	0.430	8	1431.46

structure of the detection probability component of the occupancy model was retained, with only the covariate structure describing ψ being varied.

In the third step of the model selection process, we had a candidate set of 12 models by varying covariate model structures on cell-level occupancy parameter ψ while using our best supported structure for replicate-level detection probability p_t (large prey + livestock + proportion of habitat). Comparisons between 10 higher-ranked models are reported in Table 2. We note all these models fit the data well (Δ AIC < 1.69), and therefore, we used model averaging to derive final parameter estimates (Burnham & Anderson 2002).

ESTIMATES OF OCCUPANCY AND OTHER PARAMETERS

We used parametric bootstrapping (Efron 1982) to derive the estimates of variance for the total fraction of the area occupied ψ for all models (see Appendix S2, Supporting Information). The final parameter estimates derived for tiger habitat occupancy and sign detection probabilities from model averaging are reported as follows:

$\hat{\theta}_0(\hat{SE}[\hat{\theta}_0])$, probability of tiger presence on the first replicate = 0.418 (0.0787).

$\hat{\theta}(\hat{SE}[\hat{\theta}])$, probability of tiger presence on a replicate, given absence on previous replicate = 0.194 (0.0399).

$\hat{\theta}'(\hat{SE}[\hat{\theta}'])$, probability of tiger presence on a replicate, given presence on previous replicate = 0.730 (0.0857).

$\hat{p}_t(\hat{SE}[\hat{p}_t])$, the probability of detecting a tiger sign on a replicate, given presence of tigers on the replicate = 0.17 (0.168).

$\hat{\psi}(\hat{SE}[\hat{\psi}])$, the total fraction of area occupied by tigers in MMTL = 0.665 (0.0857).

Thus, of the 21 167 km² potential tiger habitat available in MMTL, we estimate that tigers actually occupied 66%, or an area of 14 076 km² ($SE = 1814$ km²). In contrast, a naïve estimate derived from the traditional ‘presence-versus-absence’ approach is only 7 537 km² and underestimated true occupancy by *c.* 47%.

As hypothesized, tiger distribution appears to be patchy across MMTL because of ecological as well as management-related factors. Therefore, we examined the β coefficient values for different covariates we expected to influence tiger habitat occupancy. These coefficient values/signs, which express the strength/direction of their expected influence (MacKenzie *et al.* 2006), are reported in Table 3. The β coefficient estimates from 10 plausible models (Table 2) were similar. Relative density of all prey, and larger prey, and the proportion of available tiger habitat were key determinants of tiger presence, indicated by positive β values associated with these covariates (Table 3). Moreover, relative intensity of livestock presence, our surrogate measure of human disturbance, proved to be a negative

Table 3. Model-specific β coefficient estimates for covariates determining tiger occupancy ψ in Malenad–Mysore Tiger Landscape (MMTL). Models were used to determine tiger occupancy in MMTL. Number of sites = 205. Covariates considered all prey (AP), large prey (LP), livestock (LVS) and proportion of available habitat (PH)

Model	$\hat{\beta}_0(\hat{SE}[\hat{\beta}_0])$	$\hat{\beta}_{AP}(\hat{SE}[\hat{\beta}_{AP}])$	$\hat{\beta}_{LP}(\hat{SE}[\hat{\beta}_{LP}])$	$\hat{\beta}_{LVS}(\hat{SE}[\hat{\beta}_{LVS}])$	$\hat{\beta}_{PH}(\hat{SE}[\hat{\beta}_{PH}])$
ψ (AP + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	-2.347 (1.173)	2.181 (1.162)	–	–	3.089 (1.469)
ψ (LP + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	-2.257 (1.156)	–	2.109 (1.163)	–	3.057 (1.473)
ψ (LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	0.108 (1.011)	–	–	-1.561 (0.931)	2.928 (1.589)
ψ (PH), θ (.), θ' (.), p_t (LP + LVS + PH)	-0.712 (0.963)	–	–	–	3.077 (1.747)
ψ (AP + LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	-1.325 (1.569)	1.527 (1.343)	–	-1.002 (1.020)	2.974 (1.439)
ψ (LP + LVS + PH), θ (.), θ' (.), p_t (LP + LVS + PH)	-1.212 (1.556)	–	1.431 (1.349)	-1.034 (1.022)	2.956 (1.444)
ψ (.), θ (.), θ' (.), p_t (LP + LVS + PH)	1.218 (0.442)	–	–	–	–
ψ (AP), θ (.), θ' (.), p_t (LP + LVS + PH)	-0.244 (0.917)	2.009 (1.309)	–	–	–
ψ (LVS), θ (.), θ' (.), p_t (LP + LVS + PH)	1.815 (0.677)	–	–	-1.537 (1.024)	–
ψ (LP), θ (.), θ' (.), p_t (LP + LVS + PH)	-0.201 (0.908)	–	1.986 (1.326)	–	–

influence on local tiger presence (with negative β values; Table 3).

Given variations in the densities of tigers and prey at some sites (Karanth *et al.* 2004) and effectiveness of protection across MMTL, we expected substantial variations in site-level tiger abundances and consequently in site-level probabilities of tiger occupancy.

We note that the two covariates contributed significantly to the replicate-level variation in sign detection probability p_t ($\Delta\text{AIC} = 50.95$ between the top-ranked model in Table 1 and the model that does not have a covariate model structure on p_t). However, evidence for the effect of these covariates on cell-level tiger occupancy ψ was not as strong ($\Delta\text{AIC} = 1.57$ between the top model in Table 2 and the model that does not have a covariate model structure on ψ). Furthermore, the covariate relationships were all in predicted directions, suggesting that these covariates have a strong influence on cell-specific tiger abundance. If these variations in cell-specific tiger abundance are the key determinant of variations in sign detection probabilities, then the estimated cell-specific occupancy rates could potentially be linked to variations in relative tiger abundance using some of the new occupancy models proposed by Royle & Nichols (2003) or Nichols *et al.* (2007). We also graphically mapped these variations in cell-specific occupancy probabilities across the entire landscape (Fig. 3).

Discussion

OCCUPANCY MODELS FOR CARNIVORE SURVEYS

To address increasing threats to large carnivores (Ceballos *et al.* 2005), substantial investments are being made on landscape-scale sign surveys. Although these surveys use sophisticated GIS analyses (tigers: Wikramanayake *et al.* 2005; jaguars: Sanderson *et al.* 2002; lions: Bauer & Van Der Merwe 2004), they are fundamentally rooted in the traditional 'presence-versus-absence' approach to inference. Our study showed that such naïve estimates of occupancy can be substantially biased downward because detection parameters associated

with the actual sampling process not being reliably estimated (in our case θ , θ' , and p_t being < 1). Our results reaffirm the value of using occupancy modelling approach to explicitly deal with the difficult problem of imperfect detections. Similarly, development of a specific probabilistic model of the process of searching for tiger signs along trails (Hines *et al.* 2010) proved important. Occupancy models using spatial replicates and incorporating *a priori* hypotheses generated results that could be reasonably interpreted in terms of ecological or management factors (see Results).

Overall, we demonstrate the benefits of designing carnivore sign surveys based on species biology (e.g. tiger home range size and movements on trails) as well as on field survey protocols (e.g. distances walked and spatial coverage of cells). By modelling just three key covariates (available habitat, prey density and human disturbance levels), we were able to provide reasonable explanations for the patterns of tiger distribution. We note that tiger surveys sometimes sacrifice ecological clarity and model parsimony by fitting many covariates relying on omnibus statistical tools such as regressions (e.g. Jhala, Gopal & Qureshi 2008).

MEASURING TIGER DISTRIBUTION AND ABUNDANCE

Local tiger presence is strongly governed by prey density and protection effectiveness, which cannot be remotely sensed. Landscape analyses not augmented by such field data (e.g. Dinerstein *et al.* 2006; Ranganathan *et al.* 2008) therefore have inherent limitations for modelling tiger distributions. Site occupancy estimates from our models permit rapid field assessment of tiger population status across large landscapes (Fig. 3). Temporal extensions of these models (MacKenzie *et al.* 2003) can monitor tiger range contractions or expansions. Overall, we suggest that occupancy modelling offers a robust alternative to previous tiger sign survey methods, such as effort-adjusted encounter rates (Johnsingh *et al.* 2004), adjusted track count-based estimates (Hayward *et al.* 2002) and extrapolations from sign encounter rates (Smith *et al.* 1999a,b; Wikramanayake *et al.* 2005; Carroll & Miquelle 2006; Barlow *et al.* 2008).

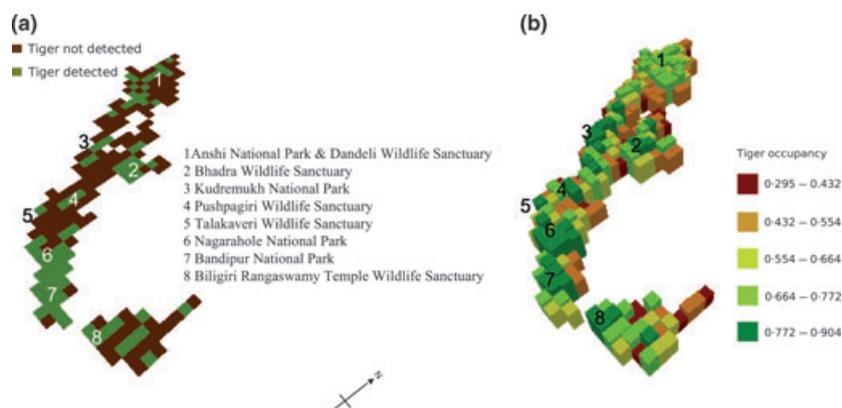


Fig. 3. Patterns of spatial variation in probability of site occupancy of tigers in the Malenad–Mysore Landscape of Karnataka (MMTL). (a) Based on naïve estimate derived from the traditional presence-versus-absence approach and (b) based on occupancy analysis under the model developed by Hines *et al.* (2010).

We note, however, that recent reports by Jhala, Gopal & Qureshi (2008) suggest that spatially replicated sign surveys can estimate tiger distribution reliably without explicitly modelling imperfect detections. On the contrary, our results show replicate-level tiger sign detection probability can be as low as 17%, which, if ignored, would lead to underestimates of occupancy. We find these differences puzzling and worth further exploration.

Our survey did not fully meet the assumptions of abundance models of occupancy (Royle & Nichols 2003; Nichols *et al.* 2007; Conroy *et al.* 2008). We are currently exploring further applications of such abundance models of occupancy, which can be integrated with rigorous site-specific tiger density estimates from camera trapping to reliably estimate tiger numbers across large landscapes.

IMPLICATIONS FOR THE MANAGEMENT OF WILD TIGER POPULATIONS

Prey depletion by human hunters was first hypothesized as a critical factor driving local declines of tiger populations by Karanth & Stith (1999). Although alternative models hypothesize a greater influence of direct hunting (Chapron *et al.* 2008), the prey depletion model has since then been supported by rigorous field studies of tiger:prey density ratios (Karanth *et al.* 2004), as well as a long-term population dynamics study (Karanth *et al.* 2006). This study finds support for the models proposing that ungulate prey densities are strong determinants of tiger presence at the landscape scale also (Karanth *et al.* 2010).

Our results (Figs 1 and 3) show that tigers have persisted better in MMTL compared with far more extensively forested, sparsely populated and economically underdeveloped landscapes in India, a pattern earlier reported by Jhala, Gopal & Qureshi (2008). Their persistence appears to be dependent upon a few effectively protected 'source populations' (Figs 1 and 3), which are reproducing above replacement levels (Karanth *et al.* 2006). A recent global conservation analysis (Walston *et al.* 2010) shows that about 70% of wild tigers now survive in source populations occupying just 6% of the habitat. These sources are currently identified based on anecdotal evidence. Our survey approach can rapidly and objectively identify such 'sources' for targeting conservation efforts.

Walston *et al.* (2010) are concerned that the widely promoted 'landscape approach' to tiger conservation (e.g. Wikramanayake *et al.* 2005; Dinerstein *et al.* 2006) does not adequately prioritize protection of source populations and therefore may not help in arresting the current tiger decline. The proponents of the 'landscape approach', however, insist that conservation investments should continue to target wider regions. The population assessment approach we present provides a basis for reliably monitoring tiger meta-populations by integrating site-level, intensive, capture-recapture surveys with cost-effective, landscape-scale sign surveys. Furthermore, this approach of confronting alternative ecological/management predictions with survey data may also prove useful for future adaptive management (Walters 1986; Williams, Nichols &

Conroy 2002) of wild tiger populations. We also believe these methods are relevant to efficient monitoring of spatial distributions and abundances of many other wide-ranging large carnivores whose signs are relatively easily detected.

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References

- Barlow, A.C.D., Ahmed, M.I.U., Rahman, M.M., Howlader, A., Smith, A.C. & Smith, J.L.D. (2008) Linking monitoring and intervention for improved management of tigers in the Sundarbans of Bangladesh. *Biological Conservation*, **141**, 2032–2040.
- Bauer, H. & Van Der Merwe, S. (2004) Inventory of free-ranging lions *P. leo* in Africa. *Oryx*, **38**, 26–31.
- Bevington, P.R. & Robinson, D.K. (2003) *Data Reduction and Error Analysis for the Physical Sciences*. McGraw-Hill, New York.
- Boyce, M.S. & McDonald, L.L. (1999) Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution*, **14**, 268–272.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. Springer-Verlag, New York.
- Carroll, C. & Miquelle, D.G. (2006) Spatial viability analysis of Amur tiger *Panthera tigris altaica* in the Russian Far East: the role of protected areas and landscape matrix in population persistence. *Journal of Applied Ecology*, **43**, 1056–1068.
- Ceballos, G., Ehrlich, P.R., Soberón, J., Salazar, I. & Fay, J.P. (2005) Global mammal conservation: what must we manage? *Science*, **309**, 603–607.
- Chapron, G., Miquelle, D.G., Lambert, A., Goodrich, J.M., Legrande, S. & Colbert, J. (2008) The impact on tigers of poaching versus prey depletion. *Journal of Applied Ecology*, **45**, 1667–1674.
- Conroy, M.J., Runge, J.P., Barker, R.J., Schofield, M.R. & Fonnesebeck, C.J. (2008) Efficient estimation of abundance for patchily distributed populations via two-phase, adaptive sampling. *Ecology*, **89**, 3362–3370.
- Das, A., Krishnaswamy, J., Bawa, K.S., Kiran, M.C., Srinivas, V., Kumar, N.S. & Karanth, K.U. (2006) Prioritization of conservation areas in the Western Ghats, India. *Biological Conservation*, **133**, 16–31.
- Dinerstein, E., Loucks, C., Wikramanayake, E., Ginsberg, J., Sanderson, E., Seidensticker, J., Forrest, J., Bryja, G., Heydlauff, A., Klenzendorf, S., Leimgruber, P., Mills, J., O'Brien, T.G., Shrestha, M., Simons, R. & Songer, M. (2006) The fate of wild tigers. *BioScience*, **57**, 508–514.
- Directorate of Census Operation. (2004) *Primary Census Abstract for Andhra Pradesh, Karnataka & Lakshadweep*. Technical Report Vol. X. 00-063-2001-Cen-CD. Office of the Registrar General and Census Commissioner, Government of India, New Delhi.
- Efron, B. (1982) *The Jackknife, the Bootstrap and Other Resampling Plans*. Society for Industrial and Applied Mathematics, Philadelphia, PA.
- Engler, R., Guisan, A. & Rechsteiner, L. (2004) An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. *Journal of Applied Ecology*, **41**, 263–274.
- Gillespie, D.T. (1992) *Markov Processes: An Introduction to Physical Scientists*. Academic Press, London, UK.
- Gu, W. & Swihart, R.K. (2004) Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*, **116**, 195–203.
- Hayward, G.D., Miquelle, D.G., Smirnov, E.N. & Nations, C. (2002) Monitoring Amur tiger populations: characteristics of track surveys in snow. *Wildlife Society Bulletin*, **30**, 1150–1159.

- Hines, J.E. (2006) PRESENCE2 – Software to estimate patch occupancy and related parameters. Version 2.4. USGS-PWRC. <http://www.mbr-pwrc.usgs.gov/software/presence.html>.
- Hines, J.E., Nichols, J.D., Royle, J.A., 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.
- Hirzel, A.H., Haussler, J., Chessel, D. & Perrin, N. (2002) Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? *Ecology*, **83**, 2027–2036.
- Jhala, Y.V., Gopal, R. & Qureshi, Q. (2008) *Status of the Tigers, Co-predators, and Prey in India*. National Tiger Conservation Authority, Government of India, New Delhi and Wildlife Institute of India, Dehradun.
- Jhala, Y.V., Qureshi, Q. & Gopal, R. (2011) Can the abundance of tigers be assessed from their signs? *Journal of Applied Ecology*, **48**, 14–24.
- Johnsingh, A.J.T., Ramesh, K., Qureshi, Q., David, A., Goyal, S.P., Rawat, G.S., Rajapandian, K. & Prasad, S. (2004) *Conservation Status of Tiger and Associated Species in the Terai Arc Landscape, India*. Final Technical Report, Wildlife Institute of India, Dehradun, pp. viii + 110.
- Karanth, K.U. & Stith, B.M. (1999) Prey depletion as a critical determinant of tiger population viability. *Riding the Tiger: Tiger Conservation in Human Dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson), pp. 100–113. Cambridge University Press, Cambridge, UK.
- Karanth, K.U. & Sunquist, M.E. (2000) Behavioral correlates of predation by tiger, leopard and dhole in Nagarhole, India. *Journal of Zoology*, **250**, 255–265.
- 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, USA*, **101**, 4854–4858.
- Karanth, K.U., Nichols, J.D., Kumar, N.S. & Hines, J.E. (2006) Assessing tiger population dynamics using photographic capture-recapture sampling. *Ecology*, **87**, 2925–2937.
- Karanth, K.K., Nichols, J.D., Karanth, K.U., Hines, J.E. & Christensen, N.L. (2010) The shrinking Ark: patterns of mammal extinctions in India. *Proceedings of the Royal Society-B*, **227**, 1971–1979.
- 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.
- Krishnaswamy, J., Kiran, M.C. & Davande, S. (2003) *Eco-climatic Vegetation Classification for the Western Ghats Using Multi-season NDVI*. Ashoka Trust for Research in Ecology and the Environment, Bangalore.
- MacKenzie, D.I. & Royle, J.A. (2005) Designing efficient occupancy studies: general advice and tips on allocation of survey effort. *Journal of Applied Ecology*, **42**, 1105–1114.
- 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., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization and local extinction when species are detected imperfectly. *Ecology*, **84**, 2200–2207.
- 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*. Elsevier, San Diego.
- Madhusudan, M.D. & Mishra, C. (2003) Why big, fierce animals are threatened: conserving large mammals in densely populated landscapes. *Battles Over Nature: Science and the Politics of Conservation* (eds V. Saberwal & M. Rangarajan), pp. 31–55. Permanent Black, New Delhi.
- Magoun, A.J., Ray, J.C., Johnson, D.S., Valkenburg, P., Dawson, F.N. & Bowman, J. (2007) Modeling wolverine occurrence using aerial surveys of tracks in snow. *Journal of Wildlife Management*, **71**, 2221–2229.
- Manley, P.N., Zielinski, W.J., Schlesinger, M.D. & Mori, S.R. (2004) Evaluation of a multiple-species approach to monitoring species at the ecoregional scale. *Ecological Applications*, **14**, 296–310.
- Miquelle, D.G., Smirnov, E.N., Merrill, T.W., Myslenkov, A.E., Quigley, H.B., Hornocker, M.G. & Schleyer, B. (1999) Hierarchical spatial analysis of Amur tiger relationships to habitat and prey. *Riding the Tiger: Tiger Conservation in Human Dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson), pp. 71–99. Cambridge University Press, Cambridge, UK.
- Miquelle, D.G., Stephens, P.A., Smirnov, E.N., Goodrich, J.M., Zaumyslova, O.Y. & Myslenkov, A.E. (2005) Tigers and wolves in the Russian Far East: competitive exclusion, functional redundancy and conservation implications. *Large Carnivores and the Conservation of Biodiversity* (eds J.C. Ray, J. Berger, K.H. Redford & R. Steneck), pp. 179–207. Island Press, Washington, DC.
- Mondol, S., Karanth, K.U., Kumar, N.S., Gopalaswamy, A.M., Andheria, A. & Ramakrishnan, U. (2009) Evaluation of non-invasive genetic sampling methods for estimating tiger population size. *Biological Conservation*, **142**, 2350–2360.
- Nichols, J.D., Hines, J.E., MacKenzie, D.I., Seamans, M.E. & Gutierrez, R.J. (2007) Occupancy estimation and modelling with multiple states and state uncertainty. *Ecology*, **88**, 1395–1400.
- Ranganathan, J., Chan, K.M.A., Karanth, K.U. & Smith, J.L.D. (2008) Where can tigers persist in the future? A landscape-scale, density-based population model for the Indian subcontinent. *Biological Conservation*, **141**, 67–77.
- Rayar, K. (2010) *Assessing Potential Tiger Habitats in Cauvery Wildlife Sanctuary, Karnataka Using Occupancy Modeling Approaches*. MS thesis, Tata Institute of Fundamental Research, National Centre for Biological Sciences, Bangalore, India.
- Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Models and Inference in Ecology: The Analysis of Data from Populations, Metapopulations and Communities*. Academic Press, New York.
- Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.
- Sanderson, E.W., Redford, K.H., Chetkiewicz, C.-L.B., Medellin, R.A., Rabinowitz, A., Robinson, J.G. & Taber, A.B. (2002) Planning to save a species: the jaguar as a model. *Conservation Biology*, **16**, 58–72.
- Smith, J.L.D., McDougal, C. & Miquelle, D. (1989) Scent marking in free ranging tigers, *Panthera tigris*. *Animal Behavior*, **37**, 1–10.
- Smith, J.L.D., McDougal, C., Ahearn, S.C., Joshi, A. & Conforti, K. (1999a) Metapopulation structure of tigers in Nepal. *Riding the Tiger: Tiger Conservation in Human-dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson), pp. 176–189. Cambridge University Press, Cambridge.
- Smith, J.L.D., Tunhikorn, S., Tanhan, S., Simcharoen, S. & Kanchanasaka, B. (1999b) Metapopulation structure of tigers in Thailand. *Riding the Tiger: Tiger Conservation in Human-dominated Landscapes* (eds J. Seidensticker, S. Christie & P. Jackson), pp. 166–175. Cambridge University Press, Cambridge.
- Sunquist, M.E. (1981) Social organization of tigers (*Panthera tigris*) in Royal Chitwan National Park, Nepal. *Smithsonian Contributions to Zoology*, **336**, 1–98.
- Tyre, A.J., Possingham, H.P. & Lindenmayer, D.B. (2001) Inferring process from pattern: can territory occupancy provide information about life history parameters? *Ecological Applications*, **11**, 1722–1737.
- Walston, J., Robinson, J.G., Bennett, E.L., Breitenmoser, U., da Fonseca, G.A.B., Goodrich, J. et al. (2010) Bringing the tiger back from the brink—the six percent solution. *PLoS Biology*, **8**, e1000485 doi: 10.1371/journal.pbio.1000485.
- Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Macmillan, New York.
- Wikramanayake, E., Mcknight, M., Dinerstein, E., Joshi, A., Gurung, B. & Smith, D. (2005) Designing a conservation landscapes for tigers in human-dominated environments. *Conservation Biology*, **18**, 839–844.
- Williams, B.K., Nichols, J.D. & Conroy, M.J. (2002) *Analysis and Management of Animal Populations*. Academic Press, San Diego.

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Supporting Information

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

Appendix S1. A general computing expression adapted from Hines et al. (2010) for modelling detection histories, h_j , obtained for detections of tiger sign along a continuous trail, composed of spatial replicates.

Appendix S2. Estimation of mean and standard deviation of the fraction of total Malenad–Mysore Tiger Landscape (MMTL) occupied by tigers.

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