Journal of Applied Ecology

Journal of Applied Ecology 2009, **46**, 1189–1200 doi: 10.1111/j.1365-2664.2009.01710.x

Patterns and determinants of mammal species occurrence in India

Krithi K. Karanth[1,2]*, James D. Nichols[3], James E. Hines[3], K. Ullas Karanth[4] and Norman L. Christensen[1]

[1]*Nicholas School of Environment, PO Box 90328, Duke University, Durham NC 27708, USA;* [2]*Department of Ecology, Evolution and Environmental Biology, Columbia University, NY 10027, USA;* [3]*U.S. Geological Survey Biological Resources Division, Patuxent Wildlife Research Center, 12100 Beech Forest Road, STE 4037, Laurel, MD 20708 4019, USA; and* [4]*Wildlife Conservation Society India Program, 403 Seebo Apts, 26-2 Aga Abbas Ali Road, Bangalore 560 042, India*

Summary

1. Many Indian mammals face range contraction and extinction, but assessments of their population status are hindered by the lack of reliable distribution data and range maps.

2. We estimated the current geographical ranges of 20 species of large mammals by applying occupancy models to data from country-wide expert. We modelled species in relation to ecological and social covariates (protected areas, landscape characteristics and human influences) based on *a priori* hypotheses about plausible determinants of mammalian distribution patterns.

3. We demonstrated that failure to incorporate detection probability in distribution survey methods underestimated habitat occupancy for all species.

4. Protected areas were important for the distribution of 16 species. However, for many species much of their current range remains unprotected. The availability of evergreen forests was important for the occurrence of 14 species, temperate forests for six species, deciduous forests for 15 species and higher altitude habitats for two species. Low human population density was critical for the occurrence of five species, while culturally based tolerance was important for the occurrence of nine other species.

5. Rhino *Rhinoceros unicornis*, gaur *Bos gaurus* and elephant *Elephas maximus* showed the most restricted ranges among herbivores, and sun bear *Helarctos malayanu*s, brown bear *Ursus arctos* and tiger *Panthera tigris* were most restricted among carnivores. While cultural tolerance has helped the survival of some mammals, legal protection has been critically associated with occurrence of most species.

6. *Synthesis and applications*. Extent of range is an important determinant of species conservation status. Understanding the relationship of species occurrence with ecological and socio-cultural covariates is important for identification and management of key conservation areas. The combination of occupancy models with field data from country-wide experts enables reliable estimation of species range and habitat associations for conservation at regional scales.

Key-words: detection, distribution, India, land cover, mammals, occupancy, parks, people, range, spatial modelling

Introduction

Many species now face large-scale range contraction and extinction (Channell & Lomolino 2000a,b; Laliberte & Ripple 2004; Cardillo *et al*. 2005). Human activities have locally extirpated animals and fragmented their habitats, thus influencing current species distribution patterns (Woodroffe & Ginsberg 1998; Sanderson *et al*. 2003). Determining where species occur and which species are threatened is a fundamental step in their conservation. Extent of range is widely recognized as an important criterion used to classify species according to conservation status. Examining the importance of nature reserves, different

*Correspondence author. E-mail: krithi.karanth@gmail.com

land-cover–land-use types, human densities and human cultural tolerance to species distribution and occurrence is critical to improving mammal conservation efforts (Cardillo *et al.* 2004).

Large mammals are often keystone species that maintain ecosystem stability and biodiversity (Terborgh 1988). They are particularly vulnerable to local extirpations leading to drastic range contractions or even extinctions. Geographical endemism and inherent rarity exacerbated by human impacts have now pushed 25% of terrestrial mammal species close to extinction (Ceballos *et al.* 2005). Many species have disappeared from over 50% of their historical ranges (Ceballos & Ehrlich 2002). Large body sizes, unique habitat requirements, and associated life-history traits increase the vulnerability of mammals to extinction (Brashares 2003; Michalski & Peres 2005).

Assessments of distributions of mammal species at the regional or subcontinental scale are difficult to obtain from direct field surveys of animals. This lack of basic information on species distributions significantly hinders mammal conservation (Brashares, Arcese & Sam 2001; Parks & Harcourt 2002). Most surveys (Channell & Lomolino 2000b; Sanderson *et al.* 2003; Ceballos *et al.* 2005) use questionnaires, static range maps or other forms of expert opinion as basic data. We note that such surveys are commonly affected by the problem of species being present at some locations but going unreported. As a result estimates of habitat occupancy are biased low, and the relationship between animal presence and habitat covariates remains poorly understood (MacKenzie *et al.* 2003; Tyre *et al.* 2003; Gu & Swihart 2004).

India harbours ~450 mammal species, has been occupied by humans for over 50 000 years (Wells 2002), but also has a 'modern' conservation history of regulating land uses to protect natural areas for over a century (Blythe 1863; Prater 1948; Rangarajan 2001). A country-wide wildlife reserve system was set up in the 1970s. In the last 100 years, rapid economic and human demographical growth has intensified human impacts on mammal species and their habitats (Forest Survey of India 2000; Das *et al.* 2006). Conservative estimates suggest that 20% of Indian large mammals face extinction, and several have disappeared from > 90% of their original range (Madhusudan & Mishra 2003). The need for basic information on current mammal distributions and on ecological and social determinants of their persistence is acute.

We conducted a country-wide survey based on field work of local experts and analysed resulting data using occupancy modelling to estimate the present geographical ranges of 20 large mammal species in India. We modelled species occurrence in relation to associated ecological and social covariates to elucidate observed species distribution patterns. These covariates (protected areas, landscape characteristics

Table 1. Environmental and Social covariates and *a priori* predictions about their influence on habitat occupancy of large mammals in India

Covariate category	Variables	Predictions for occupancy
1. Protected areas (pa, park)	(a) Presence or absence of protected area (b) Proportion of cell covered by a protected area (5 categories: 0, 1–25%, 26–50%, 51–75% and 76–100%)	Presence of protected areas and forest cover favours brown bear, black bear, gaur, elephant, rhino, Asiatic wild dog, tiger, leopard, sambar, muntjac, chital and sloth bear
2. Land cover–land use (fc, lc)	(a) Presence or absence of forest cover (b) Ten categories derived from 23 original categories. Categories were evergreen forests, deciduous forests, temperate forests, barren, salt pan, scrub, cultivated, snow, water and rural-urban areas. Actual covariate within each category was the number of pixels of the specified habitat within the cell	Evergreen forests favour sun bear, black bear, gaur, Asiatic wild dog, tiger, leopard, sambar, muntjac, chital, sloth bear and sun bear Deciduous forests favour all species Temperate forests favour brown bear and black bear Scrub-grassland favours all species except brown, black bear, tiger Barren and Salt Pan favour wolf, hyena, nilgai, blackbuck and chinkara Cultivated areas favour most herbivores and jackal
3. Elevation (elv)	Average elevation in a cell. Transformed by dividing by maximum elevation and multiplying by 10. Range of values between 0 and 10	Higher elevations favour brown bear, black bear and sun bear Low and Mid elevations favour gaur, wild pig, jackal, wolf, Asiatic wild dog, tiger, leopard, sambar, muntjac, chital, nilgai, blackbuck, chinkara, sloth bear and hyena
4. Human population density (ppl)	Total number of people for every cell. Log transformation used	Lowers occupancy for most species except wild pig and jackal
5. Cultural intolerance (tol)	Ranked states from most to least tolerant states (1 to 3). Two states were ranked as most tolerant, nine as least tolerant, and the remaining states as medium tolerance	Higher for herbivores (especially black buck, chinkara and nilgai) and lower for carnivores and wild pig

Covariates: pa, park presence/absence; park, percentage of cell covered; fc, forest cover presence/absence; elv, elevation (transformed); ppl, log (human population density); tol, cultural intolerance.
Land-cover and land-use categories are evergreen, temperate, deciduous, scrub–grassland, barren, cultivated, rural–urban, snow, salt pan and water.

Table 2. Best Models for predicting occupancy for each species

Species	Top-ranked model(s) with lowest AIC	w_i	Model AIC	*n*	ΔAIC
Chital *Cervus axis*	ψ (e + t + s + d + park + tol) p (e + t + s + d + park + tol)[2]	0·37	4612·83	14	0·00
	ψ (e + t + s + d + park + tol + ppl) p (e + t + s + d + park + tol + ppl)[2]	0·24	4613·69	16	0·86
	ψ (e + s + d + c + b + park + tol + ppl) p (e + s + d + c + b + park + tol + ppl)[1]	0·17	4614·33	18	1·50
	ψ (e + s + d + c + park + tol + ppl) p (e + s + d + c + park + tol + ppl)[1]	0·12	4615·02	16	2·19
Sambar *Cervus unicolor*	ψ (e + s + d + c + park + ppl + tol) p (e + s + d + c + park + ppl + tol)[1]	0·76	4709·36	16	0·00
	ψ (e + s + d + c + b + park + ppl + tol) p (e + s + d + c + b + park + ppl + tol)[1]	0·21	4711·90	18	2·54
Muntjac *Muntiacus muntjak*	ψ (e + t + s + d + park + ppl + tol) p (e + t + s + d + park + ppl + tol)[2]	0·88	4069·63	16	0·00
	ψ (e + s + d + park + ppl + tol) p (e + s + d + park + ppl + tol)[1]	0·06	4074·93	14	5·30
Blackbuck *Antilope cervicapra*	ψ (e + s + sp + d + c + b + park + tol) p(e + s + sp + d + c + b + park + tol)[1]	0·67	3140·45	18	0·00
	ψ (e + s + d + c + b + park + tol + ppl) p(e + s + d + c + b + park + tol + ppl)[1]	0·18	3143·03	18	2·58
	ψ (s + d + c + b + tol) p (s + d + c + b + tol)[1]	0·07	3145·05	12	4·60
Nilgai *Boselaphus tragocamelus*	ψ (s + d + c + b + park + tol) p (s + d + c + b + park + tol)[2]	0·80	2910·74	14	0·00
	ψ (s + d + c + b + tol) p (s + d + c + b + tol)[2]	0·20	2913·51	12	2·77
Chinkara *Gazella bennetti*	ψ (e + s + d + c + b + park + ppl + tol) p (e + s + d + c + b + park + ppl + tol)[1]	0·93	3112·26	18	0·00
Wild pig *Sus scrofa*	ψ (e + t + s + d + b + c + sp + sn + u + park + tol)	0·56	7600·88	24	0·00
	p (e + t + s + d + b + c + sp + sn + u + park + tol)[3]	0·44	7601·37	26	0·49
	ψ (e + t + s + d + b + c + sp + sn + u + park + tol + ppl)				
	p (e + t + s + d + b + c + sp + sn + u + park + tol + ppl)[3]				
Gaur *Bos gaurus*	ψ (e + s + d + park + ppl + tol) p (e + s + d + park + ppl + tol)[1]	0·59	2091·49	14	0·00
	ψ (e + s + d + c + park + ppl + tol) p (e + s + d + c + park + ppl + tol)[1]	0·15	2094·19	16	2·70
	ψ (e + t + s + d + park + ppl + tol) p (e + t + s + d + park + ppl + tol)[2]	0·11	2094·81	16	3·32
	ψ (e + s + d + c + b + park + ppl + tol) p (e + s + d + c + b + park + ppl + tol)[1]	0·10	2094·97	18	3·48
Elephant *Elephas maximus*	ψ (e + s + d + c + b + park + ppl + tol) p (e + s + d + c + b + park + ppl + tol)[1]	0·87	2376·17	18	0·00
	ψ (e + s + d + park + ppl + tol) p (e + s + d + park + ppl + tol)[1]	0·04	2382·08	14	5·91
Rhino *Rhinoceros unicornis*	ψ (elv + park) p (elv + park)[3]	0·98	172·98	6	0·00
Black bear *Ursus thibetanus*	ψ (e + t + s + d + tol + park) p (e + t + s + d + tol + park)[2]	0·87	1180·54	14	0·00
	ψ (e + t + s + d + tol + park + ppl) p (e + t + s + d + tol + park + ppl)[2]	0·03	1187·29	16	6·75
Brown bear *Ursus arctos*	ψ (e + t + s + d + park) p (e + t + s + d + park)[2]	0·81	602·24	12	0·00
	ψ (e + t + s + d + park + ppl) p (e + t + s + d + park + ppl)[2]	0·12	606·29	14	3·85
Sloth bear *Melursus ursinus*	ψ (e + s + d + c + b + park + ppl) p (e + s + d + c + b + park + ppl)[1]	1·00	4331·15	18	0·00
Sun Bear *Helarctos malayanu)*	ψ (elv + park) p (elv + park)[3]	0·21	176·54	6	0·00
	ψ (park) p (.)[3]	0·08	178·50	3	1·96
	ψ (park) p (.)[3]	0·07	178·58	3	2·04
	ψ (park) p (park)[3]	0·07	178·71	4	2·17
	ψ (elv + park) p (.)[3]	0·04	179·63	4	3·09
	ψ (t) p (.)[1]	0·03	180·18	3	3·64
	ψ (.) p (t)[1]	0·03	180·25	3	3·71
	ψ (.) p (e + t + s + d)[2]	0·03	180·44	6	3·90
	ψ (elv) p (elv)[3]	0·02	180·90	4	4·36
	ψ (.) p (e)[1]	0·02	181·11	3	4·57
Jackal *Canis aureus*	ψ (e + t + s + d + b + c + sp + sn + u + park + ppl + tol)	0·64	6769·68	26	0·00
	p (e + t + s + d + b + c + sp + sn + u + park + ppl + tol)[3]	0·35	6770·88	22	1·20
	ψ (e + t + s + d + b + c + sp + park + ppl + tol)				
	p (e + t + s + d + b + c + sp + park + ppl + tol)[3]				

Table 2. (Continued)

Species	Top-ranked model(s) with lowest AIC	w_i	Model AIC	n	ΔAIC
Hyena *Hyaena hyaena*	ψ (e + s + d + c + b + ppl + park + tol) p(e + s + d + c + b + ppl + park + tol)[2]	1·00	4962·94	18	0·00
Wolf *Canis lupus*	ψ (e + t + s + sp + d + c + b + ppl) p (e + t + s + sp + d + c + b + ppl)[2]	1·00	4917·22	18	0·00
Asiatic wild dog *Cuon alpinus*	ψ (e + t + s + d + tol + park) p (e + t + s + d + tol + park)[2]	0·82	2243·83	14	0·00
	ψ (e + s + d + c + tol + park + ppl) p (e + s + d + c + tol + park + ppl)[1]	0·15	2247·17	16	3·34
Tiger *Panthera tigris*	ψ (e + s + d + c + b + park + ppl + tol) p (e + s + d + c + b + park + ppl + tol)[1]	0·94	2641·22	18	0·00
Leopard *Panthera pardus*	ψ (e + t + s + d + b + c + sp + sn + u + park + ppl + tol + elv) p (e + t + s + d + b + c + sp + sn + u + park + ppl + tol + elv)[3]	0·99	5452·65	28	0·00

Top-ranked models are shown, w_i is the AIC model weight, n is the number of parameters in the model and ΔAIC is the difference in values between lowest AIC model and each model. All models are shown in Supporting Information Appendices S1 and S2.
e, evergreen; t, temperate; s, scrub–grassland; d, deciduous; c, cultivated; b, barren; sn, snow; u, urban–rural; sp, salt pan; park, park proportion; ppl, human population density; tol, cultural intolerance; elv, elevation.
[1]Individual species models.
[2]Group-based models.
[3]General models.

and human influences) allowed us to test hypotheses about plausible determinants of species distribution patterns. We expected the presence of protected areas to have a positive effect and human population density to have a negative effect on the persistence of many species. We expected human cultural tolerance to show subregional variations and have different effects on herbivores and carnivores. The expected effects of landscape covariates varied among species. We developed species-specific occupancy models based on these hypotheses to test our predictions, and we developed corresponding distribution maps.

Materials and methods

OCCUPANCY MODELLING, EXPERT FIELD SURVEYS AND STUDY DESIGN

Inferences about species distribution are complicated by locations that are not surveyed and by non-detection of species that are present in locations that are surveyed. Although the problem of non-detection and 'false absences' occurrence has been recognized for some time (e.g. Preston 1948; Connor & McCoy 1979; Rosenzweig 1995), satisfactory approaches for its solution have only been developed relatively recently. Approaches for inference about species distributions based on so-called presence-only data (locations of species detections) have been developed (e.g. Anderson 2003; Phillips, Anderson & Schapire 2006) but are susceptible to various problems associated with sampling and non-detection.

Occupancy studies are designed to provide inferences about the presence of target organisms in geographical sample units in the presence of imperfect detection. Occupancy models use some form of replication to deal with false absences, situations where species may be present but not always detected by observers (detection probabilities < 1, MacKenzie *et al.* 2002, 2006). We used a grid-based sampling approach and divided the country into 1326 grid cells (average cell size 2818 km^2). We chose this grid cell size as it was practical to get sufficient replication of reports by local experts on presence of multiple species, as well as other data on ecological and social covariates for the entire country only at this scale.

For each mammal species, we used existing information (Prater 1948; Menon 2003) to identify subsets of cells for which species occurrence was biogeographically and ecologically plausible and excluded areas where the species was historically absent.

As a result of the scale of our survey, we obtained species presence–absence data from knowledgeable Indian wildlife experts based on their field observations rather than conduct our own field surveys. Survey forms were completed by these experts (> 100) between January and August 2006. Experts were selected based on their knowledge of particular regions and species. Experts were explicitly instructed to indicate the presence of each species only if they had personally observed either the species or its direct signs (tracks or scats) in the field within the specific grid cell(s) of interest in the past year. They were instructed not to indicate presence of a species if there was any uncertainty (e.g. in identifying scats or tracks to species) associated with an observation. Therefore, we did not interpret reports of non-detection to mean absence of the species, but a reported detection was interpreted as reflecting presence of the species. By emphasizing that all reports of presence had to represent certainty, we sought to eliminate problems of false presences (e.g. Royle & Link 2006). The number of observers (experts) surveyed per cell ranged between two and 37, providing the replicate detection–non-detection data needed to estimate occupancy. We used program PRESENCE (v 2.0; Hines 2006) to model detection probabilities and estimate occupancy for all 20 species.

ESTIMATION AND MODELLING OF OCCUPANCY AND DETECTION PROBABILITY

We estimated occupancy using the single-season models developed by MacKenzie *et al.* (2002, 2006), which use the method of maximum likelihood. For each species, we fit multiple models, representing different hypotheses about the processes that generated the data. The models were ranked in order of parsimony, and model weights were calculated using Akaike's Information Criterion (AIC; Burnham & Anderson 2002, 2004). The AIC weights sum to 1 for all members in a model set, and represent relative measures of the appropriateness of a given model relative to other models in the model set. We used model averaging based on AIC model weights in situations where there were multiple models that were supported by the data.

Our approach to inference yields unconditional estimates of occupancy, $\hat{\psi}_i$ for each cell, *i*, within the area deemed plausible for species occurrence. These values reflect the probability that cell *i* is occupied by the focal species, based on the covariate values associated with the cell. These probabilities can be viewed as expectations associated with a stochastic process and do not represent realizations of this process. Thus, we are not conditioning on the cells with detections (by assigning them probabilities of occurrence of 1) and then estimating conditional occupancy probabilities only for cells at which the species was not detected (see discussions in MacKenzie *et al.* 2006, pp. 97–98 and 123–125). The unconditional occupancy estimates were then summed over all cells to estimate the overall proportion of plausible land area occupied by the species: $\hat{\psi}^* = (\sum_{i=1}^{s} \hat{\psi}_i)/s$, where *s* is the number of cells designated as plausible. This value was used to estimate the overall proportion of land (expressed at the scale of cells) within India that is occupied by the species: $\hat{\psi}_{IN} = \alpha\hat{\psi}^*$, where $\alpha =$ the proportion of land in all of India that was assigned to be plausible for the species. This proportion, α, was estimated by dividing the number of cells used in our analysis for a species by the total number of cells (1326) in India.

COVARIATES

In most field situations, occupancy and detection probabilities are not constant across all sample units (Royle 2005) but instead vary by site characteristics. We model occupancy and detection probabilities as functions of covariates using logit link functions (MacKenzie *et al.*

Table 3. Estimated beta coefficients for the top ranked models for herbivores

Species/covariates	Chital	Sambar	Muntjac	Blackbuck	Nilgai	Chinkara	Wild pig	Gaur	Elephant	Rhino
Constant	−1·45	4·80	−2·99	3·88	3·16	9·07	3·15	−12·77	−22·53	13·04
Evergreen	1·17	1·95	1·75	0·02	NA	−1·52	4·64	1·11	3·83	NA
Temperate	−0·14	NA	−0·39	NA	NA	NA	−0·22	NA	NA	NA
Scrub	−0·32	0·15	−0·78	−1·14	0·69	0·47	−0·37	0·50	0·11	NA
Snow	NA	NA	NA	NA	NA	NA	−0·003	NA	NA	NA
Rural–urban	NA	NA	NA	NA	NA	NA	0·25	NA	NA	NA
Salt pan	NA	NA	NA	0·12	NA	NA	0·05	NA	NA	NA
Deciduous	0·48	0·52	0·68	0·16	0·47	0·54	0·03	0·41	−0·28	NA
Cultivated	NA	0·13	NA	0·29	0·20	NA	0·06	NA	−0·41	NA
Barren	NA	NA	NA	0·46	−0·08	0·42	0·34	NA	−0·72	NA
Elevation	NA	NA	NA	NA	NA	NA	NA	NA	NA	−4·96
Park	0·74	0·61	0·50	0·12	0·13	0·49	0·22	0·06	−0·51	−12·78
Population density	NA	−0·58	−0·37	NA	NA	−0·53	NA	0·46	1·46	NA
Tol (intolerance)	0·28	0·78	3·20	−2·91	−2·47	−3·37	−0·93	1·88	2·57	NA

Table 4. Estimated beta coefficients for the top ranked models for carnivores

Species/covariates	Black bear	Brown bear	Sloth bear	Sun bear	Jackal	Hyena	Wolf	Asiatic wild dog	Tiger	Leopard
Constant	−5·85	−1·61	−7·93	−0·68	−0·14	2·31	0·59	−9·21	−10·33	12·74
Evergreen	0·35	−6·35	−0·21	NA	0·17	0·06	0·21	0·66	0·31	1·57
Temperate	15·87	4·70	NA	NA	0·12	NA	1·10	0·01	NA	5·18
Scrub	−0·28	−0·10	0·53	NA	−0·03	−0·32	0·28	−0·02	−0·01	−0·18
Snow	NA	NA	NA	NA	−0·27	NA	NA	NA	NA	−1·35
Rural–urban	NA	NA	NA	NA	0·06	NA	NA	NA	NA	0·57
Salt pan	NA	NA	NA	NA	0·04	NA	0·70	NA	NA	−0·40
Deciduous	−0·63	−0·10	0·80	NA	0·15	0·61	0·76	0·38	0·41	0·45
Cultivated	NA	NA	−0·29	NA	0·09	0·17	0·56	NA	0·10	0·13
Barren	NA	NA	0·75	NA	0·06	0·06	−0·22	NA	−0·29	0·38
Elevation	NA	NA	NA	−1·08	NA	NA	NA	NA	NA	−0·32
Park	−0·71	1·68	0·50	2·86	0·32	0·36	NA	0·29	0·91	0·50
Population density	NA	NA	0·76	NA	0·39	−0·19	NA	NA	0·42	−0·99
Tol (intolerance)	2·99	NA	−0·69	NA	−1·92	−0·60	−0·22	3·29	0·96	−0·23

2006). For example, the logit of the probability of a site being occupied is expressed as

$$\text{Logit}(\psi_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots\ldots + \beta_u x_{iu},$$

which is a linear function of the u covariates associated with site i, with one intercept term β_0 and u regression coefficients that need to be estimated (MacKenzie *et al.* 2006).

Based on ecological and social contextual knowledge, we selected covariates most likely to influence the distribution of large mammals in India. These include designated wildlife protected area in the cell, landscape characteristics and human influences. Data on protected areas are from the World Database on Protected Areas (http://www.unep-wcmc.org/wdpa) and were further refined using topographic maps and expert knowledge from India. The data were used to create two measures as covariates – presence or absence of a protected area in a cell, and proportion of cell covered by a protected area (Table 1). We selected presence or absence of forest cover in a cell, land cover–land use data, and elevation as covariates representing landscape characteristics. Land cover–land use data were derived from Global Land Cover Facility 2000 (Bartholomé & Belward 2005) and refined using Joshi *et al.* (2006) and Roy *et al.* (2006). We consolidated land-cover and land-use categories from 23 to 10, and used the total number of pixels in each category for every grid cell. This allowed us to build a reasonable and easily interpretable model set (Table 1). Elevation data were obtained from CGIAR-CSI SRTM 100 m (CGIAR-CSI 2004) Digital Elevation Data (2004). We calculated the average elevation in every grid cell, divided by the maximum, and transformed this to range between 0 and 10.

To measure human influence, we used human population density and 'human cultural tolerance' towards mammal species that exist in India. Human population density data were derived from LandScan Global Population Data 2000 (http://www.ornl.gov/gist) (Dobson *et al.* 2000; Budhendra *et al.* 2002). We calculated human population density for every cell, and log transformed this variable. We developed a 'human cultural tolerance' variable from prior personal observations, socio-cultural knowledge and hunting patterns of local communities in the different states of India (Rangarajan 2001; Madhusudan & Karanth 2005; Datta 2007; K. K. Karanth and K. U. Karanth, pers. obs.). India is a multi-cultural country and the State boundaries were reorganized in the 1950s and 1960s in recognition of the fact that linguistic affinities represent overall diversity effectively. Furthermore, effectiveness of anti-hunting law enforcement that shapes the degree of hunting pressure is influenced by each State's administrative culture (based on factors like efficiency, corruption, management policies and quality of field personnel). For example, States such as Madhya Pradesh and Karnataka have a relatively strong culture of law enforcement, whereas the ethnically tribal hill states in north-eastern India have poor law enforcement and much higher levels of illegal hunting. Therefore, we believe this covariate effectively represents both local people's cultural tolerance and the official law enforcement effectiveness. We grouped States from most tolerant to least tolerant (Table 1). The western states of Rajasthan and Gujarat were classified as most tolerant, seven north-eastern hill states, Chhattisgarh and Jharkhand were classified as least tolerant, and all other states as medium tolerance.

We fit several general, group and individual species-based occupancy models (Table 2). We grouped the species based on *a priori* knowledge of their general habitat preferences (Table 2). Group 1 had 14 species that are believed to prefer more closed habitat types (deciduous, evergreen, temperate and scrub-grassland areas). Group 2 had six species believed to prefer more open habitat types (scrub-grassland, salt pan, barren and cultivated areas). We also ran occupancy models tailored to reflect hypothesized habitat preferences of individual species. For rare species (e.g. sun bear *Helarctos malayanus*), our model set was smaller and restricted to simpler models. For each species, we estimated the total area (expressed as number of cells) currently occupied by summing occupancy across all cells (Table 5).

Table 5. Estimated occupancy for large mammals in India

Species	Common name	x/s	Naïve estimate of ψ	$\Sigma\hat{\psi}_i$	$\hat{\psi}$	$\hat{\psi}_{IN}$
Cervus axis	Chital	481/1009	0·48	483·23	0·48	0·36
Cervus unicolor	Sambar	539/1124	0·48	721·82	0·63	0·53
Muntiacus muntjak	Muntjac	430/1096	0·39	505·41	0·47	0·39
Antilope cervicapra	Blackbuck	342/970	0·35	588·02	0·61	0·44
Boselaphus tragocamelus	Nilgai	518/883	0·57	557·03	0·63	0·42
Gazella bennetti	Chinkara	387/883	0·44	430·95	0·49	0·32
Sus scrofa	Wild pig	987/1229	0·80	1113·78	0·91	0·84
Bos gaurus	Gaur	167/799	0·21	252·04	0·31	0·19
Elephas maximus	Elephant	198/963	0·20	340·36	0·35	0·26
Rhinoceros unicornis	Rhino	13/163	0·08	75·62	0·46	0·06
Ursus thibetanus	Black bear	130/301	0·43	201·62	0·67	0·15
Ursus arctos	Brown bear	71/170	0·42	91·92	0·54	0·07
Melursus ursinus	Sloth bear	464/1116	0·42	762·37	0·68	0·57
Helarctos malayanus	Sun bear	18/131	0·14	40·00	0·30	0·03
Canis aureus	Jackal	963/1229	0·78	1030·58	0·83	0·78
Hyaena hyaena	Hyena	588/1029	0·57	671·13	0·65	0·51
Canis lupus	Wolf	575/1094	0·52	894·79	0·82	0·67
Cuon alpinus	Asiatic wild dog (Dhole)	211/1106	0·19	330·99	0·30	0·25
Panthera tigris	Tiger	249/1189	0·21	323·81	0·27	0·24
Panthera pardus	Leopard	647/1229	0·52	904·21	0·73	0·68

The number of cells in which a species was detected $= x$ and the number of plausible cells within which a species might occur $= s$. The naïve estimate of occupancy for plausible cells is $\psi = x/s$. $\hat{\psi}_i$ is the estimated occupancy probability for the ith cell and $\hat{\psi} = \Sigma\hat{\psi}_i/s$ is the average of the estimated probabilities of occupancy for plausible cells, computed as the sum of occupancy probabilities for all plausible cells divided by the number of cells. $\hat{\psi}_{IN}$ is $\Sigma\hat{\psi}_i$ divided by 1326 (the total number of cells in India).

A PRIORI PREDICTIONS

Modelling covariates enabled us to evaluate predictions from *a priori* hypotheses about factors influencing probabilities of occupancy and detection. For protected area covariates, we predicted higher occupancy for 10 species that prefer dense habitat cover (Table 1). We selected land-cover covariates that are ecologically relevant (Table 1; Supporting information Appendices S1 and S2). We also predicted elevation to affect occupancy, with higher altitude predicted to yield increased occupancy for three bear species and reduced occupancy for other species (Table 1). We expected human population density to have a negative relationship with occupancy for most species (except wild pig *Sus scrofa* and jackal *Canis aureus*, which adapt to settlements, and nilgai *Boselaphus tragocamelus*, chinkara *Gazella bennetti*, and blackbuck *Antilope cervicapra* that are culturally tolerated in some areas). For the cultural tolerance covariate, we expected greater tolerance for and thus higher occupancy for herbivores as opposed to carnivores. Models include effects of covariates on probabilities of occupancy, detection, and both occupancy and detection. Detailed predictions are shown in Table 1. Latin names are in Table 2.

Results

PROPORTION OF PROTECTED AREA

The proportion of protected area was included in at least one of the top models for 19 species (exception for wolf *Canis lupus*; Table 2). The β parameters were positive for 16 species (Tables 3 and 4), indicating that the proportion of land set aside as protected area is important to species occupancy. Our predictions were correct for 10 forest-dwelling species, but extended to other species as well.

LAND COVER AND ELEVATION

Different combinations of land-cover types appeared important for different species. Evergreen forest was in the top model for 17 species (all except nilgai, rhino *Rhinoceros unicornis* and sun bear Table 2). The β parameters for evergreen forest were positive for 14 of these species and negative for three (chinkara, brown bear *Ursus arctos*, sloth bear *Melursus ursinus*). Our predictions were supported for all species except sloth bear. Temperate forest was in the top model for nine species, β parameters were positive for six species, and were negative for the other three species (Tables 3 and 4). Our predictions were found true for these species and extended to jackal, wolf, hyena *Hyaena hyaena* and leopard *Panthera pardus*. Deciduous forest was in the top model of 18 species (exceptions were rhino and sun bear; Table 2). The β parameters for deciduous forests were positive for 15 species. Negative β parameters for elephant *Elephas maximus*, brown and black bear *Ursus thibetanus*, indicate that our predictions were correct for all except

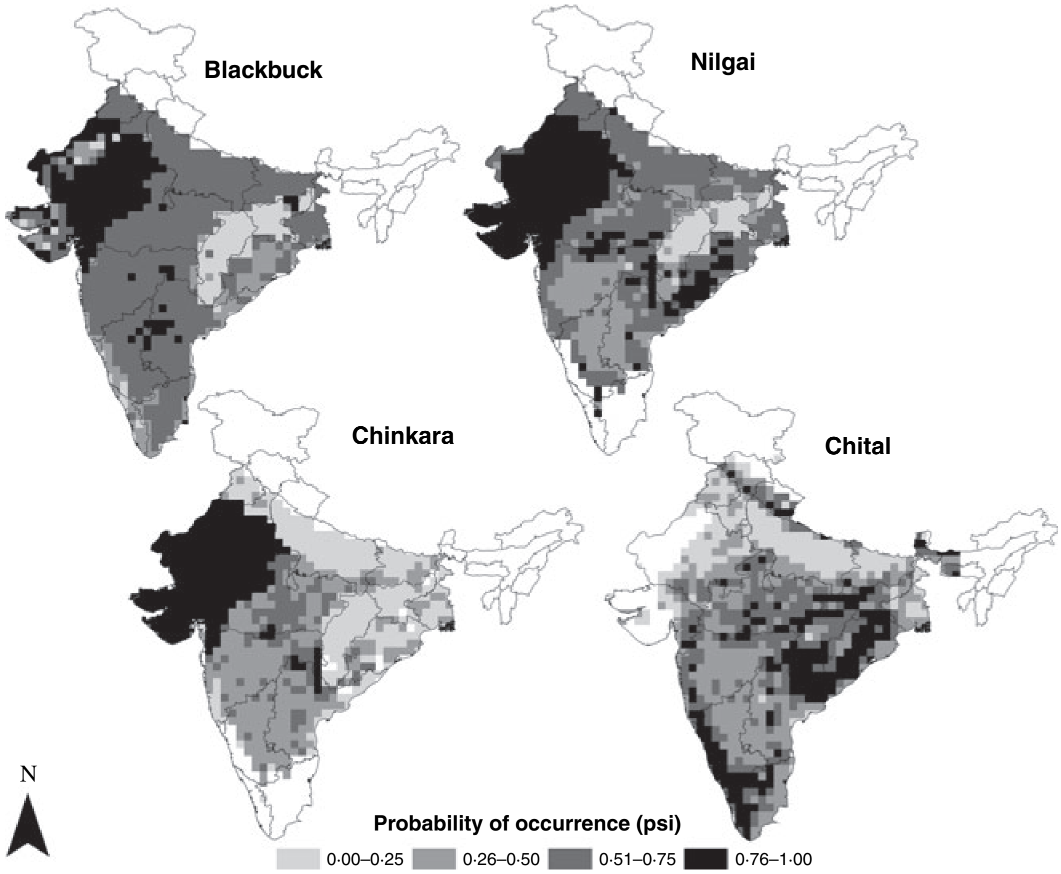

Fig. 1. Estimated probabilities of occurrence for blackbuck *Antelope cervicapra*, nilgai *Boselaphus tragocamelus*, chinkara *Gazella bennetti* and chital *Cervus axis*.

these three species. For details of other land-cover and land-use types and their effects on individual species occurrence, see Tables 2–4.

Elevation was included in the top models for three species (rhino, sun bear and leopard) with negative β parameters for all three. Our predictions were not confirmed for a positive relationship with elevation for three bear species brown bear, black bear and sun bear.

HUMAN POPULATION DENSITY AND CULTURAL TOLERANCE

Human population density was included in the top model for 10 species, and in additional models receiving substantive support for seven species. The β parameters were negative for three herbivores (sambar *Cervus unicolor*, muntjac *Muntiacus muntjak*, chinkara), and two carnivores (hyena and leopard). This suggests that human population density affects occupancy of some species, with some species adapting better to people (jackal) or coming into less contact with people (gaur *Bos gaurus*, elephant, sloth bear and tiger *Panthera tigris*) than others.

Human cultural tolerance was included in the top models for 17 species. The β parameters were negative for nine species (reflecting increased probability of occurrence with increasing tolerance), and positive for the eight others (Tables 3 and 4). The species with negative β parameters are adaptable and generally tolerated species (blackbuck, nilgai, chinkara, wild pig, sloth bear, jackal, hyena, wolf and leopard). Species with positive β parameters are mainly restricted to protected areas or are feared by people. Our predictions were supported for most species.

ESTIMATED AREA OCCUPIED BY DIFFERENT MAMMALS

We summed occupancy estimates and developed predicted occurrence and distribution maps for all 20 species (Table 5; Figs 1–5). For all species, the estimated proportion of cells occupied by a species was higher than the naïve occupancy, especially so for sambar, blackbuck, wild pig, gaur, elephant, rhino, black bear, brown bear, sloth bear, sun bear, wolf, Asiatic wild dog *Cuon alpinus* and leopard (Table 5; Figs 1–5). The most widespread species were jackal (total $\hat{\psi}_{IN} = 0{\cdot}78$; Fig. 5) and wild pig (total $\hat{\psi}_{IN} = 0{\cdot}91$; Fig. 2). The most restricted species were rhino ($\hat{\psi}_{IN} = 0{\cdot}06$; Fig. 2), and sun bear ($\hat{\psi}_{IN} = 0{\cdot}03$; Fig. 4). Among herbivores the $\hat{\psi}$ values (estimated probability that an average plausible cell is occupied) ranged from 0·31 to 0·91. The herbivores with the most restricted ranges are rhino, gaur and elephant (Table 5). For carnivores, $\hat{\psi}$ values ranged more widely from 0·27 to 0·83. The

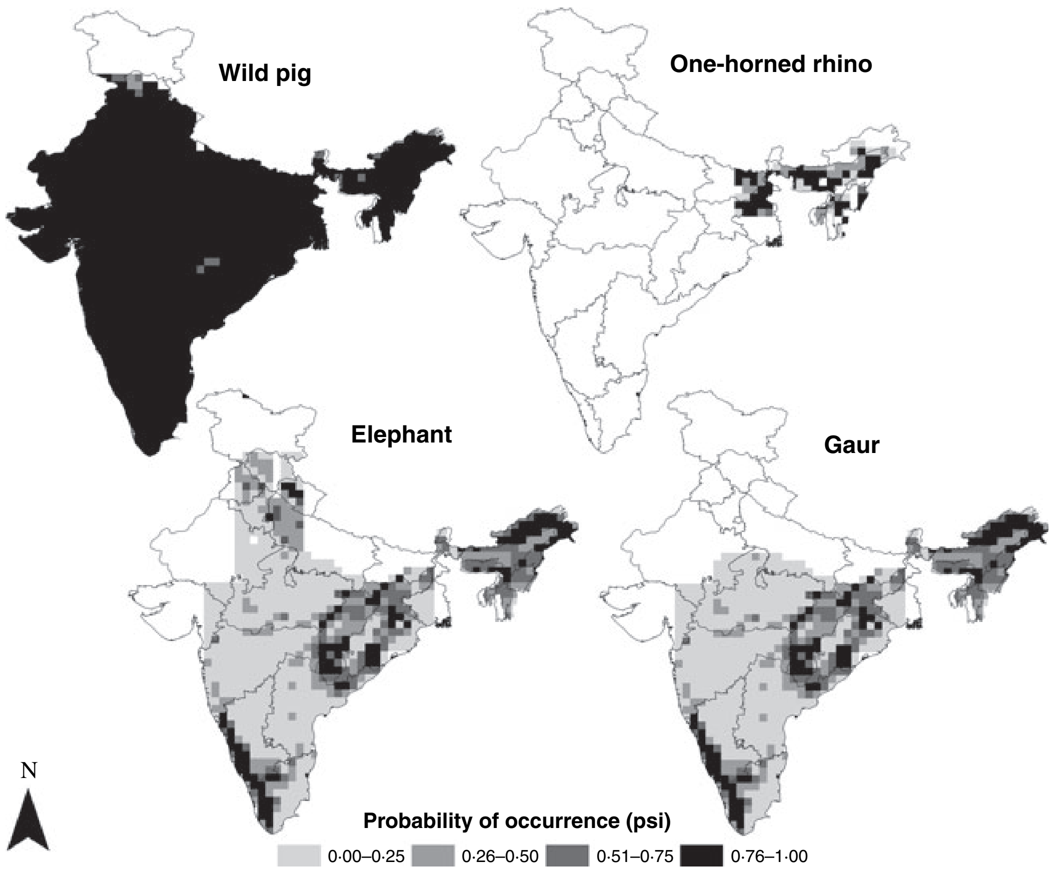

Fig. 2. Estimated probabilities of occurrence for wild pig *Sus scrofa*, rhino *Rhinoceros unicornis*, elephant *Elephas maximus* and gaur *Bos gaurus*.

carnivores most restricted in range are sun bear, brown bear and tiger (Table 5).

Discussion

Range maps are widely used to understand species distribution, focus conservation efforts and classify species by conservation status. In India, current range maps for most large mammal species are unreliable. We used occupancy modelling to map species distributions and investigate determinants of species occurrence. Our results show that failure to incorporate detection probability in surveys and analyses substantially underestimates overall habitat occupancy of all species (Table 5). We recommend that distribution surveys based on animal 'presence versus absence' data should be designed *a priori* to incorporate imperfect detections to overcome this bias.

In future analyses of species range, we believe, it will be useful to investigate auto-logistic models that explicitly model focal cell occupancy as a function of occupancy of cells within a specified neighbourhood (e.g. Augustin, Mugglestone & Buckland 1996). These models have been recently used for inference about occupancy in the presence of non-detection (Sargeant *et al.* 2005; Royle & Dorazio 2008), and we expect them to see greater use as software becomes available to facilitate implementation.

We found protected areas are key determinants of of 16 species, particularly those which are restricted regionally, or require forested habitats. Many species (e.g. tiger, Asiatic wild dog and elephant) that had a wide distribution < 100 years ago (K.K. Karanth, J.D. Nichols, U.K. Karanth, J.E. Hines & N.L. Christensen, unpublished), are now primarily restricted to protected areas (Figs 2, 3 and 5). Although India's protected areas are small (average size < 300 km^2) and fragmented, their carrying capacities for large mammals are high (Karanth *et al.* 2004). Improving protection and monitoring animal population status will be critical to their survival. Given that protected areas occupy < 4% of the country's land area now, expanding India's nature reserves, reducing their fragmentation and improving connectivity, as well as enhancing legal and traditional protection mechanisms, should be conservation policy priorities.

Maintaining landscape diversity, connectivity and compatibility of mammal habitats with human land uses will be also important for species whose habitats are substantially outside protected reserves (e.g. blackbuck, chinkara, wild pig, hyena, jackal, sloth bear, wolf and leopard; Figs 1–5). Rapid ongoing land-use changes (driven by human demographic growth) and

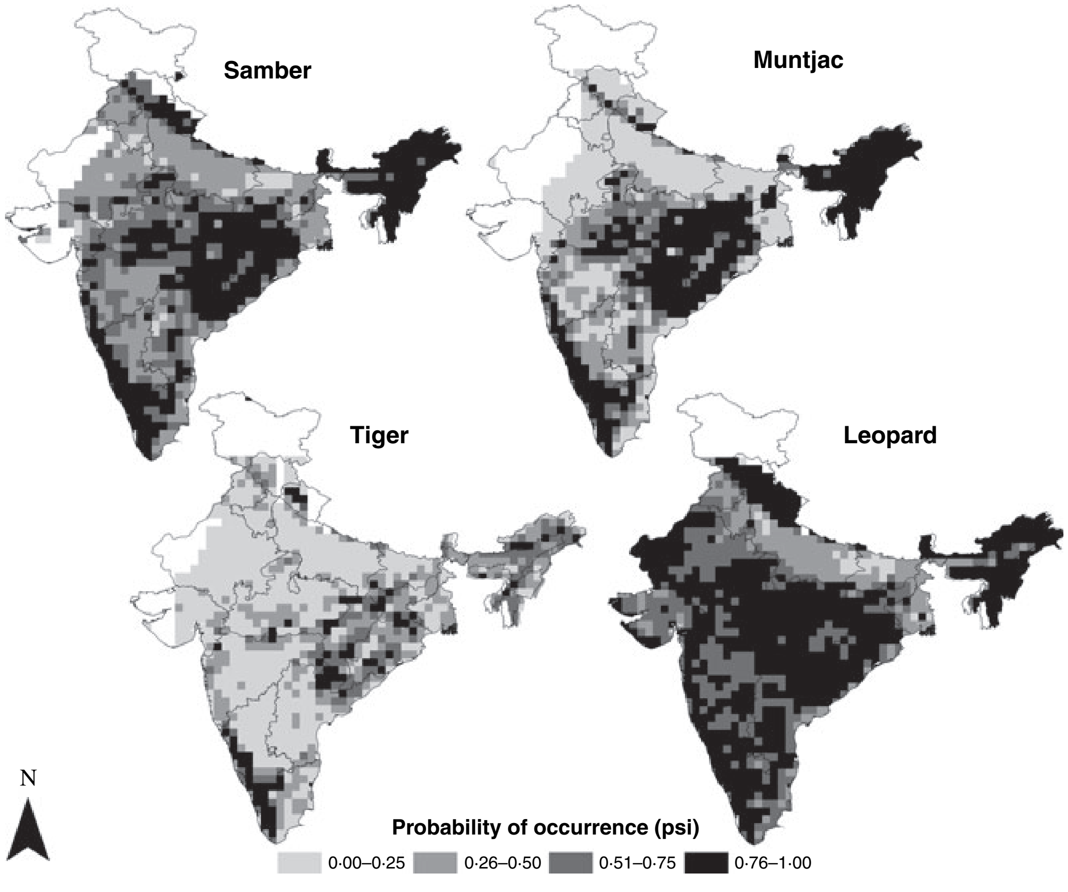

Fig. 3. Estimated probabilities of occurrence for sambar *Cervus unicolor*, muntjac *Muntiacus muntjak*, tiger *Panthera tigris* and leopard *Panthera pardus*.

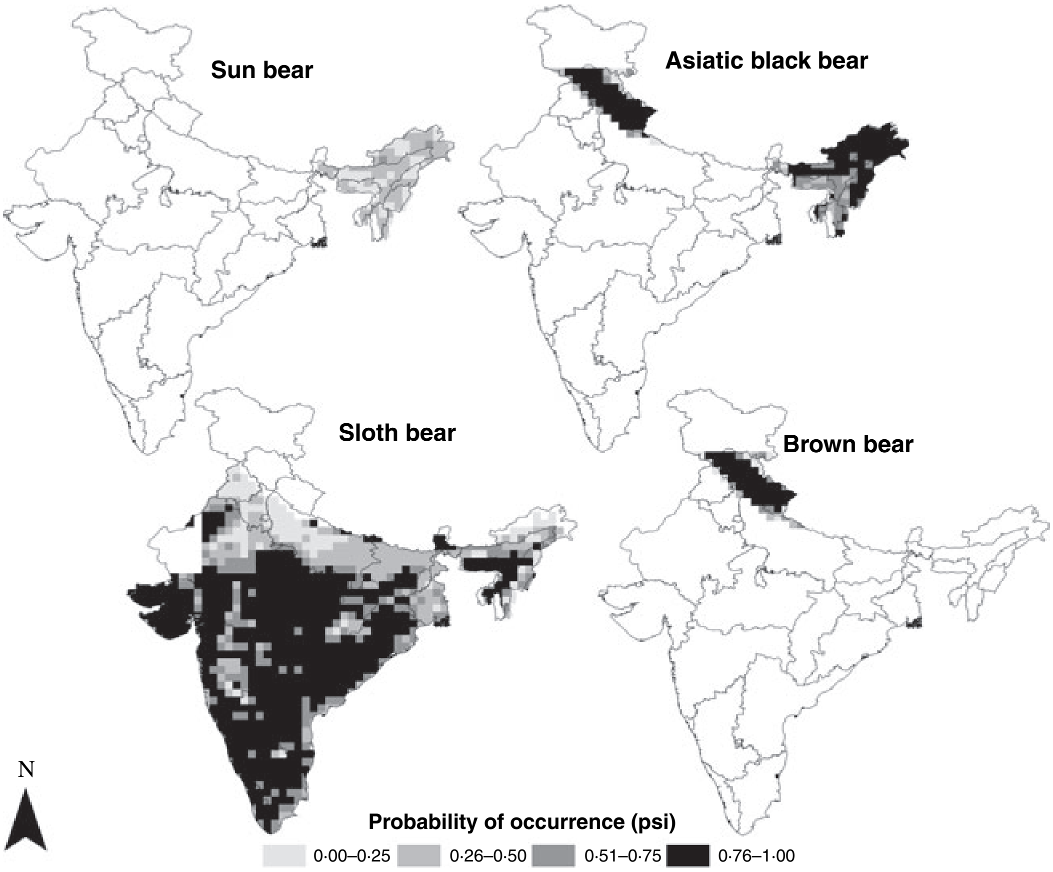

Fig. 4. Estimated probabilities of occurrence for sun bear *Helarctos malayanus*, black bear *Ursus thibetanus*, sloth bear *Melursus ursinus* and brown bear *Ursus arctos*.

economic development present significant challenges to protecting these species.

Forest clearance for agriculture in historical times has actually benefited species such as blackbuck, chinkara, nilgai, wolf and jackal. Species that are likely to benefit from the predominant Hindu cultural tolerance include nilgai, blackbuck and chinkara (in parts of Northern and Western India), gaur (in central and southern India), and elephants, macaques and langurs across much of their range, exemplifying this phenomenon unique to the Indian subcontinent. Our results support previous studies (Newmark 1995, 1996; Woodroffe & Ginsberg 1998; Brashares *et al.* 2001; Parks & Harcourt 2002; Treves & Karanth 2003; Cardillo *et al.* 2004) showing human demography and land use are important factors in mammal distribution, but cultural tolerance is a unique additional positive factor in India despite high human densities. It is particularly noteworthy that all legal hunting has been virtually banned for over 30 years in India taking advantage of this cultural ethos. Therefore, policies such as game harvesting or trophy hunting appear to be inappropriate as conservation tools in India despite their potential utility elsewhere in the world.

The ranges of several of the studied species of large mammals have contracted greatly. Some of these species will require expanded protected areas with strong law enforcement if they are to survive, while others will require additional strategies based on modifying human land uses based on traditional social tolerance or current non-consumptive utilitarian values. Our results are likely to be useful in crafting conservation strategies that appropriately blend protected areas, land-use changes, law enforcement and cultural traditions to ensure the persistence of India's large mammals at large regional scales.

Acknowledgements

The authors are enormously grateful to the wildlife experts N. Akhtar, R. Ali, S. Amu, A. Aiyadurai, Y. V. Bhatnagar, R. Borges, A. Chandola, S. Chandola, D. Chetry, K. Choudhary, S. Choudhry, H. Dang, S. Dasgupta, S. Dattatri, A. Dutta, P. S. Easa, D. V. Girish, H. Ghuleria, D. Ghose, S. P. Goyal, B. Hegde, Hilaluddin, D. Jathanna, B. Jetva, Y. V. Jhala, A. J. T. John Singh, S. Jones, J. Joshua, K. Kakati, K.U. Karanth, K. Kathju, D. K. Kashyap, R. Kaul, M. Khanduja, J. Kulkarni, A. Kumar, N. S. Kumar, S. Kumar, H. Kumara, A. Lobo, P. Mehta, B. Mohanty, S. Molur, S. Mukherjee, L. Nehemiah, N. Patil, S. Pawar, S. Pradhan, S. Radhakrishna, A. Rahmani, N. Rajamani, S. Rajesh, S. Ram, G. S. Rawat, G. V. Reddy, V. Rishi, A. D. Roy, P. K. Sen, K. Sharma, N. Sharma, K. Sathasivam, J. N. Shah, G. Shahabuddin, D. Sharma, V. Srinivas, G. Sundar, A. Tamim, S. Tiwari, P. Trivedi, H. Tyabji, N. Ved, R. Vyas, R Wangchuk, T. Wangyal, and their associates who completed the surveys. We thank S. L. Pimm, D. L. Urban, C.N. Jenkins, M. Vale, N. S. Kumar, P. M. Kumar, Duke University, Center for Wildlife Studies and Wildlife Conservation Society's India Program. Karanth received funding from the Conservation, Food and Health Foundation, Forest History Society, Duke International Travel, IDEA Wild, Roger Williams Park Zoo, AZFA Clark Waldram Conservation Fund, and Cleveland Zoo. We thank the editors and referees for their constructive comments that led to substantial improvements to the manuscript.

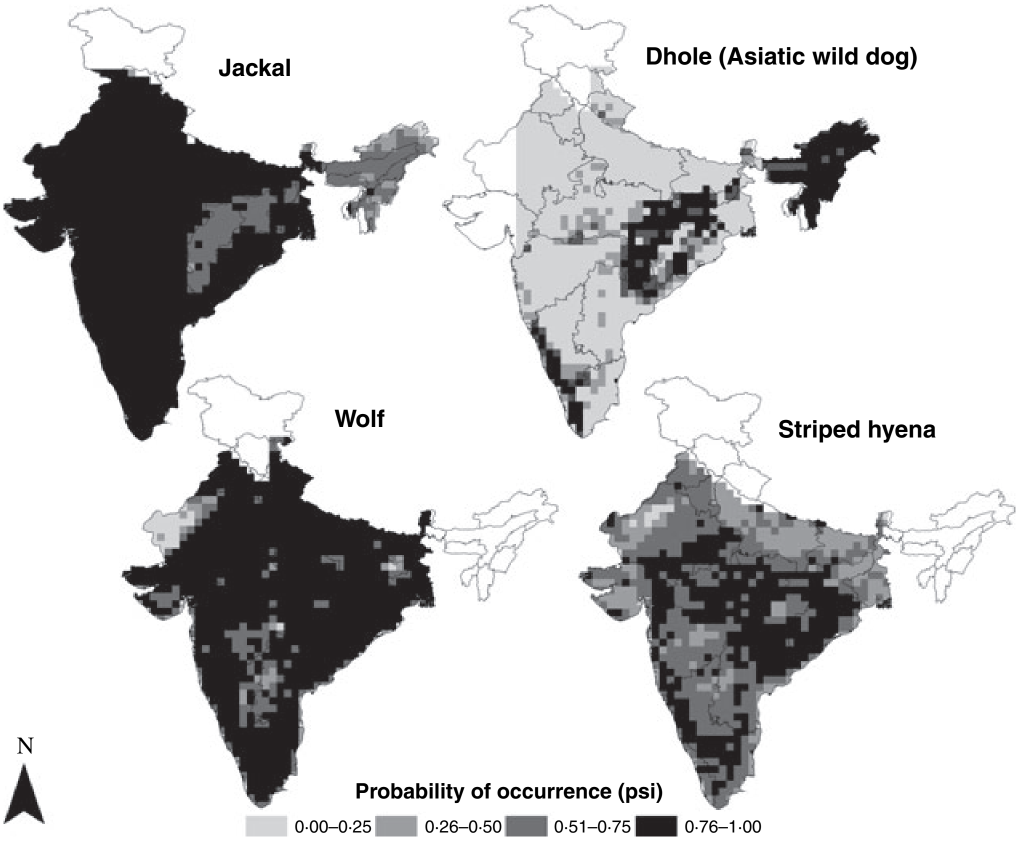

Fig. 5. Estimated probabilities of occurrence for jackal *Canis aureus*, Asiatic wild dog *Cuon alpinus*, wolf *Canis lupus* and hyena *Hyaena hyaena*.

References

Anderson, R.P. (2003) Real vs. artefactual absences in species distributions: test with *Oryzomys albigularis* (Rodentia: Muridae) in Venezuela. *Journal of Biogeography*, **30**, 591–605.

Augustin, N.H., Mugglestone, M.A. & Buckland, S.T. (1996) An autologistic model for the spatial distribution of wildlife. *Journal of Applied Ecology*, **33**, 339–347.

Bartholomé, E. & Belward, A.S. (2005) GLC2000: a new approach to global land cover mapping from earth observation data. *International Journal of Remote Sensing*, **26**, 11051–11077.

Blythe, E. (1863). *Catalogue of the Mammalia in the Museum Asiatic Society*. Savielle and Cranenburgh. Bengal Printing Committee Ltd, London, UK.

Brashares, J.S. (2003) Correlates of extinction in West Africa. *Conservation Biology*, **17**, 734–743.

Brashares, J.S., Arcese, P. & Sam, M.K. (2001) Human demography and reserve size predict wildlife extinction in West Africa. *Proceedings of the Royal Society of London*, **268**, 2473–2478.

Budhendra, B., Bright, E., Coleman, P. & Dobson, J. (2002) LandScan: locating people is what matters. *Geoinformatics*, **5**, 34–37.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodal Inference: A Practical Information × Theoretic Approach*. Springer-Verlag, New York, NY.

Burnham, K.P. & Anderson, D.R. (2004) Multimodal inference: understanding AIC and BIC in model selection. *Sociologial Methods and Research*, **33**, 261–304.

Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Beilby, J. & Mace, G.M. (2004) Human population density and extinction risk in the world's carnivores. *Public Library of Science Biology*, **2**, 909–914.

Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L. & Purvis, A. (2005) Multiple causes of high extinction risk in large mammal species. *Science*, **309**, 1239–1241.

Ceballos, G. & Ehrlich, P.R. (2002) Mammal population losses and the extinction crisis. *Science*, **296**, 904–907.

Ceballos, G., Ehrlich, P.R., Soberon, J., Salazar, I. & Fay, J.P. (2005) Global mammal conservation: what must we manage? *Science*, **309**, 603–607.

CGIAR-CSI (2004) SRTM data V1, International Centre for Tropical Agriculture (CIAT). http://srtm.csi.cgiar.org (accessed June 2006).

Channell, R. & Lomolino, M. (2000a) Trajectories to extinction: spatial dynamics of the contraction of geographic ranges. *Journal of Biogeography*, **27**, 169–179.

Channell, R. & Lomolino, M. (2000b) Dynamic biogeography and the conservation of endangered species. *Nature*, **403**, 84–86.

Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species-area relationship. *American Naturalist*, **113**, 791–833.

Das, A., Krishnaswamy, J., Bawa, K.S., Kiran, M.C., Srinivas, V., Kumar, N.S. & Karanth, U.K. (2006) Prioritization of conservation areas in the Western Ghats, India. *Biological Conservation*, **133**, 16–31.

Datta, A. (2007). Protecting with people in Namdapha: threatened forests, forgotten people. *Making Conservation Work* (eds G. Shahabuddin & M. Rangarajan), pp. 165–209. Permanent Black, New Delhi.

Dobson, J.E., Bright, E.A., Coleman, P.R., Durfee, R.C. & Worley, B.A. (2000) LandScan: a global population database for estimating populations at risk. *Photogrammetric Engineering and Remote Sensing*, **66**, 8410–8857.

Forest Survey of India (2000) *State of the Forest Report*. Forest Survey of India, Dehradun.

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.

Hines, J.E. (2006). *Program PRESENCE (Version 2)*. http://www.mbr-pwrc.usgs.gov/software/doc/presence/presence.html.

Joshi, P.K.K., Roy, P.S., Singh, S., Agrawal, S. & Yadav, D. (2006) Vegetation cover mapping in India using multi-temporal IRS Wide Field Sensor (WiFS) data. *Remote Sensing of Environment*, **103**, 1100–1112.

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

Laliberte, A.S. & Ripple, W.J. (2004) Range contractions of North American carnivores and ungulates. *BioScience*, **54**, 123–138.

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., Hines, J.E., Knutson, M.G. & Franklin, A.D. (2003) Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.A. & Hines, J.E. (2006). *Occupancy Modeling and Estimation*. Academic Press, San Diego, CA.

Madhusudan, M.D. & Karanth, U.K. (2005). Local hunting and large mammal conservation. *Wildlife Conservation, Research and Management* (eds Y.V. Jhala, R. Chellam & Q. Qureshi), pp. 60–67. Wildlife Institute of India, Dehradun.

Madhusudan, M.D. & Mishra, C. (2003). Why big, fierce animals are threatened: conserving large mammals in densely populated landscapes. *Battles Over Nature: Science and Politics of Conservation* (eds V. Saberwal & M. Rangarajan), pp. 31–55. Permanent Black, New Delhi.

Menon, V. (2003) *A Field Guide to Indian Mammals*. Dorling Kindersley India Pvt. Limited, Delhi.

Michalski, F. & Peres, C.A. (2005) Anthropogenic determinants of primate and carnivore local extinctions in a fragmented forest landscape of southern Amazonia. *Biological Conservation*, **124**, 383–396.

Newmark, W.D. (1995) Extinction of mammal populations in western North American national parks. *Conservation Biology*, **9**, 512–526.

Newmark, W.D. (1996) Insularization of Tanzanian parks and the local extinction of mammals. *Conservation Biology*, **10**, 1549–1556.

Parks, S.A. & Harcourt, A.H. (2002) Reserve size, local human density, and mammalian extinctions in U.S protected areas. *Conservation Biology*, **16**, 800–808.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Prater, S.H. (1948) *The Book of Indian Animals*. Bombay Natural History Society, Bombay.

Preston, F.W. (1948) The commonness, and rarity, of species. *Ecology*, **29**, 254–283.

Rangarajan, M. (2001) *India's Wildlife History*. Permanent Black, New Delhi.

Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Roy, P.S., Joshi, P.K., Singh, S., Agrawal, S., Yadav, D. & Jegannathan, C. (2006) Biome mapping in India using vegetation type map derived using temporal satellite data and environmental parameters. *Ecological Modelling*, **1107**, 148–158.

Royle, J.A. (2005) Site occupancy models with heterogeneous detection probabilities. *Biometrics*, **62**, 97–102.

Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis of Data From Populations*. Acadmic Press, San Diego, CA.

Royle, J.A. & Link, W.A. (2006) Generalized site occupancy models allowing for false positive and false negative errors. *Ecology*, **87**, 835–841.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2003) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.

Sargeant, G.A., Sovada, M.A., Slivinski, C.C. & Johnson, D.H. (2005) Markov chain Monte carlo estimation of species distributions: a case study of the swift fox in western Kansas. *Journal of Wildlife Management*, **69**, 483–497.

Terborgh, J.W. (1988) The big things that run the world- a sequel to E.O Wilson. *Conservation Biology*, **2**, 402–403.

Treves, A. & Karanth, U.K. (2003) Human-carnivore conflict and perspectives on carnivore management worldwide. *Conservation Biology*, **17**, 1491–1499.

Tyre, A.J., Tenhumberg, B., Field, S.A., Niejalke, D., Parris, K. & Possingham, H.P. (2003) Improving precision and reduction bias in biological surveys, by estimating false negative error rates in presence-absence data. *Ecological Applications*, **13**, 1790–1801.

Wells, S. (2002) *The Journey of Man: A Genetic Odyssey*. Princeton University Press, Princeton, NJ.

Woodroffe, R. & Ginsberg, G.R. (1998) Edge effects and extinctions of populations inside protected areas. *Science*, **280**, 2126–2128.

Received 19 March 2009; accepted 19 August 2009
Handling Editor: Andy Royle

Supporting Information

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

Appendix S1. Models included in the model sets for all species.

Appendix S2 Models included in the model sets for groups of species.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.