Determinants of occupancy and burrow site selection by Indian crested porcupine in Keoladeo National Park, Bharatpur, Rajasthan, India

Aditi Mukherjee[1,2], Honnavalli Nagaraj Kumara[1,*] and Subramanian Bhupathy[1,†]

[1]Sálim Ali Centre for Ornithology and Natural History, Anaikatty (Post), Coimbatore 641 108, India
[2]Manipal University, Madhav Nagar, Manipal 576 104, India

We examined factors responsible for spatial occupancy and burrow site selection for permanent occupancy by Indian crested porcupine in Keoladeo National Park, Bharatpur, Rajasthan, India. We employed occupancy framework to examine a priori hypotheses and to obtain detection histories of faecal droppings and burrow occurrence. The detection probability ($0.19 \pm 0.05_{SE}$) and occupancy ($0.28 \pm 0.05_{SE}$) of burrow sites were lower than those of faecal deposits ($0.33 \pm 0.029_{SE}$ and $0.71 \pm 0.06_{SE}$) respectively. The rodents avoided areas with water cover and selected those closer to the boundary of nearby agricultural fields at higher elevation as burrow sites. None of the considered covariates influenced their spatial occupancy. This study infers the strategic placement of burrows by these apex ecosystem engineers, also providing crucial ecological niche for various other co-occupants.

Keywords: Burrows, *Hystrix indica*, occupancy modelling, site selection, spatial occupancy.

ALL organisms adjust to different ecological conditions imposed on them by the environment and the conformity between them constitutes 'adaptation of an organism'[1]. Although animals can adapt and occupy almost every possible habitat, they inhabit only a limited set of ecological conditions eventually shaping species occupancy in a particular habitat[2]. Thus, understanding the influence of specific environmental variables upon occurrence of species in a habitat is a prerequisite for management and subsequent development of conservation action plans[3,4]. Identifying these specific conditions or factors is therefore crucial in understanding species occupancy or site selection for a specific activity.

A species not only occupies a habitat, but also selects an appropriate site for refuge either daily or seasonally, which is an essential requirement for the persistence of any population. Suitable burrowing sites for fossorial animals, play a crucial role in the successful rate of reproduction and rearing of offspring[5–8], and also provide protection against weather extremes, fire and predation[9–12]. Several physical, biological and ecological factors significantly influence the refuge site-selection by populations at various spatial scales[13]. Thus, understanding these factors across a landscape is imperative to manage the concerned species.

For some mammals, burrows are a crucial form of engineered shelters[10,14]. The Indian crested porcupine *Hystrix indica*, Kerr, 1792 is one such nocturnal, highly elusive, ecologically generalist, large (11–15 kg) burrowing rodent[15,16] that uses complexly engineered burrow-networks[17]. Its distribution ranges from Turkey, Sinai Peninsula, the eastern Mediterranean, Southwest and Central Asia (including Afghanistan and Turkmenistan) to Pakistan, India, Nepal, China and Sri Lanka[18–21], and reaching an altitude up to 2400 m in the Himalayan mountains[17]. The porcupine is herbivorous, feeding on both hypogeal and epigeal parts of plants, including roots, bulbs, succulent tubers, ripe fallen fruits and bark of certain tree species[22–24]. Usually porcupines occupy self-constructed burrows consisting of a long entrance tunnel, multiple exits and a large inner chamber[17,25,26]. Porcupines are known to have permanent burrows within their territory along with several others; nevertheless, site fidelity is observed for several years if not disturbed[27].

Having a widespread distribution, the Indian crested porcupine has a broad habitat tolerance[20,28] and is common enough to be considered as a serious pest in parts of its range[29–31], thus it is accorded the status of 'least concern' by the IUCN Redlist. Despite their pest status, the porcupines significantly contribute to ecosystem functions by dispersing vegetative propagules of plants (geophytes)[32,33], their diggings capture water, organic matter and seeds[34], they provide appropriate refuge sites for other species[35] and are potential prey species[36–38]. In view of this, the Indian crested porcupine is classified as an 'allogenic engineer' capable of altering the environment

---

[*]For correspondence. (e-mail: honnavallik@gmail.com)
[†]Deceased 28 April 2014.

through physical state changes in biotic or abiotic materials, via mechanical or other means[39,40]. The burrows of Indian crested porcupine in particular are a crucial refuge for many species[35,38,41], at least in certain stage of their life cycle, especially during the breeding season. Therefore, an understanding of the biology of Indian crested porcupine and its burrowing behaviour is a crucial prerequisite for the management of not just these rodents, but also other mutually tolerant species co-occupying their burrows.

Keoladeo National Park (KNP), in semi-arid areas of Bharatput, Rajasthan, India, is one of the important Ramsar sites and IUCN World Heritage sites[42]. It is a closed dynamic system having a conspicuous seasonally flooded wetland with an array of mixed habitat types[43]. Indian crested porcupine is one of the major mammal inhabitants and apex ecosystem engineer in the Park (Figure 1). Their burrows are an important ecological niche as they are also co-occupied by golden jackal, striped hyaena, Indian rock python, monitor lizard and bat species (Figure 1)[38]. The Park has the highest density of near-threatened Indian rock python in India[44]; it is presumed that the availability of a large number of burrows in the Park is the major reason for such high density. Often Indian rock pythons are seen congregating in huge numbers (>10) around these burrows during winters[38,45]. These burrows therefore appear to be highly significant in the region, as they provide appropriate microhabitat, especially to the poikilothermic pythons which solely depend on porcupine burrowing sites for refuge.

High seasonal variation in temperature and seasonal flooding make the Park's ecosystem highly dynamic; thus an understanding of the spatial occupancy and site selection for burrowing by the porcupine is necessary. The present article aims to examine the factors that are responsible for the spatial occupancy and site selection for permanent occupancy of porcupines in KNP.

Figure 1. Indian crested porcupine (ICP) *Hystrix indica* emerging from its burrow in Keoladeo National Park (KNP), Bharatpur (camera-trap image).

Methods

Study area

Keoladeo National Park (27°7.6′–27°12.2′N, 77°29.5′–77°33.9′E) is in Bharatpur district of Rajasthan. The total area of the Park is 29 sq. km, of which 20.5 sq. km is terrestrial and 8.5 sq. km is a wetland area. It falls under the semi-arid zone (Province 4A) of India[46], covered by dry–mixed–deciduous babul forest[47]. It is a man-made freshwater ecosystem with a natural depression on the floodplain of two minor tributaries of the River Yamuna: Gambhir and Banganga. It is a monsoonal wetland, receiving water from nearby reservoirs every year during August–September (post monsoon). The Park lies on the Central-Asian Flyway of the Asia-Pacific Global Migratory Flyway and is an important global wintering ground for migratory waterfowl that breed in the Palearctic region[43]. The terrestrial habitat contributes three times the area of the Park's wetland, providing a favourable habitat for resident migratory birds, reptiles and mammals[48].

Identification of covariates

The Indian crested porcupine is a generalist species that covers long distances (up to 8 km) from its permanent dwelling sites during foraging[22,24,49], as shown in the case of *Hystrix cristata*[50]. Thus, food resource availability may play an important role in the occurrence of porcupine in KNP. Soils that can be easily excavated for food resources may also affect their habitat use. Therefore, vegetation parameters and soil type may influence the spatial occupancy of porcupine in the Park. These porcupines are nocturnal in habit, and forage during the night resulting in negligible detections. However, the distinctive faecal droppings are easy to detect and hence are the only visible and easily detectable sign of the species in the fields. Unlike other porcupines that have latrine sites near their burrows[51], the Indian crested porcupine is not reported to use any such sites for defecation and their faecal pellets are easily observed randomly (Figure 2). Faecal deposits have been used as an indirect indicator of species occurrence to assess habitat use by large mammals and their occupancy[52–54] including rodents[55]. Detecting faecal deposits in the field is least expensive and easy; thus it is considered as an indicator of spatial occupancy for the porcupine. We identified five ground-based covariates: tree density (TRDE), mean tree height (TRHT), mean shrub height (SHHT), shrub density (SHDE) and soil type (ST) which may influence the occupancy of porcupine. We used herb density (HEDE) as a covariate to model detection probability that could influence the detection of indirect signs like faecal deposits.

Although the porcupine is a habitat generalist, in KNP with varying temperature, their burrows serve as surrogate for 'permanent occupancy' of the species. The Park experiences seasonal flooding causing inundation of certain parts, which occasionally results in permanent damage to the burrow systems[45]. Thus, higher elevation and greater distance from the point of maximum level of water-stand may positively influence the likelihood of occurrence of the burrows, whereas the per cent water cover would have a negative influence. The Park is also surrounded by vast agricultural fields having monoculture of seasonal crops like *Triticum aestivum*, *Brassica campestris*, *Sesamum indicum* and tuberous vegetables like *Solanum tuberosum* and *Solanum melongena*, which are reported to be part of the diet of Indian crested porcupine[31]. They are known to venture out to such nearby fields for regular foraging[25,56]. Thus the burrowing sites would likely be closer to the Park's boundary surrounding the fields, thus making it easier for the porcupine to sneak out. Hence, greater distance from the Park's boundary would negatively influence the likelihood of occurrence of the burrows. The available literature reveals that many species prefer soil types having clay and silt content with loamy texture due to their ability to hold moulded form easily when wet. They appear to be vital constituents for construction of burrows in kangaroo rats[57,58], pocket gophers[59], ground squirrels, deer mice, montane vole[58] and prairie dogs[60]. The type of soil enhances durability of the burrows, which is also expected to play a role in site selection for burrowing by the porcupine. This resulted in the identification of one ground-based covariates – soil type (ST) and four remotely sensed covariates – grid with per cent water cover (WATER), mean elevation of the grid (ELE), distance from the Park boundary (BOU) and distance from the point of maximum level of water-stand (DIWET), which may influence the occurrence of burrows. We used duration of search (TIME) as a covariate to model detection probability that could influence the detection of burrows. Table 1 shows the predicted response of the Indian crested porcupine to each of these covariates.

Figure 2. Distinctive faecal pellets of ICP in KNP.

Survey design

The study area was overlaid with 25 ha grid layer with a total of 137 grids. To locate the faecal deposits of porcupine and measure the habitat covariates, a diagonal line (707 m) was fixed for each grid as a sampling line for assessment (Figure 3). Sampling plots (20 × 20 m) were laid at a regular interval of 177 m on 10 m either side of the transect line inscribed as spatial replicates. Additionally, to locate the burrows, each grid (25 ha, i.e. 500 × 500 m) was sub-divided into four (250 × 250 m) sub-grids (Figure 3), and each sub-grid was considered as a spatial replicate. Spatial replicates suitable for single-season survey[61–63] were chosen to construct the detection histories due to limitation of manpower and logistics; nocturnal activity cycle of the species resulted in negligible detection and ease of detecting distinctive faecal deposits was the only indicator of the species in the field.

Field methods

Field surveys were conducted from September 2013 to November 2014. Grids were realized on ground using a GPS (Garmin® eTrexVist™). Sampling for the burrow sites was carried out during the dry season to have access to majority of the landscape. Each grid which was further subdivided into four sub-grids was systematically walked to locate the burrows in a zigzag search trail with the help of two efficient local trackers. The geo-coordinates for all the detected burrows were recorded using handheld GPS.

Table 1. Predicted species response to each covariate based on a priori hypotheses for Indian crested porcupine

Type	Covariates	ψ	p
Droppings	TRDE	+	0
	TRHT	+	0
	SHHT	+	–
	SHDE	+	–
	HEDE	0	–
	ST	+	0
Burrows	WATER	–	0
	ST	+	0
	ELE	+	0
	TIME	0	+
	BOU	–	0
	DIWET	+	0

TRDE, Tree density; TRHT, Mean tree height; SHHT, Mean shrub height; SHDE, Shrub density; HEDE, Herb density; ST, Soil type; WATER, Grid with per cent water cover; ELE, Mean elevation of the grid; TIME, Duration of search; BOU, Distance from Park boundary and DIWET, Distance from the point of maximum level of water-stand. '+' signifies a positive effect on the response variable, '–' signifies a negative effect on the response variable and '0' signifies that the covariate has no effect on the response variable. ψ: Probability of occurrence and p: species detection probability.

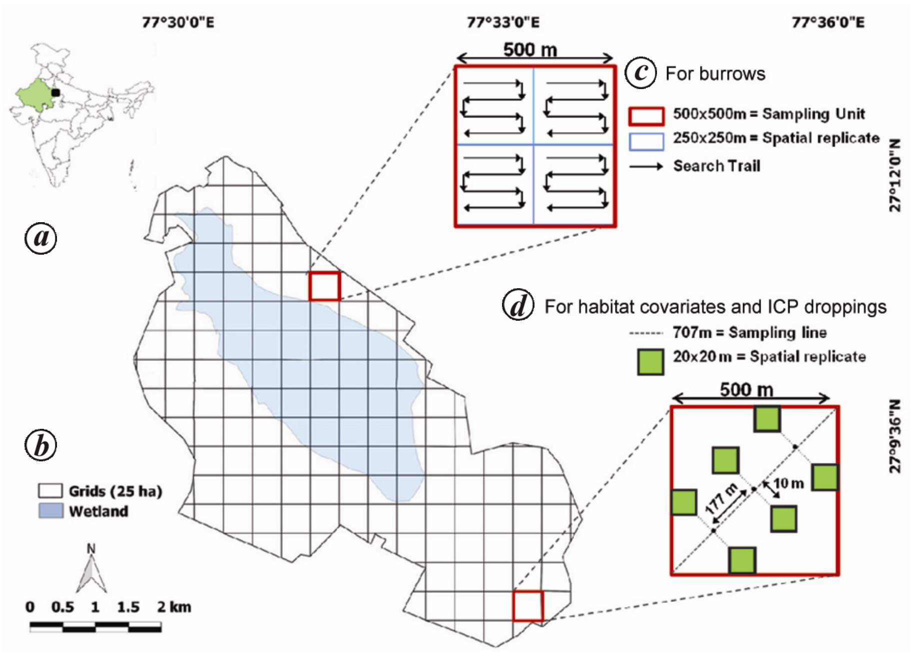

Figure 3. ***a***, Location of KNP in India. ***b***, Map of KNP overlaid with the sampling grids (25 ha). ***c***, Details of the sampling protocol in each grid for locating burrows. ***d***, Details of the sampling protocol for measuring habitat covariates and presence/absence of ICP faecal droppings.

A sub-grid was recorded as 'occupied' if the burrow was detected (four spatial replicates).

We overlaid the grids on the shapefiles of the study area with maximum standing water, which were obtained from the Rajasthan Forest Department. The per cent water-standing area was calculated based on its proportion in each grid. ASTER-GDEM data were downloaded from the USGS Earth-Explorer followed by processing them in open-source Quantum-GIS software (ver. 2.4.0). With this, a digital elevation map was developed that helped determine the mean elevation of each grid. The distance covariates 'BOU' and 'DIWET' were digitally determined for each grid using measuring tool in Quantum-GIS software. Out of 137 grids, 91 formed the sampling unit for faecal deposits covering the terrestrial area of the Park, as others were either floodplains or outside the jurisdiction of the Park. A straight diagonal line across each grid was chosen as a sampling line and the plots were laid on either side of the grids at fixed intervals. A full-sized grid (25 ha) with complete accessibility had six such plots (spatial replicates). A total of 546 such plots were sampled for the presence of porcupine faecal deposits to determine its occupancy, enumerate the vegetation parameters, and collect soil samples for assessing the soil type. If plots or sub-grids could not be sampled, either due to inaccessibility resulting from waterlogging or due to logistic reasons such as areas falling outside the jurisdiction of the Park; the replicate was treated as a missing observation[64].

For the enumeration of trees, shrubs and herbs, nested quadrates of 20 × 20 m (one), 5 × 5 m (one) and 1 × 1 m (four) respectively were laid within these plots. Species with GBH (girth at breast height) >10 cm were considered as woody species. The plant species were recorded and their taxonomic identification was done following Prasad *et al.*[65]. Quantitative community characteristics, including tree height and shrub height were determined using a range finder (Nikon Forestry Pro). The stand density for the trees, shrubs and herbaceous layer, i.e. total number of individuals per unit area was determined for each plot[66–68]. All the quantitative community characteristics assessed for each plot were then extrapolated to grid level, which was further analysed as five habitat covariates, namely TRHT, SHHT, TRDE, SHDE and HEDE, influencing porcupine occupancy.

Apart from the plots, soil samples were also collected from each burrow site and soil type was assessed using feel-analysis method[69]. We classified soil types based on the preference for burrowing by the porcupine – clay loam (CL), silty clay loam (SCL) and silty loam (SL) appeared to be the most preferred soil types in decreasing order. With this, a scoring of 0–10 was given to each grid considering the proportion of the three preferred soil types (0, none of the three soil types present; 1, higher percentage of SL; 2, higher percentage of SCL; 3, equal percentage of all three soil types; 4, higher percentage of CL; 5, 100% SL; 6, 50–75% CL/SCL; 7, >75% SCL + others; 8, 100% SCL; 9, >75% CL + others, and 10, 100% CL). Scoring was in a hierarchical order where a score of '10' indicates that a grid has the highest probability of occurrence of the burrows, whereas a score of '1' indicates vice-versa.

Table 2. Summary of model selection procedure for factors affecting detection probability of Indian crested porcupine in KNP, Bharatpur

Type	Model	$\hat{p}$	AIC$_c$	ΔAIC$_c$	w_i	K
Droppings	ψ (.), p(.)	0.33	558.54	0.00	1.00	2
	ψ (.), p(SHDE)	0.50	587.39	28.85	0	3
	ψ (.), p(HEDE)	0.50	589.73	31.19	0	3
	ψ (.), p(SHHT)	0.50	589.85	31.31	0	3
Burrows	ψ (.), p(.)	0.19	230.75	0.00	0.50	2
	ψ (.), p(TIME)	0.19	230.75	0.00	0.50	3

$\hat{p}$, Estimated species detection probability; AIC$_c$, AIC corrected for small sample bias; ΔAIC$_c$, Difference in AIC$_c$ values between each model and the model with the lowest AIC$_c$; w_i, AIC$_c$ model weight; K, Number of parameters estimated by the model and DHDE, Shrub density.

Table 3. Summary of model selection procedure for Indian crested porcupine occupancy in KNP

Model	$\hat{\psi}$	($\hat{SE}$)	AIC$_c$	ΔAIC$_c$	w_i	K
Droppings						
ψ (.), p (.)	0.71	0.06	558.54	0.00	0.40	2
ψ (TRDE + SHHT + ST), p (.)	0.62	0.08	558.83	0.29	0.35	5
ψ (TRDE + SHHT + SHDE + ST), p (.)	0.62	0.09	560.83	2.29	0.13	6
ψ (SHHT + ST), p (.)	0.62	0.07	561.55	3.01	0.09	4
ψ (SHHT), p (.)	0.49	0.04	565.76	7.22	0.01	3
ψ (ST), p (.)	0.63	0.05	566.06	7.52	0.01	3
ψ (TRDE), p (.)	0.49	0.04	567.09	8.55	5.60E-03	3
ψ (TRHT), p (.)	0.50	0.04	569.75	11.21	1.50E-03	3
ψ (SHDE), p (.)	0.49	0.03	570.45	11.91	1.00E-03	3
Burrows						
ψ (WATER + BOU + ELE), p (.)	0.61	0.18	214.02	0.00	0.78	5
ψ (WATER + BOU), p (.)	0.59	0.20	218.73	4.71	0.07	4
ψ (WATER), p (.)	0.60	0.21	219.65	5.63	0.05	3
ψ (WATER + ELE), p (.)	0.62	0.06	219.90	5.88	0.04	4
ψ (BOU + ELE), p (.)	0.57	0.15	220.31	6.29	0.03	4
ψ (BOU), p (.)	0.53	0.10	221.74	7.72	0.02	3
ψ (ELE), p (.)	0.51	0.07	225.57	11.55	2.4E-03	3
ψ (.), p (.)	0.28	0.05	230.75	16.73	2.0E-04	2
ψ (ST), p (.)	0.60	0.19	233.84	19.35	0.00	3
ψ (DIWET), p (.)	0.50	0.06	233.77	19.75	0.00	3

ψ: Estimated occupancy parameter; $\hat{SE}$, Associated standard error.

Table 4. Covariates influencing the Indian crested porcupine occupancy ranked on the basis of summed model weights of covariates, with beta coefficient and associated standard error

Covariate	Summed AIC$_c$ weights	β-coefficients ($\hat{SE}$)
Droppings		
SHHT	0.58	0.69 ± 0.32
ST	0.58	0.17 ± 0.07
TRDE	0.48	0.60 ± 0.31
SHDE	0.13	0.12 ± 0.27
TRHT	1.50E-03	−0.32 ± 0.23
Burrows		
WATER	0.95	−12.28 ± 9.94
BOU	0.91	−9.02 ± 4.52
ELE	0.86	8.57 ± 5.10
ST	0.00	0.08 ± 0.17
DIWET	0.00	−0.09 ± 0.35

Occupancy estimation

Detection histories of the porcupine faecal deposits and burrows were constructed for each spatial replication (sub-grids and plots), where '1' indicates detection, '0' indicates non-detection and '–' indicates a missing observation. We z-transformed the data on covariates to rescale and normalize them prior to occupancy analysis. The two model parameters, i.e. probability that a grid is occupied by the species (ψ) and detection probability (p) were estimated using likelihood functions[64]. The data were analysed using single-season models in program PRESENCE ver. 9.0 (refs 70, 71) to derive maximum likelihood estimates of model parameters. Based on prior knowledge on the biology of Indian crested porcupine, it was speculated that the covariates indexing vegetation structure, soil type, elevation and distance from the point of maximum level of water-stand would positively affect occupancy and burrow site selection; whereas covariates indexing water cover and distance from the Park boundary (agricultural fields) would negatively affect it. A stepwise approach was used, that is to model the effects of covariates on detection (p) at first, and then modelled occupancy (ψ). Three ground-based covariates – SHHT, SHDE and HEDE – affected the probability of detecting droppings along the search trail, while covariate TIME, i.e. duration of search affected the probability of detecting burrows. Hence these covariates were used to model the detection probability (p). To avoid biased inferences resulting from multi collinearity in predictor variables, Pearson correlation analysis was performed, which did not identify autocorrelation among the covariates; thus a combination of covariates was used in one model and all selection models were uncorrelated. Subsequently a candidate set of nine a priori models was formulated to investigate the influence of covariates on porcupine occurrence; whereas a candidate set of 10 a priori models was formulated to investigate the influence of covariates on burrow site selection for permanent occupancy. Model selection, computation of model weights and averaging of parameters followed Burnham and Anderson[72]. Models were ranked according to Akaike Information Criterion (AIC) adjusted for a small sample size ($\mathrm{AIC_c}$)[72]. Models were tabulated in ascending order of $\Delta\mathrm{AIC_c}$ values. To establish the relative influence of each covariate on occurrence, computed model weights were summed over all models containing the particular covariate[72]. We report the estimate of occupancy as mean ± standard error.

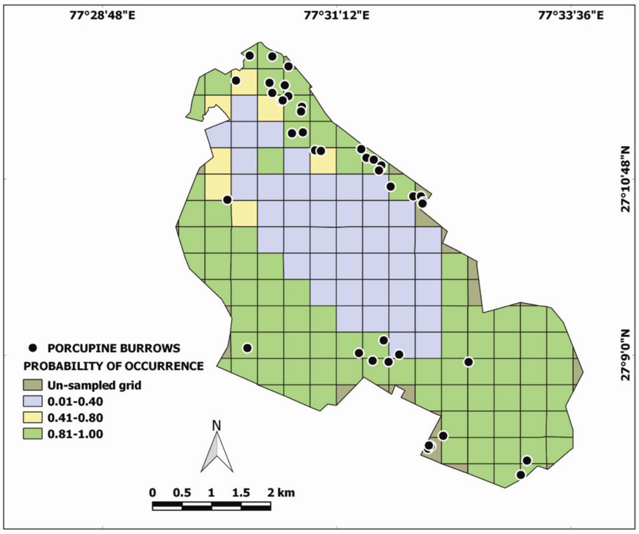

Figure 4. Estimated ICP burrow occupancy data generated for each grid, which were extracted from the best-fitting model, [ψ (WATER + BOU + ELE), p(.)]. Unsampled grid cells comprised those that were not sampled.

Results

Habitat factors affecting the occupancy of Indian crested porcupine in KNP

From 91 sites with 6 sampling occasions, the estimated species detection probability ($\hat{p}$) was $0.33 \pm 0.029_{\mathrm{SE}}$. None of the covariates influenced detection probability (w_i (SHDE) = 0, w_i (HEDE) = 0, w_i (SHHT) = 0; Table 2); so we ran subsequent models without SHDE, HEDE and SHHT as a function of p (Table 3). The naïve occupancy estimate was 0.64 and proportion of sites occupied (ψ) was 0.72. The model-averaged occupancy estimate from top-ranked model ψ(.), p(.) and the associated standard error gave an estimate of $\hat{\psi} = 0.71 \pm 0.06_{\mathrm{SE}}$. Summed model weights of the covariates indicated that SHHT (0.57), ST (0.57) and TRDE (0.48) were the major determinants of occupancy of porcupine over other covariates (Table 4). Further, the occupancy of porcupine was positively correlated to SHHT ($\beta_1 = 0.69 \pm 0.32$), ST ($\beta_1 = 0.17 \pm 0.07$) and TRDE ($\beta_1 = 0.60 \pm 0.31$).

Habitat factors affecting burrow site selection and permanent occupancy of Indian crested porcupine in KNP

A total of 41 porcupine burrow systems were recorded in the Park during sampling (Figure 4). From 137 sites with 4 sampling occasions, the estimated detection probability ($\hat{p}$) of burrow sites was $0.19 \pm 0.05_{\mathrm{SE}}$. Since both null (.) and duration of search (TIME) equally influenced the detection probability (w_i(.) = 0.50, w_i (TIME) = 0.50; Table 2), we chose (.) over (TIME) and ran subsequent models without TIME as a function of (p) (Table 3). The naïve occupancy estimation for occurrence of burrows was 0.17 and proportion of sites occupied (ψ) for permanent occupancy was 0.29. The model-averaged occupancy estimate from top-ranked model ψ(WATER +BOU + ELE), p(.) and the associated standard error gave an estimate of $\hat{\psi} = 0.61 \pm 0.18_{\mathrm{SE}}$. The second best model included ψ(WATER + BOU), p(.) and the associated standard error gave an estimate of $\hat{\psi} = 0.59 \pm 0.20_{\mathrm{SE}}$. Summed model weights for WATER (0.95), BOU (0.91) and ELE (0.86) were more than those for ST (0.004) and DIWET (0.00) (Table 4). Burrow site selection for permanent occupancy by porcupine was thus negatively correlated to both per cent water cover (WATER: $\beta_1 = -12.28 \pm 9.94$) and distance from the Park boundary or nearest agricultural field (BOU: $\beta_1 = 9.02 \pm 4.52$), and positively correlated to mean elevation (ELE: $\beta_1 = 8.57 \pm 5.10$). Site selection for permanent occupancy was mapped based on the occupancy estimates for each grid using the best fit model (Figure 4). Overall, 31.4%, 5.8% and 65.0% of the sampled 137 grid cells were classified as low ($\hat{\psi}$ = 0.01–0.40), medium ($\hat{\psi}$ = 0.41–0.80), and high ($\hat{\psi}$ = 0.81–1.00) respectively.

Discussion

The detection probability ($0.19 \pm 0.05_{SE}$) and occurrence ($0.28 \pm 0.05_{SE}$) of Indian crested porcupine burrow sites was lower than the detection probability ($0.33 \pm 0.029_{SE}$) and occupancy ($0.71 \pm 0.06_{SE}$) of their faecal deposits, indicating that certain factors are responsible for their site selection for permanent occupancy, irrespective of their uniform spatial occupancy. Porcupines were found throughout the terrestrial area of the Park (67 out of 91 sampled grids); however, per cent water-cover, distance from the Park boundary surrounded by agricultural fields and elevation of the landscape determined the selection for burrowing site. All the 41 recorded burrow systems (in 23 out of 137 sampled grids) were found confined to areas with no floodplains, closer to the agricultural fields and at a higher elevation than the average elevation of the park. These findings suggest that habitat in general and preferable feeding habits do not influence shelter requirements or permanent occupancy.

Null model $\psi(.)$, $p(.)$ remained as the top-ranked model with the lowest $\mathrm{AIC_c}$ value for occupancy of porcupine. It is apparent that none of the habitat covariates played any significant role in its occupancy. However, North American porcupine *Erethizon dorsatum* in Canada showed habitat selection pattern at tree level as their bodies are modified for climbing and manoeuvring in trees for resting, feeding on bark, fruit and leaves, and for avoiding predators[73,74]. Similarly, concentration of preferred food items determined the habitat utilization of Indian crested porcupine in Israel[75] and Cape porcupine *Hystrix africaeaustralis* in South Africa[76]. In southern Tuscany, Italy, the crested porcupine *Hystrix cristata*, avoided cultivations and selected habitats with dense vegetation, providing cover and food within the study area (second-order selection) and within home ranges (third-order selection); in the warm period, porcupines selected agricultural areas representing a minor proportion of the study site[50]. Exceedingly generalist feeding behaviour of Indian crested porcupine[31]; high abundance of resource material and lack of any fierce predator in KNP are possible reasons that the porcupines cover long distances away from their permanent burrowing site for foraging and hence occupy entire landscapes.

Among the five covariates chosen to assess burrow site selection by the porcupine, a combination of per cent water cover, distance from the boundary and mean elevation had the highest model weight ($w_i = 0.78$), indicating an increase in the probability of permanent occupancy with simultaneous decrease in area with water cover, decrease in distance from the boundary and increase in mean elevation of the area. The Park has a depression at the centre forming a wetland and experiences post-monsoon flooding in low-lying areas due to release of water from nearby reservoirs. However, low-lying, water-logged areas are not suitable sites for burrowing, as seasonal flooding causes inundation which might result in permanent damage to the burrow systems. It was observed that even though the water cover reduced considerably during dry season, porcupines did not attempt to dig burrows for permanent settling in those regions.

Another covariate: 'distance from the park boundary' had the second highest model weight ($w_i = 0.07$), which indicates that the probability of permanent occupancy increases with closer proximity of the Park's boundary surrounded by agricultural fields. This affirms previous findings highlighting the affinity of Indian crested porcupine to agricultural fields[25,56]. However, these findings are in contrast with a study in Drakensberg Midlands, South Africa[77], where the area available under cropland negatively influenced occupancy and the extent of wetland area positively influenced it. Along with per cent water cover and distance from the boundary, mean elevation also influenced the probability of permanent occupancy that increased with increase in mean elevation of an area. The Park lies at an average elevation of 174 m amsl and digital elevation mapping of the area revealed the range of elevation between 148.2 and 204.0 m amsl. Though there is not much undulation in the area, even a minor elevation seems to have influenced the placement of burrows by the porcupines. All the 41 burrow systems were dug above an elevation of 170 m, which is also the maximum water level mark when the wetland is completely inundated to a depth of approximately 1.5–2.0 m. Burrow site-selection and location of the burrow systems on higher elevation, thus provide protection against permanent damage from surface run-off and inundation during monsoonal rainfall and post-monsoon flooding. Another covariate: soil type with lower summed model weight ($w_i = 0.00$; $\beta_1 = 0.08 \pm 0.17_{SE}$) was not useful for explaining burrow site selection and occurrence, possibly because there is not much discrepancy between the use and availability of the most preferred soil types (clayey and silty) by the porcupine from the region. These are the most widespread soil types found in the Park and are also preferred by other burrowing rodents[57–60].

These results strongly support three of the five a priori hypotheses namely, 'per cent water cover' negatively influencing the permanent occupancy and likelihood of 'occurrence' of the burrows; 'distance from the boundary' surrounded by the agricultural fields negatively influencing the burrow site-selection and the 'elevation' positively influencing the occurrence; whereas none of the covariates (vegetation, soil type and distance from the point of maximum level of water stand) was found to significantly influence the spatial occupancy of porcupines. These results show that patterns of spatial occupancy for a species at macro level do not necessarily determine permanent occupancy at micro level, i.e. patterns observed at one scale are not necessarily good predictors of patterns obtained at other scales[78,79], and conflicting demands at different scales lead to varied selection criteria[80]. Here, the Indian crested porcupine has been used as a study model to examine how burrow site selection acts as a surrogate in determining its permanent occupancy, which otherwise is a generalist species with broader spatial occupancy. This study highlights the factors determining burrow site selection by Indian crested porcupine for permanent occupancy. The strategic locations of these earthen burrows are significant, since they also provide crucial ecological niche for various other co-occupants. Hence, it is important to conserve the natural habitats, especially those of the porcupine which is a primary excavator and a significant ecosystem engineer in extreme semi-arid conditions of KNP.

---

1. Pianka, E. R., *Evolutionary Ecology*, Addison-Wesley-Longman, San Francisco, CA, USA, 2000, 6th edn.
2. Wiens, J. J., Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution*, 2004, **58**, 193–197.
3. Mortberg, U. M., Resident bird species in urban forest remnants; landscape and habitat perspectives. *Landsc. Ecol*., 2001, **16**, 193–203.
4. Gu, W. and Swihart, R. K., Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biol. Conserv*., 2004, **116**, 195–203.
5. Haim, R. J., Aarde, V. and Skinner, J. D., Burrowing and huddling in newborn porcupine: the effect on thermoregulation. *Physiol. Behav*., 1992, **52**, 247–250.
6. Wilson, D. S., Nest-site selection: microhabitat variation and its effects on the survival of turtle embryos. *Ecology*, 1998, **79**, 1884–1892.
7. Madsen, T. and Shine, R., Life history consequences of nest-site variation in tropical pythons (*Liasis fuscus*). *Ecology*, 1999, **80**, 989–997.
8. Ciarniello, L. M., Boyce, M. S., Heard, D. C. and Seip, D. R., Denning behavior and den site selection of grizzly bears along the Parsnip River, British Columbia, Canada. *Ursus*, 2005, **16**, 47–58.
9. Campbell III, T. M. and Clark, T. W., Colony characteristics and vertebrate associates of white-tailed and black-tailed prairie Dogs in Wyoming. *Am. Midl. Nat*., 1981, **105**, 269–276.
10. Reichman, O. J. and Smith, S. C., Burrows and burrowing behavior by mammals. *Curr. Mammal*., 1990, **2**, 197–244.
11. Roper, T. J., Ostler, J. R., Schmid, T. K. and Christian, S. F., Site use in European badgers *Meles Meles*. *Behaviour*, 2001, **138**, 173–187.
12. Cudworth, N. L. and Koprowski, J. L., Importance of scale in nest-site selection by Arizona gray squirrels. *J. Wildl. Manage*., 2011, **75**, 1668–1674.
13. Endres, K. M. and Smith, W. P., Influence of age, sex, season and availability on den selection by raccoons within the Central Basin of Tennessee. *Am. Midl, Nat*., 1993, **129**, 116–131.
14. Stromberg, M. R., Subsurface burrow connections and entrance spatial pattern of prairie dogs. *Southwest. Nat*., 1978, **23**, 173–180.
15. Prater, S. H., *The Book of Indian Animals*, Diocesan Press, Madras, 1965.
16. Snyder, M. A. and Linhart, Y. B., Porcupine feeding patterns: selectivity by a generalist herbivore? *Can. J. Zool*., 1997, **75**, 2107–2111.
17. Gurung, K. K. and Singh, R., *Field Guide to the Mammals of the Indian Subcontinent*, Academic Press, San Diego, CA, USA, 1996.
18. Ellerman, J. R. and Morrison-Scott, T. C. S., *Checklist of Palaearctic and Indian Mammals, 1758–1946*. British Museum Natural History, London, 1951.
19. Saleh, M. A. and Basuony, M., A contribution to the mammalogy of the Sinai Peninsula. *Mammalia*, 1998, **62**, 557–575.
20. Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G. and Palamo, L. J., *Hystrix indica*. The IUCN Red List of Threatened Species. Version 2015.2., 2008; http://www.iucnredlist.org. accessed 24 July 2015.
21. Fattorini, N. and Pokheral, C. P., Activity and habitat selection of the Indian crested porcupine. *Ethol. Ecol. Evol*., 2012, **24**, 377–387.
22. Arshad, M. I., Khan, R. A. and Khaliq, A., Food habits of the Indian crested porcupine, *Hystrix indica*. *Pak. J. Zool*., 1990, **22**, 413–415.
23. Sharma, D. and Prasad, S. N., Tree debarking and habitat use by porcupine (*Hystrix indica* Kerr) in Sariska National Park in Western India. *Mammalia*, 1992, **56**, 351–361.
24. Roberts, T. J., *The Mammals of Pakistan (revised edn)*, Oxford University Press, Karachi, Pakistan, 1997.
25. Agrawal, V. C. and Chakraborty, S., The Indian crested porcupine, *Hystrix indica* (Kerr). In *Rodents in Indian Agriculture* (eds Prakash, I. and Ghosh, P. K.), Scientific Publishers, Jodhpur, 1992, pp. 25–30.
26. Mendelssohn, H. and Yom-Tov, Y., *Fauna Palaestina – Mammalia of Israel*, Academy of Sciences and Humanities, Jerusalem, Israel, 1999.
27. Monetti, L., Massolo, A., Sforzi, A. and Lovari, S., Site selection and fidelity by crested porcupines for denning. *Ethol. Ecol. Evol*., 2005, **17**, 149–159.
28. Alkon, P. U. and Saltz, D., Influence of season and moonlight on temporal – activity patterns of Indian crested porcupine (*Hystrix indica*). *J. Mammal*., 1988, **69**, 71–80.
29. Alkon, P. U. and Saltz, D., Patterns of crested porcupine (*Hystrix indica*) damage to cultivated potatoes. *Agric. Ecosystem. Environ*., 1985, **14**, 171–183.
30. Khan, A. A., Ahmad, S., Hussain, I. and Munir, S., Deterioration impact of Indian crested porcupine, *Hystrix indica*, on forestry and agricultural systems in Pakistan. *Int. Biodeter. Biodegr*., 2000, **45**, 143–149.
31. Hafeez, S., Khan, G. S., Ashfaq, M. and Khan, Z. H., Food habits of the Indian crested porcupine (*Hystrix indica*) in Faisalabad, Pakistan. *Pak. J. Agric. Sci*., 2011, **48**, 205–210.
32. Gutterman, Y. and Herr, N., Influences of porcupine (*Hystrix indica*) on the slopes of the northern Negev mountains – germination and vegetation renewal in different geomorphological types and slope directions. *Oecologia*, 1981, **51**, 332–334.
33. Gutterman, Y., Observations on the feeding habits of the Indian crested porcupine (*Hystrix indica*) and the distribution of some hemicryptophytes and geophytes in the Negev desert highlands. *J. Arid. Environ*., 1982, **5**, 61–268.
34. Dean, W. R. J. and Milton, S. J., Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites. *Afr. J. Ecol*., 1991, **29**, 11–16.
35. Taber, R. D., Sheri, A. N. and Ahmad, M. S., Mammals of the Lyallpur region, West Pakistan. *J. Mammal*., 1967, **48**, 392–407.
36. Kadhim, A. H. H., Distribution and reproduction of the Indian crested porcupine *Hystrix indica* (Hystricidae: Rodentia) in Iraq. *Zool. Middle East*, 1997, **15**, 9–12.
37. Mori, E., Maggini, I. and Menchetti, M., When quills kill. The defence strategy of the crested porcupine *Hystrix cristata* L., 1758. *Mammalia*, 2013, **78**, 229–234.
38. Bhupathy, S. and Ramesh, C., Ecology of the endangered Indian rock Python, *Python molurus* in Keoladeo National Park, Bharatpur, Rajasthan, India. Final Report Submitted to the Ministry of Environment and Forests, Government of India, 2010.
39. Jones, C. G., Lawton, J. H. and Shachak, M., Organisms as ecosystem engineers. *Oikos*, 1994, **69**, 373–386.
40. Wilby, A., Shachak, M. and Boeken, B., Integration of ecosystem engineering and tropic effects of herbivores. *Oikos*, 2001, **92**, 436–444.
41. Bhupathy, S. and Haque, M. H., Association of rock python (*Python molurus*) with porcupine (*Hystrix indica*). *J. Bombay Nat. Hist. Soc*., 1986, **83**, 449–450.

42. Ali, S. and Vijayan, V. S., Keoladeo National Park Ecological Study Summary Report 1980–85, Bombay Natural History Society, Mumbai, 1986.
43. Mathur, V. B., Sivakumar, K., Singh, B. and Anoop, K. R., A bibliographical Review for Identifying Research Gap Areas: Keoladeo Ghana National Park – a World Heritage site. Wildlife Institute of India, Dehradun, 2009.
44. O'Shea, M., *Boas and Pythons of the World*, New Holland Publishers, London, 2007.
45. Krishnan, S., Bhupathy, S. and Devi Prasad, K. V., Monitoring of *Python molurus molurus* in Keoladeo National Park. Bharatpur, Rajasthan. *Hamadryad*, 2009, **34**, 28–33.
46. Rodgers, W. A., Panwar, H. S. and Mathur, V. B., *Wildlife Protected Areas in India: a review (executive summary)*. Wildlife Institute of India, Dehradun, 2002.
47. Champion, H. G. and Seth, S. K., *A Revised Survey of the Forest Types of India*, Government of India Press, Nasik, India, 1968.
48. Vijayan, V. S., Keoladeo National Park – ecology study: final report (1980–1990). US Fish and Wildlife Service: Ministry of Environment and Government of India. Bombay Natural History Society, Mumbai, 1991.
49. Sever, Z. and Mendelssohn, H., Spatial movement patterns of porcupines (*Hystrix indica*). *Mammalia*, 1991, **55**, 187–206.
50. Mori, E., Lovari, S., Sforzi, A., Romeo, G., Pisani, C., Massolo, A. and Fattorini, L., Patterns of spatial overlap in a monogamous large rodent, the crested porcupine. *Behav. Process*., 2014, **107**, 112–118.
51. Woods, C. A., *Erethizon dorsatum*. *Mamm. Species*, 1973, **29**, 1–6.
52. Putman, R. J., Facts from faeces. *Mammal Rev*., 1984, **14**, 79–97.
53. Hines, J. E., Nichols, J. D., Royle, J. A., Mackenzie, D. I., Gopalaswamy, A. M., Sambakumar, N. and Karanth, K. U., Tigers on trails: occupancy modeling for cluster sampling. *Ecol. Appl*., 2010, **20**, 1456–1466.
54. Jain, M., Utpal, S. and Mukhopadhyay, S., Indirect evidences of wildlife activities in sholas of Western Ghats, a biodiversity hotspot. *Vestn. Zool*., 2011, **45**, 153–159.
55. D'Adamo, P., Guichon, M. L., Bó, R. F. and Cassini, M. H., Habitat use by coypu *Myocaster coypus* in agrosystems of the Argentinean Pampas. *Acta Theriol*., 2000, **45**, 25–34.
56. Bhargava, R. N., Rajpurohit, L. S., Prashanth, B. and Madan, S., On the porcupine (*Hystrix indica*) in western Thar Desert. *Tigerpaper*, 2001, **28**, 1–3.
57. Carter, D. C., Webster, W. D., Jones Jr, J. K., Jones, C. and Suttkus, R. D., *Dipodomys elator*. *Mamm. Species*, 1985, **232**, 1–3.
58. Laundré, J. W. and Reynolds, T. D., Effects of soil structure on burrow characteristics of five small mammal species. *Gt. Basin. Nat*., 1993, **53**, 358–366.
59. Sulentich, J. M., Williams, L. R. and Cameron, G. N., *Geomys breviceps*. *Mamm. Species*, 1991, **383**, 1–4.
60. Reading, R. P. and Matchett, R., Attributes of black-tailed prairie dog colonies in north-central Montana. *J. Wildl. Manage*., 1997, **61**, 664–673.
61. Krishna, Y. C., Krishnaswamy, J. and Kumar, N. S., Habitat factors affecting site occupancy and relative abundance of four-horned antelope. *J. Zool*., 2008, **276**, 63–70.
62. Saracco, J. F., Siegel, R. B. and Wilkerson, R. L., Occupancy modeling of black-backed woodpeckers on burned Sierra Nevada forests. *Ecosphere*, 2011, **2**(3), 1–7.
63. Das, S., Dutta, S., Sen, S., Jijumon, A. S., Babu, S., Kumara, H. N. and Singh, M., Identifying regions for conservation of sloth bears through occupancy modelling in north-eastern Karnataka, India. *Ursus*, 2014, **25**, 111–120.
64. MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A. and Langtimm, C. A., Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 2002, **83**, 2248–2255.
65. Prasad, V. P., Mason, D., Marburger, J. E. and Kumar, C. R. A., *Illustrated Flora of Keoladeo National Park, Bharatpur, Rajasthan*, Oxford University Press, Mumbai, 1996.
66. Curtis, J. T. and McIntosh, R. P., The interrelations of certain analytic and synthetic phytosociological characters. *Ecology*, 1950, **31**, 434–455.
67. Philips, E. A., *Methods of Vegetation Study*, Henry Holt and Co, New York, 1959.
68. Muller-Dombois, D. and Ellenberg, H., *Aims and Methods of Vegetation Ecology*, John Wiley, New York, USA, 1974.
69. Thien, S. J., A flow diagram for teaching texture by feel analysis. *J. Agron. Educ*., 1979, **8**, 54–55.
70. MacKenzie, D. I., Nichols, J. D., Royle, J. A., Pollock, K. H., Bailey, L. L. and Hines, J. E., *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*, Elsevier, New York, USA, 2006.
71. Hines, J. E., Program Presence (version 9): software to compute estimates patch occupancy rates and related parameters. USGS-PWRC, 2015; http://www.mbr-pwrc.usgs.gov/software/presence.html
72. Burnham, K. P. and Anderson, D. R., *Model Selection and Inference: A Practical Information-Theoretic Approach*, Springer-Verlag, New York, 1998.
73. Griesemer, S. J., Fuller, T. K. and Degraaf, R. M., Habitat use by porcupines (*Erethizon dorsatum*) in Central Massachusetts: effects of topography and forest composition. *Am. Midl. Nat*., 1998, **140**, 271–279.
74. Morin, P., Berteaux, D. and Klvana, I., Hierarchical habitat selection by North American porcupines in southern boreal forest. *Can. J. Zool*., 2005, **83**, 1333–1342.
75. Saltz, D. and Alkon, P. U., On the spatial behaviour of Indian crested porcupines *Hystrix indica*. *J. Zool*., 1989, **217**, 55–266.
76. de Villiers, M. S., van Aarde, R. J. and Dott, H. M., Habitat utilization by the Cape porcupine *Hystrix africaeaustralis* in a savanna ecosystem. *J. Zool*., 1994, **232**, 539–549.
77. Ramesh, T. and Downs, C. T., Impact of land use on occupancy and abundance of terrestrial mammals in the Drakensberg Midlands, South Africa. *J. Nat. Conserv*., 2015, **23**, 9–18.
78. McLoughlin, P. D., Case, R. L., Gau, R. J., Cluff, H. D., Mulders, R. and Messier, F., Hierarchical habitat selection by barren ground grizzly bears in the central Canadian Arctic. *Oecologia*, 2002, **132**, 102–108.
79. McLoughlin, P. D., Walton, L. R., Cluff, H. D., Paquet, P. C. and Ramsay, M. A., Hierarchical habitat selection by tundra wolves. *J. Mammal*., 2004, **85**, 576–580.
80. Fortin, D., Fryxell, J. M., O'Brodovich, L. and Frandsen, D., Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. *Oecologia*, 2003, **134**, 219–227.

ACKNOWLEDGEMENTS. We thank Mr A. S. Brar (Principal Chief Conservator of Forests Rajasthan) and Mr Anoop K. R., Dr Khyati Mathur and Mr Bijo Joy (Park Directors and Conservators) for permission to undertake field work in Keoladeo National Park (KNP) (No. 3(04)-11/CWLW/2010/9823). This article is an outcome of a research project on burrow dwelling animals in KNP, funded by the Science and Engineering Research Board of Department of Science and Technology (SERB No: SB/SO/AS-133/2012), Government of India. We thank the Director, Sálim Ali Centre for Ornithology and Natural History (SACON), Coimbatore for providing the necessary facilities and encouragement. We also thank Dr S. Babu, and Mr Avadhoot Velankar (SACON) for help in GIS and analysis; Local field trackers and Guides Randhir Singh and Jitendra Singh for their help in the field and the anonymous reviewers for their suggestions that helped improve the manuscript.

Received 9 January 2016; revised accepted 18 January 2017

doi: 10.18520/cs/v112/i12/2440-2448