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.

1. Koprowski, J. L., *Pine Squirrel* (*Tamiasciurus hudsonicus*)*: A Technical Conservation Assessment*, USDA Forest Service, Rocky Mountain Region, 2005.
2. Dobson, F. S. and Oli, M. K., The demographic basis of population regulation in Columbian ground squirrels. *Am. Nat.*, 2001, **158**, 236–247.
3. Gurnell, J., Lurz, P. W. W., Shirley, M. D. F., Cartmel, S., Garson, P. J., Magris, L. and Steele, J., Monitoring red squirrels *Sciurus vulgaris* and grey squirrels *Sciurus carolinensis* in Britain. *Mammal Rev.*, 2004, **34**, 51–74.
4. Rosenberg, D. K., Swindle, K. A. and Anthony, R. G., Influence of prey abundance on northern spotted owl reproductive success in western Oregon. *Can. J. Zool.*, 2003, **81**, 1715–1725.
5. Lawton, C. and Rochford, J., The recovery of grey squirrel (*Sciurus carolinensis*) populations after intensive control programmes. *Biol. Environ.*, 2007, **B107**, 19–29.
6. Fleury, M. and Galetti, M., Forest fragment size and microhabitat effects on palm seed predation. *Biol. Conserv.*, 2006, **131**, 1–13.
7. Fischer, R. A. and Holler, N. R., Habitat use and relative abundance of gray squirrels in southern Alabama. *J. Wildl. Manage.*, 1991, **55**, 52–59.
8. Fisher, J. T. and Merriam, G., Resource patch array use by two squirrel species in an agricultural landscape. *Landsc. Ecol.*, 2000, **15**, 333–338.
9. O'Connell, A. F., Servello, F. A., Higgins, J. and Halteman, W., Status and habitat relationships of northern flying squirrels on Mount Desert Island, Maine. *Northeast. Nat.*, 2001, **8**, 127–136.
10. Rushton, S. P., Lurz, P. W. W., South, A. B. and Mitchell-Jones, A., Modelling the distribution of red squirrels (*Sciurus vulgaris*) on the Isle of Wight. *Anim. Conserv.*, 1999, **2**, 111–120.
11. Wheatley, M., Fisher, J. T., Larsen, K., Litke, J. and Boutin, S., Using GIS to relate small mammal abundance and landscape structure at multiple spatial extents: the northern flying squirrel in Alberta, Canada. *J. Appl. Ecol.*, 2005, **42**, 577–586.
12. Derge, K. L. and Yahner, R. H., Ecology of sympatric fox squirrels (*Sciurus niger*) and gray squirrels (*S. carolinensis*) at forest–farmland interfaces of Pennsylvania. *Am. Midl. Nat.*, 2000, **143**, 355–369.
13. Haughland, D. and Larsen, K., Ecology of North American red squirrels across contrasting habitats: Relating natal dispersal to habitat. *J. Mammal.*, 2004, **85**, 225–236.
14. Martin, J. L., Joron, M. and Gaston, A. J., The squirrel connection: Influence of squirrels as songbird nest predators in Laskeek Bay. In *Laskeek Bay Research 10* (ed. Gaston, A. J.), Laskeek Bay Conservation Society, Queen Charlotte City, 2001, pp. 42–61.
15. Bayne, E. M. and Hobson, K. A., Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. *Conserv. Biol.*, 1997, **11**, 1418–1429.
16. Nupp, T. E. and Swihart, R. K., Landscape-level correlates of small-mammal assemblages in forest fragments of farmland. *J. Mammal.*, 2000, **81**, 512–526.
17. Bayne, E. M. and Hobson, K. M., Relative use of contiguous and fragmented boreal forest by red squirrels (*Tamasciurus hudsonicus*). *Can. J. Zool.*, 2000, **78**, 359–365.
18. Pearson, D. E. and Ruggiero, L. F., Transect versus grid trapping arrangements for sampling small-mammal communities. *Wildl. Soc.*, 2003, **B31**, 454–459
19. Koprowski, J. L., Alanen, M. I. and Lynch, A. M., Nowhere to run and nowhere to hide: Response of endemic Mt. Graham red squirrels to catastrophic forest damage. *Biol. Conserv.*, 2005, **126**, 491–498.
20. Carey, A. B. and Witt, J. W., Track counts as indices to abundances of arboreal rodents. *J. Mammal.*, 1991, **72**, 192–194.
21. Karanth, K. U. and Nichols, J. D. (eds), *Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia*, Centre for Wildlife Studies, Bangalore, 2002.
22. Williams, B. K., Nichols, J. D. and Conroy, M. J., *Analysis and Management of Animal Populations*, Academic Press, San Diego, 2002.
23. Thompson, S. K., *Sampling*, Wiley, New York, 1992.
24. Dobson, F. S., Regulation of population size: Evidence from Columbian ground squirrels. *Oecologia*, 1995, **102**, 44–51.
25. Amstrup, S. C., McDonald, T. L. and Manly, B. F. J., *Handbook of Capture–Recapture Analysis*, Princeton University Press, Princeton, 2005.
26. Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L., Borchers, D. L. and Thomas, L., *Introduction to Distance Sampling*, Oxford University Press, Oxford, 2001.
27. Buckland, S. T., Anderson, D. R., Burnham, K. P., Laake, J. L. Borchers, D. L. and Thomas, L. (eds), *Advanced Distance Sampling*, Oxford University Press, Oxford, 2004.
28. Healy, W. M. and Welsh. C. J. E., Evaluating line transects to monitor gray squirrel populations. *Wildl. Soc.*, 1992, **B20**, 83–90.
29. Meher-Homji, V. M., Vegetation types of India in relation to environmental conditions. In *Conservation in Developing Countries: Problems and Prospects* (eds Daniel J. C. and Serrao, J. S.), Proceedings of the Centenary Seminar of the Bombay Natural History Society, Oxford University Press, Mumbai, 1990, pp. 95–110.
30. Karanth, K. U. and Sunquist, M. E., Population structure, density and biomass of large herbivores in the tropical forests of Nagarahole, India. *J. Trop. Ecol.*, 1992, **8**, 21–35.
31. Karanth, K. U. and Nichols, J. D., Ecological status and conservation of tigers in India, Final technical report to the Division of International Conservation, US Fish and Wildlife Service, Washington DC; Wildlife Conservation Society, New York and Centre for Wildlife Studies, Bangalore, 2000.
32. Jathanna, D., Karanth, K. U. and Johnsingh, A. J. T., Estimation of large herbivore densities in the tropical forests of southern India using distance sampling. *J. Zool.*, 2003, **261**, 285–290.
33. Kumar, N. S., Ungulate density and biomass in the tropical semi-arid forest of Ranthambore, India. M Sc thesis, Pondicherry University, Puducherry, 2000.
34. Karanth, K. U., Thomas, L. and Kumar, N. S., Field surveys: Estimating absolute densities of prey species using line transect sampling. In *Monitoring Tigers and their Prey: A Manual for Researchers, Managers and Conservationists in Tropical Asia* (eds Karanth, K. U. and Nichols, J. D.), Centre for Wildlife Studies, Bangalore, 2002.
35. Thomas, L. *et al.*, Distance 5.0. Release 1. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK, 2005; http://www.ruwpa.st-and.ac.uk/distance/
36. Burnham, K. P. and Anderson, D. R., *Model Selection and Multi-Model Inference: A Practical Information–Theoretic Approach*, Springer-Verlag, New York, 2002, 2nd edn.
37. Umapathy, G. and Kumar, A., The occurrence of arboreal mammals in the rainforest fragments in the Anamalai Hills, south India. *Biol. Conserv.*, 2000, **92**, 311–319.

ACKNOWLEDGEMENTS. We are grateful to the Karnataka Forest Department for permits to carry out the field research. The study was supported by Wildlife Conservation Society, New York, the US Fish and Wildlife Service, and the National Fish and Wildlife Foundation, USA. We thank Farshid Ahrestani, the transect volunteers and forest department trainees for assistance with field data collection.