Measuring Indian giant squirrel (*Ratufa indica*) abundance in southern India using distance sampling

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A large body of work on the ecology of sciurids is based on comparing patterns of abundance across either space or time. However, in most cases investigators choose to use surrogate measures of abundance, such as indices based on species or sign encounter rates, or trapping rates. This requires the assumption that detection probabilities are equal at all sites (or time periods) sampled, an assumption that is difficult to meet under field conditions. We demonstrate the application of line transect-based distance sampling, a technique that explicitly models and accounts for detection probability, to estimate ecological densities of Indian giant squirrels in forested habitats. Line transect surveys were carried out at several sites and the number of detections included: 86 (Bandipur), 152 (Nalkeri), 110 (Sunkadakatte), 304 (Muthodi) and 236 (Lakkavalli). The encounter rates ranged from 0.179/km in Bandipur through 0.296/km (Nalkeri), 0.368/km (Sunkadakatte), and 0.625/km (Lakkavalli), to 0.779/km in Muthodi, while the estimated probabilities of detection were 0.517 (Bandipur), 0.532 (Nalkeri), 0.531 (Sunkadakatte), 0.548 (Lakkavalli) and 0.604 (Muthodi). The estimated mean squirrel densities (± standard error of the density) ranged from 2.37 (0.33) squirrels/km^2 in Bandipur through 4.55 (0.44) squirrels/km^2 in Nalkeri, 4.86 (0.62) squirrels/km^2 in Sunkadakatte, to 10.20 (0.82) squirrels/km^2 and 12.26 (1.10) squirrels/km^2 in Muthodi and Lakkavalli respectively. We discuss design, field survey and data analytic considerations for rigorously estimating squirrel density and abundance.

Keywords: Density estimation, distance sampling, Indian giant squirrel.

Introduction

FIELD studies of sciurids focussing on disciplines such as population biology[1–3], prey–predator dynamics[4], invasive species control[5], seed predation[6], habitat use and landscape ecology[7–11], competition and coexistence[12], dispersal[13], nest predation[14,15] and effects of fragmentation[16,17] have considerably advanced our understanding of both theoretical and applied ecology. Most of these studies base inferences on spatial or temporal patterns of squirrel abundance. However, due to logistical or other constraints, instead of estimating true abundance, investigators usually use surrogate measures of abundance, such as counts from acoustic and visual surveys[3,14,15,17], trapping rates (catch per unit effort) or number of individuals captured in live-trapping surveys[7,9,11,16,18], surveys of signs such as middens[19], dreys[3] and tracks[8,20] (using tracking boards, sand plots or smoked plates).

The canonical estimator for estimating population size[21,22] relates the raw 'counts' obtained to true abundance as $\hat{N} = C' / \hat{p}\alpha$, where C' is the count statistic on areas surveyed, $\hat{p}$ the estimated detection probability, and α the proportion of the total area from which the count statistic was taken. The proportion of area sampled α is usually known, but to be able to extrapolate abundance on sampled areas to areas not sampled requires that the data be collected using probability-based sampling designs such as simple random, stratified random or cluster sampling[23]. The key challenge in estimating true abundance lies in reliably estimating detection probability $\hat{p}$ since it is usually less than 1 (but see refs 13, 24), and more importantly, it often varies unpredictably over space or time. Comparing raw counts or indices at one site (or time) with those at another site (or time) requires the implicit assumption that detection probabilities are equal at the two sites (or time periods); this assumption is difficult to meet[1], and violating it may either induce or obscure patterns in measures of abundance. For example, an evaluation of various squirrel track count techniques found that there were marked discrepancies, even while comparing rank orders of track counts with true abundance[20].

To address this problem, some investigators have applied methods based on the canonical estimator, such as capture–recapture sampling[22,25] in conjunction with live-trapping and marking, where the capture process is explicitly modelled, allowing the count (number of individuals captured) to be corrected for by the estimated capture (detection) probabilities. However, due to constraints of sample size, capture probabilities cannot always be estimated from the data, forcing investigators to fall back on indices such as minimum number alive[7]. A few investigators

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have applied an alternative method, distance sampling, that permits counts of squirrels to be corrected for detection probabilities, estimated from the distribution of detections from lines or points[26,27]. For example, line transect surveys of squirrels were carried out over six years in western Massachusetts[28], and were found to be reliable and easier to implement than capture–recapture surveys. In this article, we demonstrate the use of line transect sampling to estimate densities of the Indian giant squirrel (*Ratufa indica*), a large obligate forest species, at six sites in southern India.

Study sites

Line transect surveys were carried out in Muthodi, Lakkavalli, Nalkeri, Sunkadakatte and Bandipur, all in the southern Indian state of Karnataka. Muthodi, in the southern part of Bhadra Tiger Reserve, is covered by moist deciduous forests of the *Tectona–Dillenia–Lagerstroemia* series[29] and teak plantations, and receives an annual rainfall of 2000–2540 mm. Lakkavalli, in the northern part of Bhadra, is covered by moist as well as dry decidous forests of the *Terminalia–Anogeissus–Tectona* series. Nalkeri, along the western border of Nagarahole National Park, has moist deciduous and teak dominant forests, with dry deciduous forests along its eastern edge. Annual rainfall declines from 1500 mm along the western border to 900 mm in the east. Sunkadakatte, also within Nagarahole, lies to the east, abutting the Kabini reservoir, and is dominated by dry deciduous forests, with some areas supporting moist deciduous forests. Bandipur Tiger Reserve is the driest of the sites surveyed, with patches of moist deciduous forests within extensive dry deciduous stretches. Detailed descriptions of the study sites may be found elsewhere[30–32].

Field methods

Standard line transect methodology[26,32–34] was used to estimate Indian giant squirrel densities. These surveys were carried out as part of a long-term and large-scale study of large predator–prey dynamics. In each site, permanent transects were first measured and marked. The primary considerations in establishing transects were adequate coverage of the study area, and representation of the habitat types in which herbivore densities could be expected to differ.

Two trained observers walked along the transects between 0615 h and 0830 h as well as between 1545 h and 1800 h, and recorded cluster size, sighting distance and azimuths along the transect and to the centre of the cluster in each detection. As giant squirrels sometimes occurred in clusters (animals aggregating within a 30-m radius)[30], distances and angles were recorded to the centre of each cluster. Animal density estimation was thus a two-step process: estimation of cluster density and multiplying it by the estimated cluster sizes. As we wanted to express density per unit area rather than unit volume, detections high up on trees were projected to the ground before distances were measured. Sighting distances were measured using rangefinders, and the bearings were recorded using a liquid-filled compass. Table 1 gives details of distances walked during line transect surveys in each site.

Analytical methods

The program DISTANCE[35] was used to carry out all analyses. We first carried out exploratory analyses of the data to look for evidence of evasive movement prior to detection, 'rounding' and 'heaping' of data, and to truncate outlier observations to improve subsequent model-fitting. Detection probabilities were then estimated based on models of the detection process fit to the data. If the key function[26] did not fit the data adequately, cosine adjustment terms were added sequentially to improve the fit. The fit of possible alternative models to each specific dataset was assessed using Akaike's Information Criterion (AIC) values, which trade-off the bias of simple models against the higher variance of more complex models[36]. The goodness-of-fit tests generated by program DISTANCE, visual assessments of the fit of the proposed model to the observed distance data close to the transect line and the precision of estimated detection probabilities also helped guide model selection. Using the selected model in the program DISTANCE, the estimates of the

Table 1. Survey effort (l), numbers of detections (n) and encounter rates (n/l) of Indian giant squirrels during line transect surveys in southern India

Site	Year	Effort (l, km)	Number of cluster detections (n)	Encounter rate (n/l, squirrels clusters/km)
Bandipur	1999	476	86	0.1788
Nalkeri	2000	504	152	0.2956
Sunkadakatte	2000	288	110	0.3681
Muthodi	1998	384	304	0.7795
Lakkavalli	1998	344	236	0.6250

Table 2. Details of detection functions fit to field survey data

Site	Truncation width (m)	Selected model	Adjustment terms	Selection based on
Bandipur	80	Half-normal	None	AIC
Nalkeri	72	Uniform	1 cosine term	AIC, var (p)
Sunkadakatte	88	Half-normal	None	AIC
Muthodi	80	Hazard rate	None	AIC, var (p)
Lakkavalli	52	Half-normal	None	AIC, visual fit

AIC, Akaike's information criterion. See Methods for details.

Table 3. Parameters estimated using the selected models: average detection probability between the transect and truncation distance ($\hat{p}$); effective strip width sampled ($\hat{\mu}$); cluster density ($\hat{D}_S$); expected cluster size ($\hat{E}(S)$); mean density ($\hat{D}$) and standard error of density ($S\hat{E}(\hat{D})$)

Site	$\hat{p}$	$\hat{\mu}$ (m)	$\hat{D}_S$ (clusters/km^2)	$\hat{E}(S)$	$\hat{D}$ (squirrels/km^2)	$S\hat{E}(\hat{D})$
Bandipur	0.5168	41.346	2.1622	1.0941	2.3657	0.3325
Nalkeri	0.5324	38.333	3.8561	1.1800*	4.5504	0.4372
Sunkadakatte	0.5314	46.764	3.9352	1.2358	4.8633	0.6219
Muthodi	0.6039	48.311	8.0670	1.2642	10.1980	0.8158
Lakkavalli	0.5481	28.503	10.964	1.1179*	12.2560	1.0985

*Expected cluster size corrected for size bias.

following parameters were generated: encounter rate (n/l), where n is the total number of clusters detected and l the total length of the transects walked; average probability of detection between the transect and truncation distance ($\hat{p}$); effective strip width ($\hat{\mu}$); cluster density ($\hat{D}_S$); expected cluster size ($\hat{E}(S)$) and animal density ($\hat{D}$). As there was a greater tendency to detect larger clusters (relative to smaller ones) farther away from the line, we expected the average of our cluster sizes to be a (positively) biased estimate of mean cluster size. We tested for this bias by assessing if the slope of a regression of log cluster size against detection probability was significantly different from zero (at an α of 0.15). If the regression was found to be significant, the average cluster size was corrected using the estimated slope parameter. Variance of mean density was estimated as a composite of the variances of group size, encounter rate and the probability of detection. As we had far too few spatial replicates, empirical estimation of the variance associated with encounter rate was not possible, and we estimated encounter rate variance theoretically, assuming animals are randomly distributed over the area, with the encounter rate following a Poisson distribution across transects.

Results

Table 1 gives details of survey effort and encounter rates in each site. All sites had adequate numbers of detections, allowing us to model the detection process and estimate detection probabilities. The encounter rates ranged from 0.18/km in Bandipur to 0.78/km in Muthodi. The half-normal model without any adjustment terms proved to best describe the distance data in all sites (Table 2) other than Muthodi (hazard-rate) and Nalkeri (uniform, with one cosine adjustment term). The estimated detection probabilities ranged from 0.52 in Bandipur to 0.60 in Muthodi (Table 3), and the estimated densities from 2.37 squirrels/km^2 to 12.26 squirrels/km^2.

Discussion

In all the sites, the lack of adequate spatial replication prevented us from estimating encounter rate variance empirically, and we were forced to use theoretical estimates, assuming that n/l follows a Poisson distribution across transects. This may have underestimated the true variance to some extent[26]. In our current surveys, we have addressed this issue by employing systematic sampling designs for 25–40 transects in each site. Other ways of reducing n/l variance include stratification, when transects are located in different habitat types, or through cluster sampling, when transects sample a density gradient (e.g. in the case of grizzled giant squirrel *R. macroura*, which is found in riparian forests). The variance of estimated detection probabilities can be reduced by estimating stratum-wise detection functions, or by modelling detection probability as a function of detection distance as well as habitat or environmental covariates[27]. Despite the drawbacks in our datasets, we believe that our estimates demonstrate the usefulness of explicit model-based estimation of detection probabilities, in general, and distance sampling, in particular, for the measurement of squirrel densities, especially in forest habitats.

To be able to derive such estimates, a first step is carefully measuring and marking transects, according to some probability-based study design, as described above. While this may seem to be rather effort-intensive, once such a system of transects has been established, it can be used repeatedly, with a minimum amount of clearing and re-marking each year, to carry out long-term monitoring of squirrels and other wildlife. Another consideration is that of human resources: in order to cover the distances required for the minimum sample sizes of 40–60 to model the detection function[26], it is desirable to enlist the help of highly motivated volunteer naturalists. In our experience, volunteers can be adequately trained in all aspects of data collection in 2–3 days. Finally, careful exploration of the data and fitting of appropriate models is critical to generating reliable estimates of density.

Our density estimates seem to be positively related to annual rainfall, though the proximate driver for this pattern is likely to be some structural (e.g. tree height, canopy contiguity) or compositional (e.g. abundance or spatio-temporal distribution of food) attribute of the habitat. This pattern holds true even in the case of estimates from much wetter sites in tropical evergreen forests[37]. However, the lack of sufficient datapoints precludes formal testing of these, or any other, hypotheses. This underlines the need for estimation of giant squirrel densities from a range of habitats, derived using reliable methods such as distance sampling.

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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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