Site occupancy of the Indian giant squirrel *Ratufa indica* (Erxleben) in Kalakad–Mundanthurai Tiger Reserve, Tamil Nadu, India

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The status report on the Indian giant squirrel speculates a declining population trend for the species and suggests that a further decline can be expected. Given the wide distribution of the species and the limited resources to accurately estimate abundances to monitor population trends, the proportion of the area occupied by the species could be used as an alternate state variable. Arriving at occupancy rates involves repeated detection/non-detection surveys and analysis of the data in a capture–recapture framework. We estimate the site occupancy rates for unstudied populations of Indian giant squirrel within the Kalakad–Mundanthurai Tiger Reserve (KMTR) using a model that allowed us to estimate this parameter even when the species was not detected. About 180 evidences of the occurrence of the species were recorded from 486 km of trails. The estimated occupancy rate for Indian giant squirrel in KMTR was 0.82 (with a SE of 0.08) with a detection probability of 0.71 (± 0.05). An examination of the species–habitat relationship showed that contiguous patches of moist deciduous and evergreen forests were preferred by the species. The occupancy rates were low in areas with degraded dry deciduous forests and scrub, which were associated with high levels of human disturbance. The estimates from this study provide a benchmark for long-term monitoring and metapopulation studies.

Keywords: Detection probability, Indian giant squirrel, site occupancy, species–habitat relationship.

Introduction

THE Indian giant squirrel (*Ratufa indica*) is widely distributed in peninsular India[1], in forests south of 22°N. Although widely distributed, there are few studies that have estimated the population status of the species using standard sampling techniques[2]. At present all that is available are a handful of reports relating to the presence and relative abundance of the species across its distributional range[3–6]. Recent estimates speculate a population decline of 20–30% for this species that has been attributed to loss of habitat and hunting. The total population is estimated at less than 5000 individuals occurring in fragmented subpopulations and the decline in population is expected to continue[7].

Given that there are no programmes to monitor the species across its range and that accurate population abundance estimation requires considerable amount of effort and resources[8], alternate state variables that are easily gathered will be useful to monitor the status of the species. The effort and costs further increase when the species occurs at very low densities and habitats are severely fragmented. To circumvent these problems, it has been suggested that occupancy rate can be used as a state variable using presence/absence surveys across several sampling sites[8–10]. In metapopulation studies, patch (or site) occupancy is used as a state variable to estimate local extinction and colonization probabilities[11–13].

However, one of the key problems with presence/absence (henceforth detection/non-detection) surveys is the non-detection of the target species. Non-detection does not necessarily translate to true absence of the species, but could mean that the species was present but was not detected during the surveys[9]. Failing to account for imperfect detectability will result in underestimates of site occupancy and biased estimates of local colonization and extinction probabilities[14]. This has been overcome by estimating the detection probability using a capture–recapture framework while analysing data from detection/non-detection surveys[8,9,14,15]. The method requires multiple detection/non-detection surveys to be conducted at the monitoring sites (or sampling sites) in order to estimate the detection function and to correct for non-detection[9,16,17]. Habitat covariates can be built in to reduce variance in the estimated detection probability and occupancy[9]. If counts are also available, relative abundances of target species might then be estimated by incorporating the detection probability[8,18].

In addition to reducing efforts and costs, surveys directed at site occupancy are useful for long-term monitoring,

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metapopulation studies[14,19] and for conservation planning[20,21]. Several studies have examined environmental and habitat correlates with site occupancy[22–24]. Occurrence of species in poorly sampled areas and habitat selection patterns of unstudied populations have been predicted using occupancy-based habitat models[25,26]. Site occupancy has also been used for studying populations in fragmented landscapes[27,28].

In this article, we present the site occupancy estimates for unstudied populations of the Indian giant squirrel (*Ratufa indica*) within Kalakad–Mundanthurai Tiger Reserve (KMTR), Tamil Nadu. To investigate species–habitat relationships, we formulated the following hypotheses a priori, based on existing literature[29–32]: (i) the Indian giant squirrel prefers moist or wetter forest types and (ii) they prefer large contiguous forest patches. We used remotely-sensed covariates as surrogates for habitat attributes. We illustrate how such methods can be used to study and monitor species of squirrels with limited detectability and those that are found in fragmented habitats. The work presented here is part of a larger project to estimate herbivore densities in KMTR and to develop long-term monitoring protocols.

The Indian giant squirrel *R. indica* (Erxleben) is a large-bodied squirrel, mostly solitary and territorial with arboreal, diurnal and herbivorous habits[33]. This endemic species is found in deciduous, mixed deciduous and evergreen forests south of 22°N[1,34,35]. It is listed under Schedule II of the Wildlife Protection Act (1972)[36] of India and in Appendix II of CITES (2005)[37]. The species is more widely distributed when compared to the only other large squirrel found in southern India, the grizzled giant squirrel (*Ratufa macroura*), a highly endangered species of the subcontinent.

Earlier studies have shown that the Indian giant squirrel preferentially uses large trees[32] and requires canopy continuity, especially near nest trees[29–31]. It seems to be able to adapt to some extent to disturbed forests with some gaps in the canopy[32], but cannot be found in forests regenerating from clear felling[38]. Other than habitat loss, poaching has been identified as a major threat to the species[3,7,39,40].

Study site

The KMTR (8°25′–8°53′N and 77°10′–77°35′E) is the southern-most Tiger Reserve in India, situated at the southern tip of the Western Ghats (Figure 1). The Reserve was notified in 1988 and covers an area of ~900 km^2. It ranges in altitude from about 50 m to 1867 m, and the topography is variable with steep rocky slopes in the northern and southern boundaries to gentle undulating areas on the plateau. The annual rainfall ranges from 750 mm in the rain-shadow eastern slopes to over 3000 mm in the western slopes.

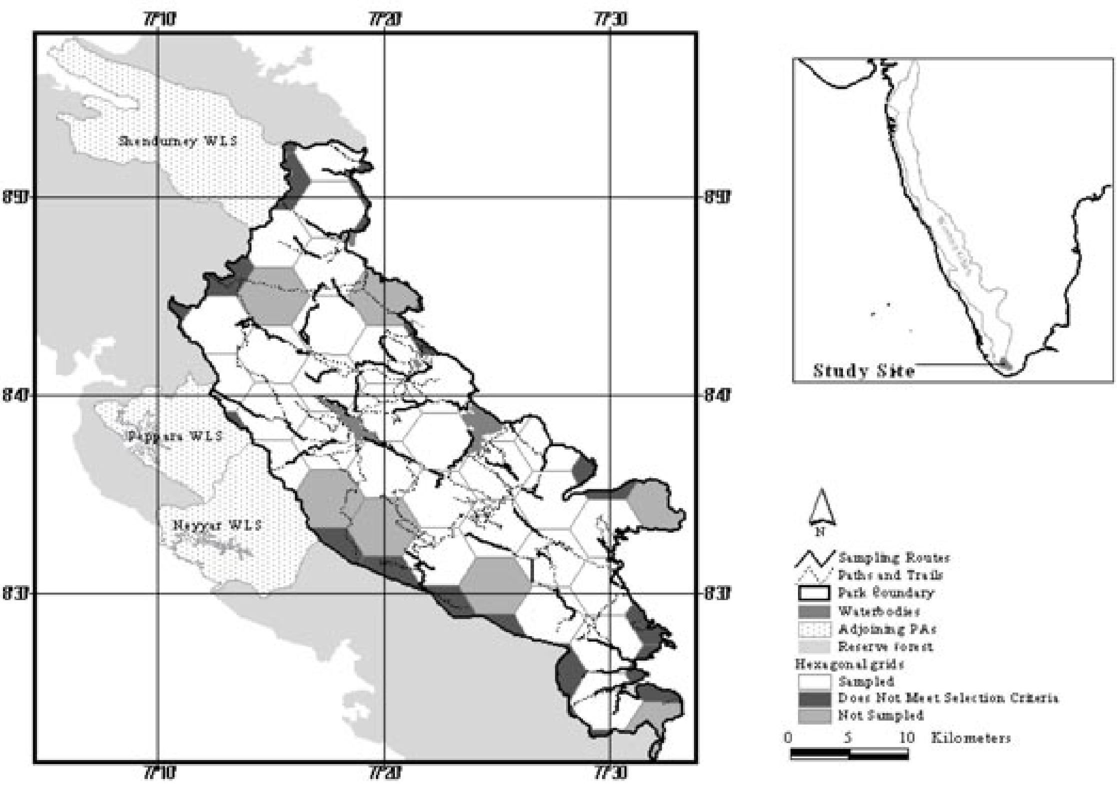

Figure 1. Map showing Kalakad–Mundanthurai Tiger Reserve, Tamil Nadu, India.

KMTR includes a large variety of habitat types, including west coast tropical evergreen forest, Tirunelveli semi-evergreen forest, southern hilltop tropical evergreen forest, southern moist mixed deciduous forest, dry teak forest, southern dry mixed deciduous forest, Carnatic umbrella thorn forest, *Ochlandra* reed breaks, pioneer Euphorbiaceae scrub and southern *Euphorbia* scrub[41].

The Reserve is noted for its high faunal and floral diversity and endemism[42,43], and, other than the Indian giant squirrel, harbours five species of squirrels (*Funambulus palmarum*, *F. sublineatus*, *F. tristriatus*, *Petaurista philippensis* and *Petinomys fuscocapillus*). There are also unconfirmed reports of the grizzled giant squirrel in the northern parts of the Reserve. Within the Reserve, there are only two concentrations of human settlements: some on the Mundanthurai Plateau and the plantations of Kakachi and Kodayar, which together constitute about 4% of the total Reserve area[41]. The eastern boundary of the Reserve is surrounded by more than 150 villages that exert considerable pressure and disturbance on the forest with respect to fodder and fuel-wood extraction. In the recent past, the implementation of an eco-development programme, had reduced[44] fuel-wood removal from the park by 95%. The western side of the park is mostly free from large human settlements, as it is contiguous with protected areas of Kerala and the reserve forests of Tamil Nadu and Kerala.

Methods

Base maps

A detailed base map of the Reserve was prepared by digitizing known features from a 1 : 50,000 scale geo-referenced Survey of India toposheet. This was updated by incorporating additional information on trails and paths, which were collected by carrying out a survey using handheld GPS units.

Field surveys

Hexagonal grids (hex) of 25 km^2 were overlaid on the map of the study area to define sampling sites. The hex size was determined to ensure that the sites were properly defined and that it was larger than the home range of the animal, enabling estimation of true occupancy rather than intensity of use; it also had to be determined by field logistics. The grids were clipped to the administrative boundary and only those sites that were larger than 10 km^2 were chosen for sampling. Using the above criteria, we identified 37 hexes, covering about 675 km^2 of the Reserve for sampling. Of the 37 hexes, seven could not be sampled, as there were no trials or paths within them. Similarly, the trails sampled across different hexes also varied based on availability of trails and paths within them. Four temporal replicates were used to collect detection/non-detection data, with every morning and evening session spread across two days, each being treated as a replicate. Trails were also chosen such that they were as far apart from each other as possible. On each sampling session, two teams of two biologists each traversed about 3 km of the existing trail network recording both sightings and calls of giant squirrels. The latitude and longitude of each evidence were noted down using a handheld GPS. The habitat description of the point location was also noted down. The hexes were sampled between February and September 2005, except for two, which were sampled in July 2004. The data were analysed using single-season models available in the program Presence[45].

The covariates used to describe each hex were average slope (Slope); percentage dry forest cover (Dry); percentage wet forest cover (Wet); area under water (Water); a Habitat Homogeneity Index (HHI) (the average area-to-perimeter ratio for different habitat type within each hex, a higher score indicating a more heterogeneous hex with several smaller patches of different forest types); and the number of habitat fragments (Frag).

The influence of these covariates on the occupancy (ψ) and the influence of time of sampling (morning/evening) on the detection probability (p) were explored. The simplest model keeping the variability in ψ and p constant was first undertaken. Each variable and combination of variables was then used as a predictor in the models to estimate ψ and p. Models were ranked on their AIC_c (Akaike's Information Criteria for small subsets) value and the best model was selected based on ΔAIC_c. To understand the influence of a covariate on occupancy, computed model weights were summed over all models containing the particular covariate[46].

Results

A total of 486 km of trails and paths were sampled and 91 direct sightings and 89 calls of giant squirrels were recorded during the study period. The frequency of evidences observed in the sampling units is provided in Figure 2.

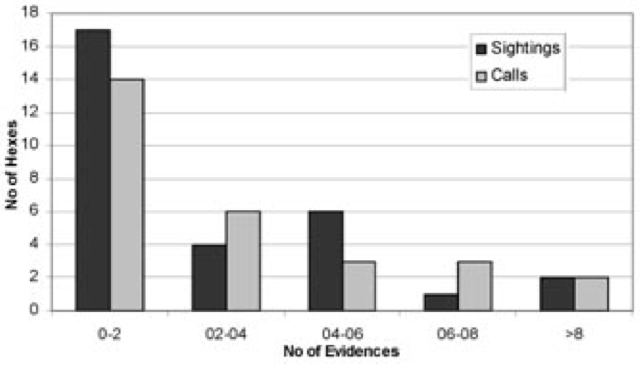

Figure 2. Frequency of evidences observed in the sampling units.

Table 1. Models assessed to estimate occupancy rates

Model	AIC_c	ΔAIC_c	AIC_c weights	$\hat{\psi}$	$\hat{SE}(\hat{\psi})$
psi(*Slope*,*HHI*), p(*Sam*)	141.18	0.00	0.25	0.814	0.087
psi(*Slope*), p(*Sam*)	141.39	0.21	0.23	0.844	0.063
psi(*Wet*), p(*Sam*)	141.50	0.32	0.22	0.797	0.055
psi(*Slope*,*HHI*,*Wet*), p(*Sam*)	142.56	1.38	0.13	0.811	0.103
psi(*Slope*,*Wet*), p(*Sam*)	142.78	1.60	0.11	0.842	0.088
psi(*HHI*), p(*Sam*)	145.66	4.48	0.03	0.806	0.073
psi(*), p(*Sam*)	145.74	4.56	0.03	0.808	0.074
psi(*), p(*)	146.72	5.54	0.02	0.808	0.074

Slope, Average slope; HHI, Habitat Homogeneity Index; Sam, sampling occasion; Wet, percentage of wet forest cover; *Constant.

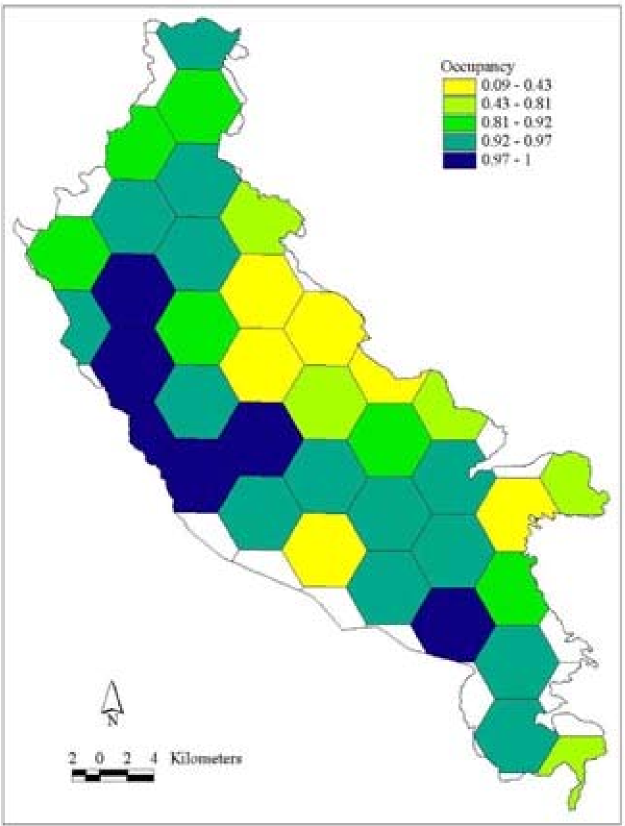

Figure 3. Rates of Indian giant squirrel occupancy across the study site. The rates have been estimated using model averaging.

No evidence of giant squirrel occurrence was recorded in six of the 30 sampled hexes. In nine hexes they were detected on every sampling occasion. Also, the number of evidences collected during morning surveys was different from that collected during the evening surveys (morning 62%, evening 38%). Given this difference, the time of sampling (morning/evening) was used as a variable to model the detection probability.

Various models were assessed (Table 1) to estimate occupancy rates. The naïve rate of squirrel occupancy (occupancy rates estimated without using a capture–recapture framework) was 0.8. In other words, giant squirrels occupied 80% of our sampled sites.

Table 2. Summed weights of covariates indicating their importance in determining occupancy

Covariate	Summed AIC_c weights	Average β coefficient	Average SE
Slope	0.722	0.147	0.071
Wet	0.457	2.670	1.968
HHI	0.407	–24.832	22.056

Slope, Average slope; Wet, Percentage of wet forest cover; HHI, Habitat Homogeneity Index.

Our analysis showed that none of the models could be judged as the best. Hence model-averaging or averaging $\hat{\psi}$ and $\hat{p}$ across all models was undertaken. This gave the estimated occupancy rate as 0.82 (with a SE of 0.08), with an average detection probability of 0.71 (± 0.05; i.e. probability of detecting squirrels on each walk). Only 29% of the sampled hexes had occupancy rates lower than 0.8. Using the first model (the model with the lowest AIC_c value; Table 1) and the same set of variables, the occupancy rates for those hexes that were not sampled were estimated (Figure 3). The difference between the sampled and the predicted occupancy rates did not appear to be different from each other ($\hat{\psi}_{\text{sampled}} = 0.8114 \pm 0.103$, $\hat{\psi}_{\text{predicted}} = 0.8111 \pm 0.099$).

The summed weights (Table 2) were calculated to infer the relative influence of each covariate on occupancy of the Indian giant squirrel. It was seen that slope, per cent wet forest and HHI were the three main factors (in that order) influencing the occupancy of this species. The β-coefficient (Table 2) shows that the HHI has a negative influence on their occupancy and per cent wet forest and slope are positively correlated to the occupancy.

Discussion

This study demonstrates how data from detection/non-detection surveys can be used to determine occupancy rates when species are not always sighted. Although our results show that the estimated occupancy did not largely differ from the naïve estimate, the study provides a framework for improving estimates. Also, given that the number of sightings differed in the morning and evening, we demonstrate the methods that can be employed to account for this variation and its influence on detection probability.

There has been no prior population estimates of the Indian giant squirrel in KMTR, and this is the first attempt to estimate occupancy rates for giant squirrels in any Indian forests. The occupancy rates estimated in this study show that the Indian giant squirrel is widely distributed in KMTR and the high detection probability shows that they are easily sighted. This indicates that the species is common in this landscape both in terms of detectability as well as distribution.

Habitat characteristics that influenced the occupancy of these squirrels in this protected area were also identified in this study. Of the six covariates used, only three influenced the occupancy of giant squirrels in KMTR. The remaining three variables (area under water, percentage dry forests and number of habitat fragments) did not have any influence. The models where these covariates were incorporated showed lower AIC values than the models where ψ and p were held constant.

Slope had the highest influence on the observed occupancy. This indicates that the giant squirrel prefers undulating terrain in KMTR. This could be an artefact of the distribution of moist and evergreen habitats, which are mostly found in highly undulating terrain in the study site. These habitats cover about half of KMTR. The positive trend with the proportion of wet forest cover and the negative trend with the habitat homogeneity indicate that the squirrels prefer large contiguous patches of the moist and wetter forest types. These findings corroborate with earlier reports on the habitat preference of the species.

Low model weights suggest that remotely sensed covariates do not explain the underlying pattern well, and account only for 25% variance even in the best model. However, this can be substantially improved if ground-based covariates are taken into consideration.

The rate of occupancy was low in areas with high percentage of degraded dry deciduous forests and scrub. This constitutes the eastern side of the park and includes areas like the Mundanthurai Plateau, Manimuttar and the lower reaches of the Kalakad range. Human disturbance, by way of settlements and tourists, is high in these grids and these areas are also severely affected by heavy fuel-wood extraction by local residents. The vegetation around settlements comprises of short trees and is dominated by thorny shrubs.

Although poaching is reported to be a major threat in other parts of its distribution range[3,47], this alone might not explain the lower occupancy rates of squirrels closer to human settlements, as poaching of the giant squirrel is not widespread in KMTR. Based on interactions with locals and field knowledge, we infer that poaching occurs at very low intensities around human settlements. Occupancy rates were also low in regions with rocky slopes and high elevation grasslands, like the Panditheri Pass bordering Kerala.

With subsequent surveys, probabilities of site colonization and extinction using multiple season models can be estimated. Such studies will be of use for future management and conservation of the species. Also, during occupancy surveys, information on presence and number of breeding animals can also be collected. It has been suggested that this can be used as an indicator of habitat quality[3,47].

The occupancy approach has several advantages over traditional density estimation techniques: it is cost-effective in terms of equipment and trained manpower, and can be carried out relatively more quickly compared to other abundance-estimation techniques like line transects and mark-recapture surveys. Although in the present study we make use of only direct evidence (sighting and loud calls), this technique also allows the use of indirect evidences like nests and pellet-droppings. In sites with very low densities, it is most likely that one will be able to detect indirect evidences more easily than direct evidence. Advances in the technique also allow estimation of animal abundances if an occupancy framework is followed while collecting data[48,49]. Often, it may suffice for field managers and conservation biologists to monitor trends in populations or trends in occupancy as a response to specific conservation/management interventions rather than monitoring actual abundances using effort-intensive methods.

1. Abdulali, H. and Daniel, J. C., Races of giant squirrel (*Ratufa indica*). *J. Bombay Nat. Hist. Soc.*, 1952, **50**, 469–474.
2. Jathanna, D. N., Kumar, S. N. and Karanth, K. U., Estimating Indian giant squirrel *Ratufa indica* abundances in forest habitats using distance sampling, In Abstracts of the Fourth International Tree Squirrel Colloquium and First International Flying Squirrel Colloquium (eds Nandini, R., Robin, V. V. and Sinha, A.), National Institute of Advanced Studies, Bangalore, 2006, p. 55.
3. Borges, R. M., Mali, S. and Ranganathan, S., The status, ecology and conservation of the Indian giant squirrel (*Ratufa indica)*, Technical Report No. 1, Wildlife Institute of India, Dehradun, 1992.
4. Sridhar, H., Effects of rainforest fragmentation and degradation on the Indian giant squirrel *Ratufa indica* and other small mammals in the Anamalai hills, southern Western Ghats, India. In Abstracts of the Fourth International Tree Squirrel Colloquium and First International Flying Squirrel Colloquium (eds Nandini, R., Robin, V. V. and Sinha, A.), National Institute of Advanced Studies, Bangalore, 2006, p. 29.
5. Babu, N. V. and Varma, S., Distribution and abundance of the Indian giant squirrel (*Ratufa indica*) in Bandipur Tiger Reserve. In Abstracts of the Fourth International Tree Squirrel Colloquium and First International Flying Squirrel Colloquium (eds Nandini, R., Robin, V. V. and Sinha, A.), National Institute of Advanced Studies, Bangalore, 2006, p. 74.
6. Kumara, H. N. and Singh, M., Distribution and relative abundance of giant squirrel and flying squirrel in Karnataka, India. *Mammalia*, 2006, **70**, 40–47.
7. IUCN 2006. IUCN Red List of Threatened Species; www.iucnredlist.org, accessed on 30 May 2007.
8. Royle, J. A. and Nichols, J. D., Estimating abundance from repeated presence–absence data or point counts. *Ecology*, 2003, **84**, 777–790.

9. 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.
10. MacKenzie, D. I. and Nichols, J. D., Occupancy as a surrogate for abundance estimation. *Anim. Biodivers. Conserv*., 2004, **27**, 461–467.
11. Hanski, I., Inferences from ecological incidence functions. *Am. Nat.*, 1992, **139**, 657–662.
12. Hanski, I., A practical model of metapopulation dynamics. *J. Anim. Ecol*., 1994, **63**, 151–162.
13. Hanski, I., Metapopulation dynamics: From concepts and observations to predictive models. In *Metapopulation Biology: Ecology, Genetics and Evolution* (eds Hanski, I. and Gilpin, M.), Academic Press, London, 1997, pp. 69–92.
14. MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G. and Franklin, A. B., Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. *Ecology*, 2003, **84**, 2200–2207.
15. Karanth, K. U. and Nichols, J. D. (eds), Monitoring tiger populations: Why use capture–recapture sampling? In *Monitoring Tigers and their Prey – A Manual for Wildlife Researchers, Managers and Conservationists in Tropical Asia*, Center for Wildlife Studies, Bangalore, 2002, pp. 153–167.
16. Stauffer, H. B., Ralph, C. J. and Miller, S. L., Incorporating detection uncertainty into presence–absence surveys for marbled murrelet. In *Predicting Species Occurrences – Issues of Accuracy and Scale* (eds Scott, J. M. *et al.*), Island Press, Washington DC, 2002, pp. 357–367.
17. 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.
18. MacKenzie, D. I. and Kendall, W. L., How should detection probability be incorporated into estimates of relative abundance? *Ecology*, 2002, **83**, 2387–2393.
19. Hanski, I., Metapopulation dynamics. *Nature*, 1998, **396**, 41–49.
20. Mortberg, U. M., Resident bird species in urban forest remnants; landscape and habitat perspectives. *Landsc. Ecol.*, 2001, **16**, 193–203.
21. Buij, R. *et al*., Patch occupancy models indicate human activity as major determinant of forest elephant *Loxodonta cyclotis* seasonal distribution in an industrial corridor in Gabon. *Biol. Conserv*., 2007, **135**, 189–201.
22. Mladenoff, D. J., Sickley, T. A., Haight, R. G. and Wydevan, A. P., A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conserv. Biol*., 1995, **9**, 279–294.
23. Buckland, S. T., Elston, D. A. and Beaney, S. J., Predicting distributional change, with application to bird distributions in northeast Scotland. *Global Ecol. Biogeogr*., 1996, **5**, 66–84.
24. Wiser, S. K., Peet, R. K. and White, P. S., Prediction of rare-plant occurrence: A southern Appalachian example. *Ecol. Appl*., 1998, **8**, 909–920.
25. Edwards, T. C. Jr, Deshler, E. T., Foster, D. and Moisen, G. G., Adequacy of wildlife habitat relation models for estimating spatial distributions of terrestrial vertebrates. *Conserv. Biol.*, 1995, **10**, 263–270.
26. Cowley, M. Jr, Wilson, R. J., Leon Cortes Jorge, L., Gutierrez, D., Bulman, C. R. and Thomas, C. D., Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *J. Appl. Ecol*., 2000, **37**, 60–72.
27. van Apeldoorn, R. C., Celada, C. and Nieuwenhuizen, W., Distribution and dynamics of the red squirrel (*Sciurus vulgaris* L.) in a landscape with fragmented habitat. *Landsc. Ecol.*, 1994, **9**, 227–235.
28. Verbeylen, G., De Bruyn, L. and Matthysen, E., Patch occupancy, population density and dynamics in a fragmented red squirrel *Sciurus vulgaris* population. *Ecography*, 2003, **26**, 118–128.
29. Patton, D. R., Abert squirrel cover requirements in southwestern ponderosa pine. US Department of Agriculture, Forest Service Research Paper RM-145, Fort Collins, Colorado, 1975.
30. Hall, J. G., A field study of the Kaibab squirrel in the Grand Canyon National Park. *Wildl. Monogr.*, 1981, **75**, 1–154.
31. Ramachandran, K. K., Ecology and behaviour of Malabar giant squirrel (*Ratufa indica maxima*) Schreber. KFRI Report 55 (Summary), Kerala Forest Research Institute, Peechi, 1988.
32. Dutta, A. and Goyal, S. P., Comparison of forest structure and use by the Indian giant squirrel (*Ratufa indica*) in two riverine forests of India. *Biotropica*, 1996, **28**, 394–399.
33. Borges, A., Figs, Malabar giant squirrels and food shortages within two tropical Indian forests. *Biotropica*, 1993, **25**, 183–190.
34. Prater, S. H., *The Book of Indian Animals*, Bombay Natural History Society, Bombay/Oxford University Press, Oxford, 1980.
35. Menon, V., *A Field Guide to Indian Mammals*, Dorling Kindersley/Penguin Books, New Delhi, 2003.
36. Wildlife (Protection) Act, India, 1972, Ministry of Law and Justice; http://envfor.nic.in/legis/wildlife/wildlife1s2.html, accessed on 15 January 2006.
37. CITES, 2005, Convention on International Trade in Endangered Species of Wild Flora and Fauna; http://www.cites.org/eng/app/appendices.html, accessed on 15 January 2006.
38. Muul, L. and Liat, L. B., Comparative morphology, food habits and ecology of some Malaysian arboreal rodents. In *The Ecology of Arboreal Folivores* (ed. Montgomery, G. G.), Smithsonian Institution Press, Washington DC, 1978, pp. 361–368.
39. Madhusudan, M. D. and Karanth, K. U., Local hunting and the conservation of large mammals in India. *Ambio*, 2002, **31**, 39–54.
40. Kumara, H. N. and Singh, M., The influence of differing hunting practices on the relative abundances of mammals in two rainforest areas on WG, India. *Oryx*, 2004, **38**, 321–327.
41. Ali, R., Enclaves in Kalakad Mundanthurai Tiger Reserve, Final report submitted to the Field Director, KMTR, 2001, p. 110.
42. Johnsingh, A. J. T., The Kalakad–Mundanthurai Tiger Reserve: A global heritage of biological diversity. *Curr. Sci*., 2001, **80**, 378–388.
43. Das, A., Krishnaswamy, J., Bawa, K. S., Kiran, M. C., Srinivas, V., Kumar, N. S. and Karanth, K. U., Prioritisation of conservation area in Western Ghats, India. *Biol. Conserv*., 2006, **133**, 16–31.
44. Dutt, S., Beyond 2000: A management vision for the Kalakad–Mundanthurai Tiger Reserve. *Curr. Sci.*, 2001, **80**, 442–447.
45. Hines, J. E., Program Presence (Version 2): Software to compute estimates patch occupancy rates and related parameters, USGS-PWRC, 2006; http://www.mbr-pwrc.usgs.gov/software/presence.html
46. Burnham, K. P. and Anderson, D. R., *Model Selection and Inference: A Practical Information–Theoretic Approach*, Springer-Verlag, New York, 1998.
47. Thorington, R. W. Jr and Cifelli, R. L., The unusual significance of giant squirrels (*Ratufa*). In *Conservation in Developing Countries: Problems and Prospects* (eds Daniels, J. C. and Serrao, J. S.), Proceedings of the Centenary Seminar of the Bombay Natural History Society, Bombay Natural History Society/Oxford University Press, Bombay, 1990, pp. 212–219.
48. Royle, J. A., N-mixture models for estimating population size from spatially replicated counts. *Biometrics*, 2004, **60**, 108–115.
49. Gopalswamy, A. M., Estimating sloth bear abundance from repeated presence–absence data in Nagarahole–Bandipur National Parks, India. M S thesis, University of Florida, USA, 2006.

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