

**Assessing animal abundance from photographic capture data
using an occupancy approach**

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Declaration

I declare that the thesis entitled "Assessing animal abundance from photographic capture data using an occupancy approach" comprises research work done by me under the guidance of Dr. Ullas Karanth, and co-guidance of Mr. Arjun Gopalaswamy. The work is original and has not been done earlier by anyone else. Part of this work, which is related to or similar to work done by other researchers, has been cited in this thesis at appropriate places. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

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Certificate

I declare that the thesis entitled "Assessing animal abundance from photographic capture data using an occupancy approach" comprises research work carried out by Kaavya Nag at the Centre for Wildlife Studies under my guidance, and the co-guidance of Mr. Arjun Gopalswamy, during the period 2007-2008, for the Degree of Master of Science in Wildlife Biology & Conservation of the Manipal University. The results presented in this thesis have not been submitted previously to this or any other university for an M.Sc. or any other degree.

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Summary

Abundance or population size is a state variable that provides the most critical information about the status of any animal population. However, it is difficult to estimate abundances of some species that are nocturnal, cryptic and not individually identifiable from natural markings, using conventional non-invasive techniques, such as distance sampling or photographic capture-recapture methods. However, recent advances in ‘occupancy modeling’ of animal presence data derived from photographic captures might provide solutions to the problems of monitoring such species. A specific occupancy approach – the Royle and Nichols (2003) model, allows for reliable estimation of abundance at best, and of an index of abundance or occupancy rate at the least, without the need for individual identification of animals. It might enable estimation of abundances of elusive and nocturnal species of small carnivore and medium sized mammals, when used in conjunction with photographic capture data derived using camera traps. In this study the Royle and Nichols (2003) approach was applied to photographic capture data to estimate abundances of some species of nocturnal and cryptic mammals.

The study was conducted in the Bhadra Wildlife Sanctuary, Karnataka, India, from January 2008 to May 2008. During this period, passive detection camera traps were used to collect presence-absence data for seven species of elusive mammals. These data were analysed using the Royle and Nichols (2003) model to estimate abundances of four species of carnivores and other nocturnal mammals, and three species of large ungulates.

The average abundance (density) of the Small Indian Civet (*Viverricula indica*) was estimated to be 0.83 ± 0.297 (SE) animals per km². Similarly, average abundance of other

species, expressed in number of animals per km² were: Stripe-necked Mongoose (*Herpestes vitticollis*) was estimated to be 0.74 ± 0.27 (SE), Indian Porcupine (*Hystrix indica*) was estimated to be 0.56 ± 0.36 (SE), Mouse Deer (*Moschiola memmina*) to be 1.52 ± 1.11 (SE). Muntjac (*Muntiacus muntjak*), Chital (*Axis axis*) and Sambar (*Cervus unicolor*) average abundance of clusters per cell was estimated to be 1.04 ± 0.66 (SE), 0.56 ± 0.33 (SE) and 1.09 ± 0.55 (SE), respectively. Most of these estimates appear to be reasonable.

This method appears to provide a novel approach to monitor the distribution and abundance of species whose elusive traits have so far, prevented non-invasive abundance estimation using conventional techniques. It can potentially be a reliable method for the monitoring of multiple species from the same field survey, thus being especially useful for community-level monitoring of animal populations and biodiversity.

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Debts of gratitude - the one kind of insolvency that one may justly consider a form of riches

- Amitav Ghosh, 2000

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GENERAL INTRODUCTION

For cryptic and elusive species that are not individually identifiable from natural markings, it is still not possible to use conventional, non-invasive techniques for abundance monitoring. Methods that use statistically sound procedures to arrive at reliable estimates of abundance (William et al. 2002) include distance sampling (Buckland et al. 2001), and photographic capture-recapture methods (Karanth & Nichols 2002, Karanth et al. 2004). However, owing to specific model assumptions and requirements, distance-sampling methods (such as line transects) can only be used on more visible species, while photographic capture-recapture can only be used for species with unique natural markings, which can therefore be individually identified (Karanth and Nichols 2002).

However, modern analytic approaches that shift focus from counting animals to counting patches or sites potentially occupied by them can permit estimating populations of even cryptic and non-uniquely identifiable species. This general approach is called occupancy modeling and estimation approach, and uses repeated presence-absence data to estimate the proportion of sites occupied or used by a species (Mackenzie et al. 2006). Two specific advances in occupancy modeling – namely the Mackenzie et al. (2002) approach and the subsequent Royle and Nichols (2003) model, can allow for the estimation of animal abundance without the need for individual identification based on detections of species presence at sites.

Therefore, for cryptic and elusive species, the use of photographic data from remotely triggered camera traps in combination with the Royle and Nichols (2003) occupancy approach can potentially provide a reliable method to estimate abundances.

Although they are of high conservation interest, small and medium sized tropical forest carnivores and other nocturnal mammals are species that tend to be data deficient, because of their cryptic and nocturnal or otherwise elusive habits (Ray and Sunquist 2001). The Western Ghats of India harbor several such animal species, for which camera trap photography combined with the Royle and Nichols (2003) approach can potentially provide a practical technique for abundance estimation. In the general context, such surveys can also be used for abundance estimation of multiple species from the same survey, therefore making animal community level monitoring more cost-effective and efficient.

This thesis is comprised of one research paper, which involves the application of the Royle and Nichols (2003) occupancy model to estimate abundances of several species of mammals from photographic capture data, and is titled:

Assessing animal abundance from photographic capture data using an occupancy approach.

This follows the journal format of *Journal of Applied Ecology*.

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The Study Species



Small Indian Civet (*Viverricula indica*)



Indian Porcupine (*Hystrix indica*)



Mouse Deer (*Moschiola memminna*)



Asian Muntjac (*Muntiacus muntjak*)



Stripe-Necked Mongoose (*Herpestes vitticollis*)



Sambar (*Cervus unicolor*)

SUMMARY

1. Non-invasive abundance monitoring of cryptic and non-uniquely identifiable species, as well as multiple species is not possible through conventional photographic capture-recapture methods or distance sampling.
2. In this study the analytic approach of Royle and Nichols (2003) was used in combination with detection/non-detection data obtained from photographic captures to estimate abundance of some mammal species in the Western Ghats of India.
3. Abundances of two species of small carnivores, two nocturnal mammals and three species of ungulates were estimated. Although estimates have high degrees of uncertainty, they provide the first abundance estimates of four species of mammals in India. Uncertainty can be reduced by improved sampling techniques.
4. *Synthesis and applications:* With investment of adequate sampling effort and field methods tailored to maximize the chances of detecting animals, the approach developed in this study provides a useful new technique for the reliable estimation of animal abundance, even for cryptic species that may not be individually identifiable. It also provides a method for the estimation of abundances of multiple species from a single cost-effective survey.

INTRODUCTION

The need to monitor animal populations

Current conservation targets to reduce biodiversity loss (Pereira & Cooper, 2006) require tracking changes in biodiversity at local, regional and global scales. They emphasize the need for systematically monitoring biodiversity components at various scales.

At the landscape and global scales, animal population monitoring can advance our understanding of ecosystem response (Halpin 1997) to factors such as habitat fragmentation and climate change, which are key factors depressing biodiversity (Opdam & Wascher, 2004).

At local scales, reliable population monitoring is required to objectively assess hunting and other anthropogenic pressures (Robinson and Bennett 2000), evaluate the success or failure of management programs and to establish benchmark data for future conservation (Carillo et al., 2000, Karanth & Nichols 2002, Williams et al. 2002). All these concerns emphasize the need for multi-species animal monitoring methods that are rigorous, reliable and cost effective.

Abundance or population size (often expressed as density or number of individual animals per unit area) is a state variable that provides the most critical information about the status of any animal population. It is therefore a preferred parameter to estimate. However, abundance estimation methods that effectively deal with complex issues of spatial sampling and imperfect detections usually require greater investment of resources (Williams et al. 2002).

Animal population monitoring: Basic Issues

Usually, abundance estimation methods must address the issue of ‘spatial sampling’: extrapolating data from sampled units to wider survey areas (Williams et al., 2002). They must also deal with the fact that not all animals present even within a sampled unit are detected during the survey, and therefore that the probability of detecting an animal in the sampled area is often less than one (Williams et al. 2002, Karanth et al. 2004). If simple count statistics (raw encounter rates) that do not account for these problems are reported as abundance values, true abundance tends to be consistently underestimated. As a result, estimating the detection probability for a given field survey and correcting the resulting count statistics to obtain a more reliable estimate of abundance and density becomes the key goal of any survey (Williams et al. 2002; Mackenzie and Nichols 2004). Therefore, in addition to field counts of animals, other ancillary data on the observation and sampling process are required to address the above issues of spatial sampling and detectability.

Reliable abundance estimation methods that incorporate these issues include techniques such as line or point transects - which are based on “distance sampling” (Buckland et al. 2001; Williams et al. 2002), and “capture-recapture sampling” (Williams et al. 2002, Borchers et al., 1998), and are most widely applied to count a variety of animal species.

For species that are easily visible and non-cryptic – typically ungulates and other diurnal mammal species - distance sampling methods (Buckland *et al.* 2001) or multiple-observer sampling (Nichols et al 2000) can provide reliable estimates of abundance.

However, when dealing with secretive, nocturnal, or otherwise evasive species, which cannot be visually detected and counted, distance sampling cannot be used. For such species, biologists must employ theoretically well-founded ‘capture-recapture’ methods (Karanth and Nichols 1998) that involve physically capturing and tagging the animals. However these capture-tagging methods are generally invasive, difficult and expensive to apply. Although non-invasive capture-recapture sampling based on ‘photographic captures’ from camera traps can be used, (Karanth and Nichols 2002; Trolle & Kery 2003; Karanth et al. 2004; Soisalo & Cavalcanti 2006), its application is restricted to species that are naturally marked and therefore individually identifiable from photographs.

Therefore, species without uniquely identifiable markings cannot be studied using this technique. For such species, photographic captures can only generate data on species presence rather than abundance estimates.

Trapping rate surveys using camera trap data

Although trapping rate surveys (e.g. Carbone et al. 2001) have been used as indicators of animal abundance, detection probability is generally not estimated while doing so. As a result, its use is controversial both on theoretical and practical grounds (Jennelle, Runge & Mackenzie 2002; Karanth et al. 2003; Rowcliffe et al. 2008). Although Rowcliffe et al. (2008) recently published an alternative approach to estimating animal abundance from photographic captures this method requires prior biological knowledge of movement rates of animals as well as completely random placement of traps, potentially rendering its use in the field difficult.

Indirect indices of species presence

Indirect indices based on sign surveys, such as track counts and scent station visitation rates can provide estimates of relative abundance of animals. However, such indices do not incorporate detectability, and must be used with caution since the assumed relationship between the indirect count statistic (scent-station counts, scat encounter rates for example) and abundance must be adequately evaluated before conclusions about abundance are made (Sargeant et al. 1998; Gese 2001).

Approaches based on species presence data

If species presence data from camera trap photos could be used to model and derive animal abundances - or at least to derive reliable indices of abundance, (which can effectively deal with imperfect detections) - it will be a major advance in animal monitoring science.

In recent years, analysis of species presence data based on a variety of sources such as direct sightings or animal sign surveys has seen major advances. In addition, the former naïve field surveys of animal presence versus absence have evolved into a rigorous, reliable modeling and estimation approach known as ‘occupancy sampling and estimation’ (Mackenzie et al. 2006).

A synthesis of these two lines of progress in wildlife research - photographic sampling of animal presence data using camera traps and modern analytic approaches that estimate habitat occupancy from animal presence data in the face of imperfect detections- has opened new doors for investigating distributions of nocturnal and elusive animal species that are non-uniquely identifiable. Some specific advances in occupancy modeling (Mackenzie et al

2002, Royle and Nichols 2003), have even opened up the possibility of deriving animal abundance from presence data as elucidated below.

Occupancy Modeling and Estimation: A brief review

Methods using this general approach are called occupancy approaches. They use detection/non-detection data obtained from a sample of 'sites' or habitat patches potentially occupied by the species of interest (Williams et al. 2002, Royle and Nichols 2003). These methods primarily aim to estimate the proportion of area occupied (ψ) by a species of interest. The estimation approaches squarely address the issue of detection probability (Mackenzie et al. 2002) by conducting repeated survey visits to several 'sites'. They therefore deal with a fundamental weakness of traditional analytic methods which cannot distinguish true absence of the animal from non-detection during the survey.

Mackenzie et al. (2002) model

The occupancy approach was first conceptualized as being analogous to a closed-population mark-recapture approach by Nichols and Karanth (2002). Mackenzie et al. (2002) developed a rigorous maximum likelihood-based estimator for the occupancy rate ' ψ ' and the detection probability ' p '.

Basic assumptions of these occupancy estimation models include:

- a) Species are never falsely detected at a site when absent,
- b) Sites are closed to changes in occupancy over the duration of the survey,
- c) Detection at a site is assumed to be independent of detection at other sites.

- d) Detection probability ' p ' is constant across sites, or is a function of some measurable covariates (e.g. habitat type, weather, time of day).

As with standard capture-recapture analytic methods, in occupancy estimation also, the potential for variation in detection probability from one time period to the next, one individual to the next or one site to the next, is an important modeling consideration (Royle and Nichols 2003). However, the Mackenzie et al. (2002) model makes a de-facto assumption that abundance is constant across all sites. This assumption is likely to result in the model underestimating true occupancy when abundance is not constant across space, which is likely to be the case in many ecological situations.

An important extension of the Mackenzie et al. (2002) approach was made by Royle and Nichols (2003) via their model, which specifically assumes that abundance is not constant across sites, and is therefore important to introduce it as a primary cause of the variation in detection probability.

The Royle and Nichols (2003) model

The Royle and Nichols (2003) model assumes that variation in animal abundance from one site to the next is probably *the* most important source of heterogeneity in detection probability among sites (Royle & Nichols 2003). They suggest that by basing heterogeneity in detection probability on varying site-specific animal abundance, it is possible to exploit this very relationship to estimate the abundance parameter, and consequently derive the probability of occupancy.

The Royle and Nichols (2003) model is formulated as:

$$p_i = 1 - (1 - r)^{N_i}$$

Where p_i is the probability of detecting at least one animal at that site, and is estimated by repeated visits to the site.

N_i is the site-specific abundance

And r is the binomial sampling probability that a particular individual is detected, or the individual animal-specific detection probability.

The Royle and Nichols (2003) approach also uses maximum likelihood methods for parameter estimation. The estimated parameters are site-specific abundance ' λ ' and animal-specific detection probability ' r '. Abundance is assumed to be a random variable with some probability distribution, normally the Poisson or Negative Binomial distribution. The Poisson distribution for abundance is used because it arises under a random distribution of animals in space and is a good starting point for modeling the abundance distribution (Royle and Nichols 2003). Although the negative binomial distribution may prove useful in instances where animal densities vary with space, the estimated parameters of this model have high variances (see Royle and Nichols 2003). However, this distribution is likely to represent the data better, when there is a large difference in abundance over the study area.

Royle & Nichols (2003) requires the general assumptions of the basic Mackenzie et al.

(2002) model, and additionally assumes that:

- a) Detection probability p_i , varies across sites *only* as a result of variation in site-specific abundance N_i .

- b) Animal-specific detection probability ' r ' is constant, and if not, it should be specifically modeled.

Considering that the occupancy model parallels the 'demographically closed, capture-recapture approach (Otis et al. 1978), it is important to meet these basic model assumptions. In order to adhere to the population closure assumption, the time interval among repeated surveys is important. The survey duration must be short in order to reduce the chance of the occupancy changing during the survey, which may arise due to possible changes in animal distribution (see Mackenzie & Royle 2005).

For the assumption that detection of an animal at one cell is independent of detection at another cell to be met satisfactorily, cells must be separated by at least one home range diameter. If the assumption of independence is relaxed, the model can still provide useful results, if average abundance per cell can be assumed to be constant. However, in such a case, the animal abundance (parameter ' λ ') needs to be interpreted as average abundance per cell, and the occupancy parameter as 'habitat use' (Royle and Nichols 2003).

For meeting the assumption of constant individual animal specific detectability (' r ') across cells, sampling effort within each cell must be uniform. It is always preferable to use temporal replicates in such a survey in order to avoid the problem of spatial sub-sampling within each cell. However, in situations in which animals are expected to move widely in relation to cell size, and for logistical advantages, spatial replicates may be used.

Application of Occupancy Estimation to Camera Trapping Studies

The Royle and Nichols (2003) approach provides a powerful tool for the estimation of abundance using replicated detection/non-detection data. It does not require individuals of a

species to be uniquely identifiable. It also proves to be particularly useful in estimating abundance (or occupancy) for a multiple set of species simultaneously (e.g., Royle and Nichols 2003; Royle 2004b; Kery et al. 2005). So far however, the Royle and Nichols (2003) approach has not been used to estimate abundances of cryptic and nocturnal species from camera trap data.

The use of a systematic, likelihood-based method that also estimates detection probabilities can provide reliable estimates of at least an index of abundance if not abundance itself, and prove to be a robust tool in community and biodiversity monitoring. It is thus possible for us to now survey and monitor a range of rare, elusive species that hitherto, could not be surveyed, with unprecedented rigor.

Scope of the present study

In this study, I used the Royle and Nichols (2003) occupancy model in combination with photographic capture techniques to estimate abundances of several cryptic nocturnal and diurnal mammal species in the Bhadra Wildlife Sanctuary, Karnataka, India. This study was specifically designed (through placement of camera traps) for small carnivores and other small and medium-sized mammals. However, I have also used the incidental photographic capture data on larger ungulate species to derive estimates of abundance, so that these could be compared with density estimates derived from distance sampling methods at the same site under an ongoing study.

In order to meet occupancy survey design assumptions for each study species, I collected information on the ecology of small carnivores, nocturnal mammals and large ungulates from prior research at the site and at other locations (See appendix A).

Within mammalian communities, tropical forest carnivores and nocturnal mammals are a typical example of species that tend to be overlooked because of their often cryptic and nocturnal habits (Ray & Sunquist 2001). As a result, basic ecological knowledge about them is rudimentary at best (Ray & Sunquist 2001), and abundance estimates are unavailable for most species. Mammals of the Western Ghats of India are one such set of species, where, basic ecological information on sympatric species of small carnivore, smaller ungulates such as the Indian chevrotain (*Moschiola memmina*) and larger nocturnal rodents such as the Indian porcupine (*Hystrix indica*) is unavailable.

For several animal species found in the Western Ghats, standard photographic capture-recapture estimation techniques cannot be used since individuals are not uniquely identifiable. For nocturnal and cryptic species among them, even distance sampling cannot be used owing to low detection probabilities and violation of basic survey assumptions. For most small carnivores, visual identification of track and scats is not possible because standard identification protocols are yet to be developed. Even species-level identification using DNA techniques from faecal matter is yet to be developed. This scenario presents a conservation challenge: conventional techniques to monitor abundances cannot be used for a whole suite of non-uniquely identifiable, cryptic and nocturnal species that are ecologically little studied and in some cases seriously threatened.

However, the new occupancy modeling of animal presence data derived from photographic capture techniques might provide solutions for monitoring of these species. This study presents one such attempt. Therefore, although this study involves development of methodology rather than testing of specific ecological hypotheses, it has relevance to

advancing both the scientific understanding and conservation of a variety of rare and endangered animal species in the study area as well as elsewhere in the world.

METHODS

Explanation of notation: In the methods, results and analysis, the following are the notations used.

' p ' is detection probability

' ψ ' is Occupancy rate, or proportion of sites occupied (or 'used').

' λ ' is the average cell-specific abundance.

' r ' is animal-specific detection probability

' T ' is the number of trials

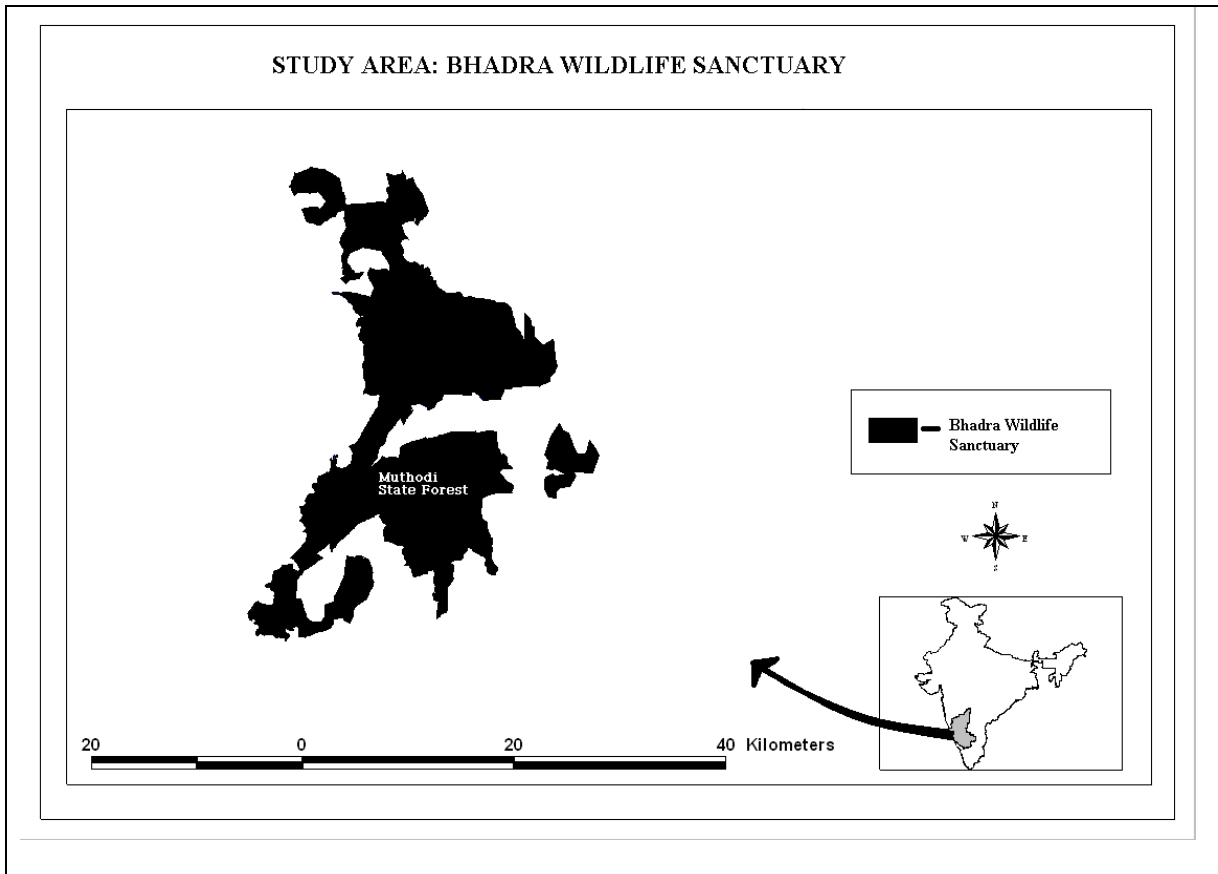
' r ' is the number of sites or cells.

' D_s ' is cluster density

' C ' is Cluster size

STUDY AREA

The 492 km² Bhadra Wildlife Sanctuary is located in the Chikmagalur district of Karnataka State, India. The altitudinal range is 700 m to 1200 m, mean annual rainfall is approximately 1800 mm and the temperature ranges between 15°C to 30°C. The terrain is gently undulating and is drained by tributaries of the Bhadra River, which form the major source of perennial water in the sanctuary. The principal vegetation type is moist deciduous and semi-evergreen forests (Jathanna et al. 2003). I selected a 100 km² area in Muthodi State forest within the sanctuary to conduct the camera trap survey.



SURVEY DESIGN

Occupancy modeling approaches are likelihood-based, and are therefore not small sample procedures (Royle and Nichols 2003). The performance of the Royle and Nichols (2003) model deteriorates at small sample sizes ($R < 100$), and small values of animal-specific detection probability ' r ' (< 0.15) (Royle and Nichols 2003). It is also generally recommended to evaluate different survey designs using simulations tailored to anticipated sampling conditions (Royle and Nichols 2003). It was expected that small carnivores and some nocturnal mammals in Bhadra Wildlife Sanctuary may have low animal-specific detectability (about 0.1 to 0.3 ' r '), and that given logistical constraints, the indicated sample size of 300 to

400 cells could not be surveyed. As a result, a simulation study was carried out prior to field data collection, in order to assess precision and bias in estimates for given sampling effort (number of cells) and trials per cell, keeping in mind target species biology (therefore low expected values of ' r ' and ' λ ').

For this study, ' r ' was expected to be around 0.2.

The total number of cells (200,150, 100, 80, 50, 30); trials per cell (32, 16, 8, 4, 2) and animal specific detection probability ' r ' (0.3, 0.2, 0.1, 0.075) were varied serially for the occupancy model under the Poisson model for abundance. 200 simulations were run using a code developed on R statistical software, for each combination of the above values of total number of cells, number of replicates and animal-specific detection probability and the parameters of ' r ' and ' λ ' were estimated. For all trials ' λ ' was kept at 4. R statistical software was used for running the simulation using a code developed by A.Gopaldaswamy*.

Study Species

I analyzed photographic capture data on the following seven species:

- 1) Small Indian Civet (*Viverricula indica*)
- 2) Stripe-Necked Mongoose (*Herpestes vitticollis*)
- 3) Mouse Deer (*Moschiola meminna*)
- 4) Indian Porcupine (*Hystrix indica*)
- 5) Indian Muntjac (*Muntiacus muntjak*)
- 6) Sambar (*Cervus unicolor*)
- 7) Chital/ Spotted Deer (*Axis axis*)

Field methods

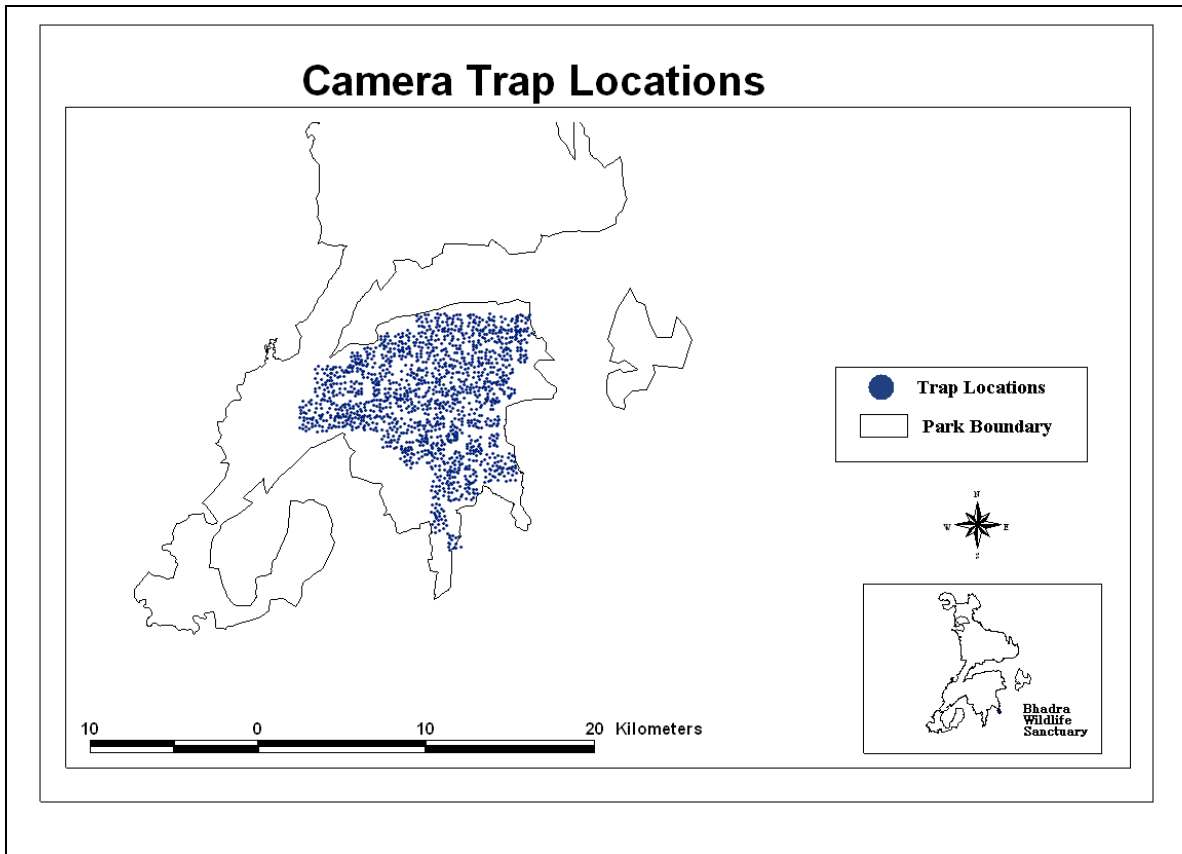
A study area of 100 km² was divided into 100 cells, each of 1 km², with 16 analog type passive detection camera traps deployed per cell. Although there were several target species, with varying home ranges (and consequently cell sizes), a cell size of 1 km² was fixed for camera trapping effort, based on logistical and time constraints, but also keeping species biology in mind (see appendix A).

I used passive analog camera traps, both Deer Cam Scouting Camera DC-200® and Stealth Cam MC2GV ®, for this study. Sixteen camera trap units were placed at locations judged to be optimal for capturing animals in all habitat types encountered within a cell (of area 1 km²), with cameras spaced roughly 130 to 200 m apart.

Geographic locations of traps were recorded using a Global Positioning System (Garmin GPS 60 ®and Garmin GPS 76 ®), and the camera settings were adjusted so that date and time of capture would be imprinted on the film.

Cameras were deployed with the intent of maximizing captures of small carnivores and medium-sized nocturnal mammals, while ensuring adequate spatial coverage. They were therefore placed at ground level, along animal trails, watercourses and streams, with the infrared beam of the unit aligned to 3 cm above ground. Dried fish was used as bait to attract any animals in the immediate vicinity of the camera traps. Cameras were deployed in each cell over one morning, left overnight, and shifted to the next cell the following day. Survey needs of meeting the closure assumption limited the sampling period to one night per cell.

Data were collected from January 2008 to April 2008, with a total of 100 cells and 1529 trap nights across all cells.



Analytical methods

Species such as small carnivores and nocturnal mammals are unlikely to attain high detection probabilities under most circumstances, owing to their cryptic nature, but also due to the duration of sampling per cell in this study. Although likelihood-based estimation is not a small sample procedure, Royle and Nichols (2003) suggest that reliable estimates can be arrived at even at sample sizes of 100 cells and low ' r ', provided that the number of replicates is high.

For this analysis, I relax the assumption of independence of captures obtained between cells, since sampled cells were adjacent to one another, but assumed that average abundance per cell remains constant. Hence the abundance parameter ' λ ' is interpreted as 'average abundance per cell'. Although equal sampling effort is required in each cell to assume constant ' r ', the number of camera traps deployed per cell varied from 11 to 16 owing to occasional camera malfunctions. (See Table 1. for proportion of cells with varying number of cameras). Since all sixteen cameras were deployed at the time of set-up, camera failures were regarded as stochastic events, which could lead to partial sampling, and hence the effect on ' r ' was not modeled. Further, the data shows no consistent trend in reduced detections when number of traps was lower. Hence I assume that estimates of ' r ' are not drastically affected by this occasional, random reduction in trapping effort.

Table 1. No. of traps deployed per cell. Total number of cells = 100

No. of traps deployed (x)	% cells with x traps
16	63
15	14
14	16
13	5
12	1
11	1

I obtained the maximum likelihood estimate (MLE) of occupancy rate for the above species using the constant ' p ' (Mackenzie et al. 2002) model implemented in the software in 'PRESENCE version 2.0' (<http://www.mbr-pwrc.usgs.gov/software/presence.html>).

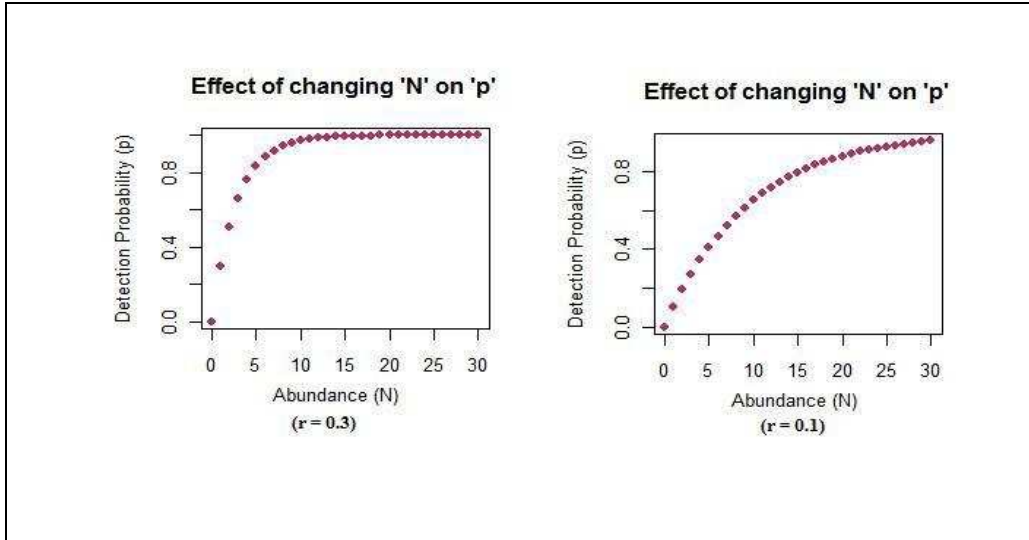
Considering that none of the target species had non-overlapping home ranges, neither were daily movement rates larger than cell sizes except possibly for Sambar (*Cervus unicolor*),

and to avoid the issue of sub-sampling, I used temporal replicates. I evaluated the performance of analyses using 12, 14 or 16 sampling occasions of one hour each (based on the species) as opposed to 6, 7, or 8 of two hours each (respectively), based on the standard errors of estimated parameters, the variance of parameters and covariance between parameters (at lower T values the covariance between ' ψ ' and ' p ' increases), and chose the appropriate model for which to report occupancy rate. Although covariance of estimated parameters increases with a reduction in the number of replicates, replicates of two hours each vis-à-vis one hour each reduces the correlation between trials. Hence wherever possible I chose longer time periods for replicates and remain biologically conservative.

However, it is unlikely that abundance is the same across all sites for these study species. This expected heterogeneity in abundance across sites is likely to induce heterogeneity in capture probabilities. This variation in ' p ' is higher when the animal specific detection probability ' r ' is low, and when site-specific abundance ' N_i ' is low; which is expected to be the case for several of the species considered in this study.

For small values of ' r ', even a small change in ' N ' will result in a large change in ' p ' for values as low as $N < 15$ (see Figure 1.). Clearly, an estimate of occupancy that does not take this into account is likely to underestimate the true occupancy. Hence I ran the heterogeneity (Royle and Nichols 2003) model under an assumption of Poisson distribution in 'PRESENCE' version 2.0, for the chosen number of trials.

Figure 1. Effect of changing abundance on detection probability, when 'r' is low.



AIC (Akaike 1973; Williams et al. 2002) values for the two competing models were compared, followed by checking parameter estimates for possible bias. In general, when 'r' is low, although bias in lambda estimates are not considerable, standard errors are high. In general, the heterogeneity model performed better than the constant p model in almost every case. I further investigated the nature of heterogeneity in abundance by assessing the fit of three candidate discrete probability models (the Poisson, the Negative Binomial and the Zero-Inflated Poisson models) as specified by a suitable discrete probability model. Although the Poisson model for abundance is a good starting point, animals may not be distributed completely randomly in space. In the event of clustering at low animal densities, the zero-inflated Poisson model is likely to better represent the spatial distribution of animals. Hence I assessed the fit of the Poisson and the Zero-Inflated Poisson. In all cases, the negative binomial model provided unreliable results and was not used as a model for inference. For this I used R statistical software, since PRESENCE only allows for the assumption of a Poisson distribution.

I also compared the abundance estimates for Chital (*Axis axis*), Sambar (*Cervus unicolor*) and Muntjac (*Muntiacus muntjac*) obtained from this study with those from distance sampling (Karanth et al., unpublished data), from the Bhadra Wildlife Sanctuary in May 2007. However, since all these species occur in groups, the estimated ' λ ' is interpreted as average number of clusters and not as individuals since the Royle and Nichols (2003) implicitly assumes that all animals are independent, which is not true for ungulates.

For estimated abundances to be converted to densities, the effectively sampled area needs to be calculated lest densities be overestimated (Williams et al. 2002). Typically, a buffer around the trapping grid is added, using information from radio telemetry studies or the mean maximum distance method (MMDM) (Wilson and Anderson 1985; Karanth and Nichols 1998), instead of assuming geographic closure within the trapping grid.

Considering that no home range size information is available for species from this area, and also since traps were placed only for 1 to 2 hours each per sampling occasion, I assume the area of each cell to be the effectively sampled area.

Hence estimated average abundance per cell (λ) is interpreted as density per km² for small carnivores and nocturnal mammals, and as density of clusters per km² for large ungulates. However, it would be preferable to estimate densities using home range size or MMDM based on information available from other studies.

RESULTS

Results of simulation study

There is relatively low bias even for low values of ' r ' (up to 0.075), provided that the number of trials remains high ($T > 5$). However, at ' r ' value of 0.02, even for high number of trials and cells, positive bias in estimates is high. Clearly therefore, for reliable estimates of lambda, ' r ' values must be as high as possible. For simulation results see Appendix B. The number of cells and replicates was decided based on simulation results, target species biology, and logistical constraints, to be 100 cells of 1 km² each.

Based on practical and logistical considerations, more than 150 cells would not have been possible to survey in the given time. Reviewing literature on target and related species indicated that home range sizes were not much more than the cell sizes, and if they were, then cell sizes could be varied post data collection. Simulation results indicated that 100 cells was a sufficient number of cells, provided ' r ' were to be 0.2 or more.

Estimation of Occupancy and abundances

Occupancy and abundance results derived from the analyses are presented species-wise here below. Results for all species are presented in Table 2. Naïve occupancy (detection-non-detection maps) for all species is presented in Figures 2 and 3.

Small Indian Civet (*Viverricula indica*)

The standard errors (SE) of ' ψ ' between $T=12$ and $T=6$ are not significantly different, for the constant p model. There is also no drastic difference in the variance of ' ψ '. Covariance between parameters is not significant either. However, estimated ' p ' value is much higher.

Hence I choose $T=6$. Seasonal home range sizes of Palm Civet and Malay Civet lie between 0.14 and 0.77 km² (Joshi et al. 1995; Colon 2001), which is smaller than the cell size. Hence under the Mackenzie et al. (2002) model, proportion of sites occupied is 0.46 (0.07).

However, AIC values of the heterogeneity model (Poisson) are better than the constant p model. The occupancy estimate from this model is higher 0.53 (0.11), but not significantly so.

Based on AIC and standard errors I choose the Poisson model for abundance. For this model, ' r ' estimates are 0.104 (0.037) and lambda estimates are 0.835 (0.304).

Stripe-necked mongoose (*Herpestes vitticollis*)

The standard errors (SE) of ' ψ ' between $T=14$ and $T=7$ are not significantly different, for the constant p model. Variance in ' ψ ' is nearly double when T is decreased, as is covariance between parameters. Although the estimated ' p ' value is higher, for lower T , I choose $T=14$. Mongooses are known to have very small home range sizes not exceeding 0.6 km². Hence proportion of sites occupied is 0.45 (0.09).

However, the heterogeneity model (Poisson) performs better than the constant p model with respect to AIC values. The occupancy estimate from this model is higher 0.52 (0.11).

Based on AIC values I choose the Poisson model to estimate abundance. For this model, ' r ' estimates are 0.044 (0.016) and lambda estimates are 0.743 (0.269).

Mouse Deer (*Moschiola memminna*)

The standard errors (SE) of ' ψ ' between $T=12$ and $T=6$ are not significantly different, for the constant p model. Variance in ' ψ ' is lower when T is decreased, although covariance is

higher between parameters. Hence I choose $T=6$. A related species, the African water chevrotain is known to have home ranges of $0.13 - 0.23 \text{ km}^2$. Hence proportion of sites occupied is reported as 0.64 (0.16).

By AIC, the constant p model performs better than the heterogeneity model, although the models are competing. This may indicate that abundances across cells are constant. The occupancy estimate from the latter model is 0.78 (0.25).

Based on AIC values I choose the Poisson model. For this model, ' r ' estimates are 0.047 (0.035) and lambda estimates are 1.52 (1.11).

Indian Porcupine (*Hystrix indica*)

The standard errors (SE) of ' ψ ' between $T=12$ and $T=6$ are not significantly different, for the constant p model. Variance in ' ψ ' is marginally higher when T is decreased, as is covariance. Considering no significant difference, I choose $T=6$, in order to reduce correlation between samples. North American porcupines are known to have home range sizes of 0.2 km^2 . Since there is no estimate of Indian porcupine (or more closely related species) home range sizes, I assume that home range size is not higher than 0.6 km^2 in the given habitat. Hence proportion of sites occupied is reported as 0.37 (0.15).

By AIC, the heterogeneity model performs better than the constant p model, although the models are competing. The occupancy estimate is 0.43 (0.2).

Based on AIC and standard error values I choose the Poisson model. For this model, ' r ' estimates are 0.06 (0.042) and lambda estimates are 0.55 (0.37).

Muntjac (*Muntiacus muntjak*)

The standard errors (SE) of ' ψ ' between T=12 and T=6 are not significantly different but high, for T = 8. Variance in ' ψ ' is nearly double when T is decreased, as is covariance although the difference is not significant. Although estimated ' p ' is lower for T =16, considering higher variance for T = 8, I choose T= 16. Average home range sizes of Reeves' muntjac (*Muntiacus reevesii*) are known to be 1.07 km². Hence proportion of sites occupied is reported as 0.54 (0.15).

By AIC, the constant p model performs better than the heterogeneity model although the models are competing. The occupancy estimate for the heterogeneity model is 0.65 (0.23). Based on AIC values I choose the Poisson model. For this model, ' r ' estimates are 0.02 (0.012) and lambda estimates are 1.04 (0.64).

Chital (*Axis axis*)

The standard errors (SE) of ' ψ ' between T=16 and T=8 are not significantly different. Variance in ' ψ ' is nearly marginally lower when T is decreased, although covariance is higher. Estimated ' p ' is higher for T =8, and I therefore choose the more conservative T = 8. Annual home range sizes of chital are known to be between 3.4 and 1.4 km² (Sankar 1994; Moe & Wegge 1994). Hence proportion of sites 'used' is reported as 0.37 (0.13).

By AIC, the heterogeneity model performs better. This is as expected, since Chital are group-living and are found clustered with respect to space. The occupancy estimate for the heterogeneity model is 0.43 (0.19).

Based on AIC values and standard errors, I choose the Poisson model. For this model, ' r ' estimates are 0.049 (0.03) and lambda estimates are 0.558 (0.334).

Sambar (*Cervus unicolor*)

The standard errors (SE) of ' ψ ' between T=16 and T=8 are not significantly different.

Variance values in ' ψ ' are close, although covariance is higher when T is decreased.

Estimated ' p ' is higher for T =8, and I therefore choose the more conservative T = 8. Mean home range sizes of Sambar are known to be between 1.4 and 4 km² (Sankar 1994). Hence proportion of sites 'used' is reported as 0.56 (0.12).

By AIC, the heterogeneity model performs better. The occupancy estimate for the heterogeneity model is 0.66 (0.18).

Based on AIC values and species biology, I choose Poisson model. For this model, ' r ' estimates are 0.05 (0.026) and lambda estimates are 1.09 (0.53).

Table 2. Results fitting Mackenzie et al. (2002), Royle and Nichols (2003) Poisson and Royle and Nichols (2003) Zero inflated poisson model to 100 cells for seven mammal species. Note: only AIC values paired in bold or italics respectively to be compared*.

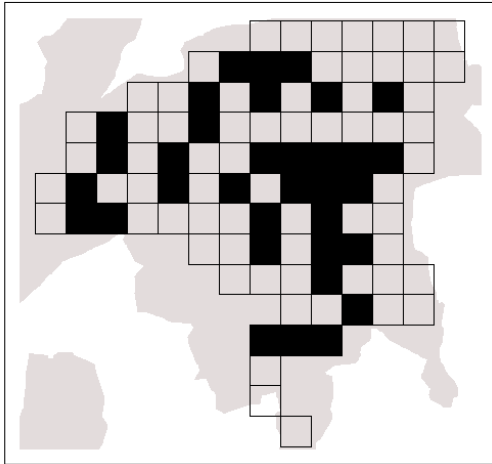
Model	ψ (SE)	p (SE)	var(ψ)	var(p)	r (SE)	λ (SE)	zp (SE)	AIC
Small Indian Civet								
MT12	0.46(0.07)	0.1(0.01)	0.0058	0.0003				
MT6	0.46(0.07)	0.2(0.035)	0.0061	0.0012				355.065
RNT6	0.53(0.1)				0.13(0.03)	0.75(0.22)		353.13
Pois					0.13(0.03)	0.75(0.22)		<i>195.193</i>
ZIP					0.08(0.07)	1.44(2.02)	0.76(0.45)	<i>197.05</i>
Stripe-Necked Mongoose								
MT14	0.45(0.09)	0.07(0.016)	0.0085	0.0003				390.07
MT7	0.52(0.12)	0.11(0.029)	0.0156	0.0009				
RNT14	0.52 (0.11)				0.044(0.015)	0.74(0.25)		387.48
Pois					0.044(0.016)	0.74(0.27)		<i>185.176</i>
ZIP					0.036(0.025)	1.2(1.55)	0.75(0.48)	<i>186.981</i>
Mouse Deer								
MT12	0.69(0.18)	0.05(0.015)	0.0318	0.0002				
MT6	0.64(0.16)	0.11(0.031)	0.0268	0.001				305.768
RNT6	0.78(0.25)				0.048(0.035)	1.52(1.18)		306.125
Pois					0.048(0.035)	1.52(1.11)		<i>174.484</i>
ZIP					0.004(0.0017)	26.34(13.36)	0.65(0.16)	<i>176.076</i>
Porcupine								
MT12	0.34(0.13)	0.05(0.021)	0.017	0.0004				
MT6	0.37(0.15)	0.09(0.04)	0.023	0.0016				175.738
RNT6	0.43(0.2)				0.06(0.04)	0.56(0.36)		175.556
Pois					0.06(0.04)	0.56(0.36)		<i>112.146</i>
ZIP					0.04(0.11)	1.24(5.94)	0.63(1.36)	<i>114.11</i>
Muntjac								
MT16	0.54(0.15)	0.038(0.012)	0.023	0.0002				322.12
MT8	0.62(0.22)	0.062(0.023)	0.046	0.0006				
RNT16	0.64(0.23)				0.02(0.01)	1.04(0.64)		322.424
Pois					0.02(0.01)	1.04(0.66)		<i>152.505</i>
ZIP					0.018(0.031)	3.83(8.48)	0.61(0.33)	<i>154.278</i>
Chital								
MT16	0.39(0.15)	0.035(0.015)	0.023	0.0002				
MT8	0.36(0.13)	0.075(0.03)	0.018	0.0009				200.819
RNT8	0.43(0.19)				0.05(0.03)	0.56(0.34)		199.952
Pois					0.05(0.03)	0.56(0.33)		<i>119.901</i>
ZIP					0.039(0.044)	1.05(2.23)	0.66(0.75)	<i>121.815</i>
Sambar								
MT16	0.54(0.11)	0.054(0.012)	0.013	0.0002				
MT8	0.56(0.12)	0.1(0.024)	0.015	0.0006				345.04
RNT8	0.66(0.18)				0.05(0.027)	1.09(0.55)		344.161
Pois					0.05(0.027)	1.09(0.55)		<i>183.92</i>
ZIP					0.022(0.013)	3.92(2.24)	0.66(0.46)	<i>186.137</i>

M indicates Mackenzie et al. (2002) model, T indicates number of trials, RN is Royle and Nichols (2003) model, Pois indicates Poisson model of abundance, ZIP indicates Zero-inflated model of abundance.

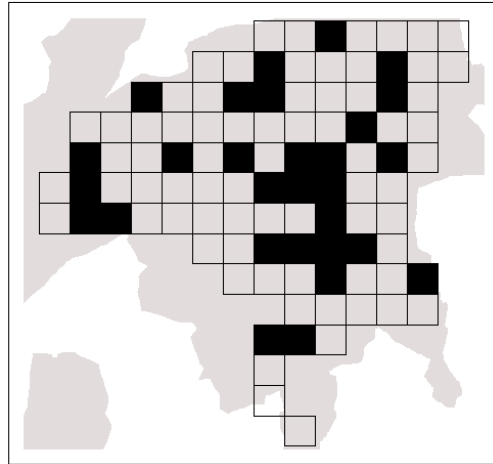
* The deviance ($-2 \times \log\text{likelihood}$) value from PRESENCE is different from the 'optim' engine in R and hence cannot be directly compared.

Figure 2. Naïve occupancy maps (small carnivores and porcupine)

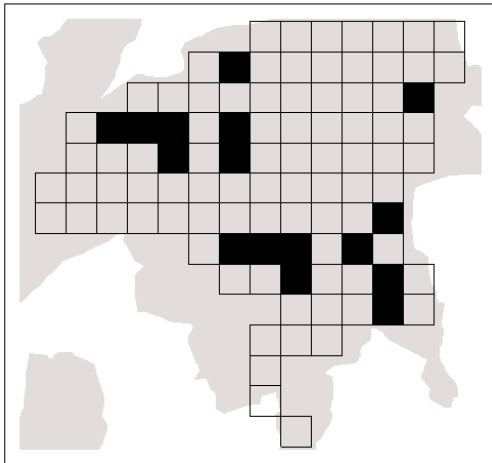
SMALL INDIAN CIVET



STRIPE-NECKED MONGOOSE



INDIAN PORCUPINE



□ NON DETECTION

■ DETECTION

■ PARK BOUNDARY

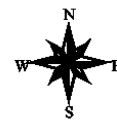
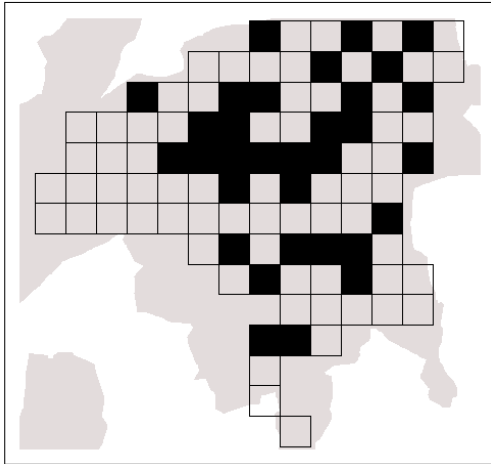
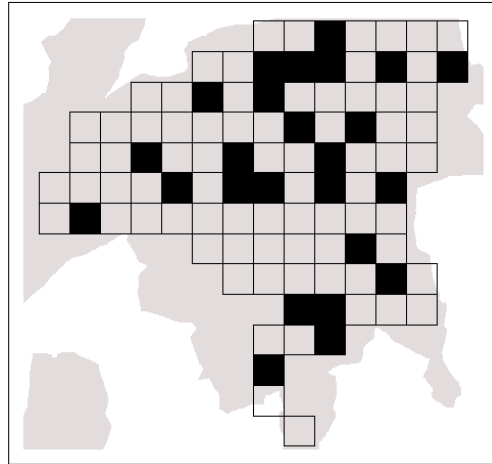


Figure 3. Naïve occupancy maps (ungulates)

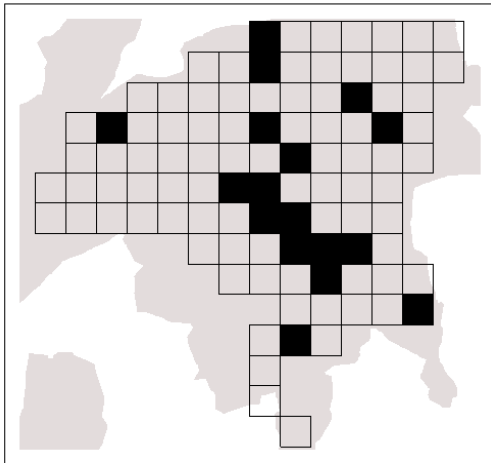
MOUSE DEER



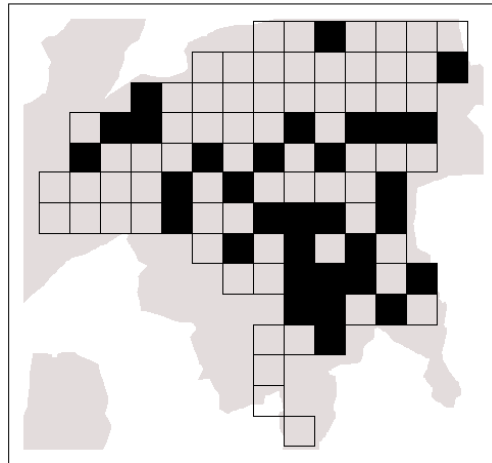
MUNTJAC



CHITAL



SAMBAR



□ NON DETECTION

■ DETECTION

■ PARK BOUNDARY



Comparison across two abundance estimation techniques

I compared ungulate densities (in this case per 1 km²) with results from Distance Sampling surveys conducted in the Muthodi State Forest of the Bhadra Wildlife Sanctuary, in May 2007 (Karanth et al. unpublished). In order to make estimates comparable across space, it is necessary to control for effectively sampled area. Hence, for this study I consider the cell to be adequately covered by trapping effort. Therefore, the estimates represent densities of clusters per km². However, cluster size values are those obtained from Distance Sampling. Results from Distance Sampling provide estimates with smaller standard errors, and therefore, uncertainty in estimates is lower.

Comparison of density estimates from trap-based occupancy and Distance Sampling

Density estimates from distance sampling have lower uncertainty in parameter estimates than those obtained from the trap-based study. Also, in comparing the two methods, the trap based study is underestimating densities of Chital (*Axis axis*) and Muntjac (*Muntiacus muntjak*) considerably. Results are reported in Table 3.

Table 3. Comparison of Distance sampling density estimates to trap-based occupancy estimates.

	Species	Muntjac	Chital	Sambar
Method				
Distance Sampling (Ds (SE) [C])		3.917 (0.858) [1.07]	2.382 (0.829) [4.19]	2.825 (0.696) [1.77]
Trap-based occupancy (N (SE) C)		1.09 (0.55) [1.07]	0.56 (0.33) [4.19]	1.04 (0.66) [1.77]

Ds is density of clusters, C is cluster size.

DISCUSSION

The results of this study show that the occupancy-based Royle and Nichols (2003) model can provide a generally useful tool for the estimation of abundance of non-uniquely identifiable and cryptic species. When parameter estimates have high standard errors (as in this study), uncertainty in estimates is high, and therefore, reliable estimates of absolute abundance may not be obtained. However, it is still possible to arrive at an index of abundance that takes detection probability into account. Such an index is comparable across temporal scales for instance, and can provide important insights into population trends.

In this study, occupancy rate (under both Mackenzie [2002] and Royle and Nichols [2003] models) and abundances of some species were expected to be higher than those estimated. However, low estimates with relatively high standard errors can be expected when ' r ' values are extremely low – such as in this study.

Nevertheless, these results do provide the first abundance estimates for the Small Indian Civet, Stripe-Necked Mongoose, Mouse Deer, and the Indian Porcupine, which will serve as benchmark information against which future estimates from the same area can be compared and refined.

This study shows that the Royle and Nichols (2003) model can indeed be used estimate abundances of a set of species for which conventional methods cannot be used. The use of this model for a suite of species that may not be uniquely identifiable provides a solution to monitoring populations of cryptic and nocturnal species in a systematic and statistically sound manner. However, its use is subject to certain caveats.

Namely, that estimates are likely to improve (lower standard errors) when animal-specific detection probabilities are improved, and also when the number of repeated visits are

increased and more sites (patches, cells) are surveyed. Therefore, it may be possible to obtain a reliable estimate of abundance, index of abundance or occupancy is possible to obtain, if sampling methods are better tailored to species biology and are designed to increase animal-specific detection probability ' r '. When home range sizes or movement rates can be established, densities may also be estimated.

Clearly, the method is not limited to the use in camera traps surveys alone. Other sign-based survey methods can also use similar analyses if animal signs can be reliably used to identify the species of interest. However, sign based surveys must be used with the knowledge that sign may not be directly related to abundance. This combination of direct and sign-based survey methods will increase the applicability of this method to a greater range of field conditions, habitats and species.

If this method can be used in a planned and systematic manner, even photo-trap data of non-target species can be used to estimate reliable indices of abundance rather than relative abundances (see TEAM network 2008). This can therefore empower community monitoring by estimating the most critical state variables, and make inferences based on population monitoring results more powerful.

In the larger conservation context of needs of biodiversity and animal community monitoring, the approach developed in this study appears to hold promise.

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APPENDIX A.

REVIEW OF TARGET SPECIES ECOLOGY

CARNIVORE BIOLOGY

Basic carnivore biology suggests that there is a clear relation between home range size and diet, and carnivores depending on a greater proportion of meat (flesh eaters and omnivores) have larger ranges than insectivores and folivores/frugivores (Gittleman & Harvey 1982). Within a carnivore species, population density is positively correlated with prey biomass (Carbone & Gittleman 2002, Karanth et al, 2003).

MONGOOSES

Most ecological information on mongooses is available from North America and Madagascar, where introductions resulted in the species becoming invasive. Although densities can be expected to be fairly high in such circumstances, basic ecology is not expected to change.

Home range estimates

Home range estimates for Indian grey mongoose (*Herpestes edwardsii*) from the Nilgiri Biosphere Reserve (single individual for a period of four months) was found to be 3.4 to 4.9 hectares (0.039 to 0.049 km²), and an overall range of 0.15 km² (Kumar & Umapathy, 1999).

Small Indian mongoose (*Herpestes javanicus*) in Mauritius was found to have a mean home range of 0.77 km² (0.25 – 1.10) (Roy *et al.*, 2002). Cape grey mongoose home range was found to range between 0.21-0.63 km² (Cavallini & Nel, 1990).

Herpestes auropunctatus, with a large proportion of fruit, vegetation and insects in the diet (0.85), have home ranges of 0.31 km² (Gittleman & Harvey 1981).

Density

Mean estimated density is only available for introduced populations of the small Indian mongoose, and as a result are likely to be higher than densities in range habitats. However, since density estimates from range countries are lacking, these may prove to be helpful priors: 6.4 animals per hectare in St. Croix, 2.4/ha in Jamaica and 4.6/ha in Puerto Rico (Horst *et al.* 2001); or 1.8 animals per hectare using capture-recapture estimates in the West Indies (Corn & Conroy 1998).

Territoriality

Small Indian mongoose are non-territorial, and home range overlap is considerable (Roy *et al.* 2002), as are Cape Grey mongooses (Cavallini & Ned, 1990).

Daily movement rates

Mean movement between captures for the small Indian Mongoose (*Herpestes javanicus*) in the West Indies was found to be 383m for males and 140m for females, and the tendency to return to the same trap was high (18% for males and 40% for females) (Tomich 1969). Cavallini and Ned (1990) found average daily movement rates to range around 80 to 90m for the Cape grey mongoose (*Galerella pulverulenta*). Roy *et al.* (2002) caught up to six different animals at an individual trap within the span of one week. This indicates low daily movement rates.

Activity pattern

Several species of mongoose are known to be diurnal (Prater 1972; Cavallini & Ned 1990; Cavallini 1995)

CIVETS

Home range estimates

A radio collaring study in the Nilgiri Biosphere reserve but in which only one small Indian civet could be tracked for four months (Kumar & Umapathy, 1999), estimated a mean monthly home range of 65 ha (20.69 - 102 ha). These are the only estimates for the small Indian civet in Southern India.

In Chitwan, Nepal, the Common Palm civet (*Paradoxurus hermaphroditus*) was found to have mean monthly home range size of 14.1 ha (Joshi *et al.*, 1995). However Rabinowitz (1991) reported a home-range size 12 times larger than that reported by Joshi *et al.* (1995) in a dry, mixed deciduous and evergreen forest in Thailand (Joshi *et al.* 1995). Palm civets in Thailand are reported to have a home range of 1.1 to 5.9 km² (Grassman 1997). Masked palm civet mean-monthly home range was reported to be 0.74 km² (0.64 – 0.98 km²) (Rabinowitz 1991). Yearly home range sizes for the Malay civet are reported to be 1.1 km² in Sabah, Malaysia (Colon 2001), while estimates in Sulawesi are 0.7 km² (Jennings *et al.*, 2006). Data used by Gittleman & Harvey 1981 suggest African civet (*Nandinia binotata*) home range size to be 0.73 km² (See Gittleman & Harvey 1981).

General carnivore biology and home range estimates from various habitat types indicate that food availability drives home range size.

Density

Estimated Malay civet densities are 1 individual per 0.46 km² in unlogged forests in Sabah (Colon 2001).

Territoriality

Territoriality has not been observed in common palm civet (Joshi et al. 1995), and large home range overlap is reported (48%) (Joshi et al. 1995).

Daily movement rates

Mean daily movement of 0.48 km was observed in Palm Civets in Thailand (Grassman 1997).

Activity pattern

Palm civets (Joshi et al. 1995) and Malay civet (Colon 2001; Jennings et al. 2006) are strictly nocturnal (18:00 to 7:00 hrs), as are most viverrid species.

PORCUPINE

Home range estimates of the North American Porcupine were 20.7 ha for males and 8.2 ha for females (Sweitzer 2003).

Density

Density of Cape porcupine 8 per km² in a semi-arid ranch in South Africa

Territoriality

The Cape Porcupine is suggested to be territorial with small exclusive territories within larger non-exclusive home ranges, and neighbours rarely encounter each other (Corbet & van Aarde 1996).

Activity pattern

Porcupines are known to be nocturnal (Prater 1972).

MOUSE DEER

Very little is known about the ecology and behaviour of the Indian chevrotain with much of the information being in the form of anecdotal observations and sight records (Prater 1971; Krishnan 1972; Raman 2004).

Home range

In the African water chevrotain, males have a home range of 23-28 ha that overlap with more than one female range (13-14 ha) (Dubost 1975; Raman 2004). Research on the south-east Asian greater and lesser mouse deer (*T. napu* and *T. javanicus*) indicates that these species also have relatively small home ranges of between 2 and 12 ha in primary tropical rainforest of Sabah, Borneo (Ahmad 1994 in Heydon and Bulloh 1997; Raman 2004).

Territoriality

Although there is no intra-sexual overlap in home range, territorial defence has not been noted.

Density

There are no published estimates of population densities and population status of the species from India. The African water chevrotain (*Hyemoschus aquaticus*) is known to occur at densities of 7.7 to 28 animals per km² in Gabon (Dubost 2001). Densities of *Tragulus javanicus* and *Tragulus napu* was over 20 animals/km² in primary rainforest in Borneo, but was lower (< 16/km²) in logged forest (Heydon & Bulloh 1997). Densities of *T. javanicus* were correlated with abundance of small fruits whilst density of *T. napu* and biomass of mouse deer were correlated to density of large standing Ficus trees, which are a keystone resource for these mouse deer in times of fruit scarcity (Heydon and Bulloh 1997). Estimates from Sumatra (O'Brien et al. 2003) also estimated densities of these two mouse deer species, at 2.0 to 6.28 animals/km².

MUNTJAC

Home range size

Average home range size of the Reeve's muntjac (*Muntiacus reevesi*) was found to be 107.7 ha (McCullough et al. 2000).

Territoriality

Home ranges and core areas overlapped, and Reeves muntjac were found to be non-territorial (McCullough et al. 2000).

Density

Density estimates (distance sampling) for Bhadra Tiger Reserve is 4.64 (±0.63) muntjac km² (Jathanna et al., 2003), while from Nagarhole National Park is 4.2 muntjac per km² (Karanth & Sunquist 1992).

CHITAL

Home range

In Sariska the mean home range of male chital stag was around 3.5 km², and that of a chital doe was around 2.5 km². The estimated annual home range of a chital doe was around 16 km² (Sankar 1994; Sankar & Acharya 2004). Annual mean home range of chital does in Karnali-Bardia was about 1.4 km², and that of stags was about 2 km² (Moe and Wegge 1994; Sankar & Acharya 2004).

Densities

In the Bhadra Tiger Reserve chital densities were estimated to be 4.51 (± 1.05) chital km⁻² (Jathanna et al. 2003).

SAMBAR

Home range

In Sariska (Sankar 1994; Sankar & Acharya 2004), the mean home range of Sambar stags was around 4 km² and for hinds was 1.7 km². In Florida the estimated mean home range of stags was around 11 km² and hinds nearly 6 km² (Shea et al 1990; Sankar & Acharya 2004).

Density

In Bhadra Tiger Reserve, density estimates are 0.89 (± 0.23) Sambar/km² (Jathanna et al., 2003).

APPENDIX B

Simulation Results: Simulation to assess effect of R and T on estimates of lambda. True lambda value was given to be 4. All trials were run for 200 simulations.

R	T	R	estimated λ	Lcl λ	Ucl λ
200	8	0.6	3.819	3.163	4.456
200	8	0.3	3.866	3.240	4.446
200	8	0.15	4.124	3.024	6.134
200	8	0.075	4.509	2.633	8.307
200	8	0.02	5.590	1.463	11.592
200	4	0.6	4.271	3.301	7.325
200	4	0.3	4.124	3.058	5.709
200	4	0.15	4.497	2.542	9.493
200	4	0.075	5.414	2.207	11.604
200	4	0.02	5.225	1.082	11.315
200	2	0.6	4.406	3.004	7.823
200	2	0.3	4.667	2.646	10.063
200	2	0.15	4.948	1.901	11.444
200	2	0.075	5.009	1.248	11.317
200	2	0.02	5.673	0.503	10.738
150	10	0.6	3.878	3.282	4.490
150	10	0.3	3.957	3.308	4.552
150	10	0.15	4.194	3.001	6.243
150	10	0.075	4.657	2.950	9.542
150	10	0.02	5.116	1.470	11.832
150	5	0.6	3.858	3.278	4.430
150	5	0.3	3.765	2.923	4.441
150	5	0.15	4.503	2.646	9.545
150	5	0.075	4.662	2.163	10.853
150	5	0.02	6.277	0.950	11.566
150	3	0.6	4.332	2.932	6.791
150	3	0.3	4.443	2.913	8.258
150	3	0.15	4.526	2.113	10.655
150	3	0.075	5.436	1.593	11.882
150	3	0.02	6.426	0.635	11.030
100	16	0.6	3.947	3.014	4.629
100	16	0.3	3.903	3.063	4.648
100	16	0.15	3.860	3.118	4.596
100	16	0.075	4.651	2.642	4.651
100	16	0.02	5.069	1.798	11.936
100	8	0.6	3.876	3.020	4.680
100	8	0.3	3.884	2.904	4.701
100	8	0.15	4.446	2.598	8.444
100	8	0.075	4.878	2.437	11.186
100	8	0.02	6.376	0.973	11.991
100	4	0.6	3.803	3.077	4.502
100	4	0.3	4.270	2.821	7.476
100	4	0.15	4.551	2.286	10.929
100	4	0.075	6.005	1.913	12.444
100	4	0.02	5.876	0.634	11.553

100	2	0.6	4.934	2.840	11.850
100	2	0.3	5.133	2.180	11.819
100	2	0.15	5.836	1.752	12.041
100	2	0.075	5.722	0.802	11.782
100	2	0.02	5.989	0.255	10.789
80	20	0.6	3.907	2.762	4.844
80	20	0.3	3.911	3.019	4.767
80	20	0.15	3.835	3.000	4.595
80	20	0.075	4.578	2.855	9.089
80	20	0.02	5.873	1.921	12.589
80	10	0.6	3.838	2.971	4.677
80	10	0.3	3.867	3.056	4.674
80	10	0.15	3.791	2.809	4.895
80	10	0.075	4.619	2.336	9.729
80	10	0.02	6.282	1.371	12.442
80	5	0.6	3.914	3.112	4.605
80	5	0.3	3.744	2.460	4.628
80	5	0.15	3.511	2.254	4.505
80	5	0.075	6.084	2.030	12.481
80	5	0.02	6.354	0.623	11.800
80	3	0.6	4.806	2.807	11.666
80	3	0.3	5.094	2.713	12.688
80	3	0.15	5.411	1.756	12.438
80	3	0.075	5.988	1.399	12.222
80	3	0.02	7.171	0.568	11.286
50	32	0.6	3.974	3.241	4.978
50	32	0.3	3.872	2.756	5.121
50	32	0.15	3.919	2.713	4.954
50	32	0.075	4.052	2.715	5.009
50	32	0.02	5.206	2.053	11.921
50	16	0.6	3.950	2.667	4.912
50	16	0.3	3.957	2.954	4.933
50	16	0.15	3.901	2.660	4.996
50	16	0.075	3.836	2.343	4.929
50	16	0.02	6.330	1.560	12.798
50	8	0.6	3.836	2.845	4.847
50	8	0.3	3.874	2.782	4.840
50	8	0.15	3.829	2.670	4.772
50	8	0.075	3.543	1.909	2.670
50	8	0.02	7.146	0.908	12.295
50	4	0.6	3.822	2.790	4.643
50	4	0.3	3.849	2.574	4.826
50	4	0.15	5.892	1.922	2.574
50	4	0.075	5.800	1.654	12.798
50	4	0.02	2.487	0.477	3.635
50	2	0.6	5.538	2.464	12.297
50	2	0.3	5.334	2.051	11.901
50	2	0.15	6.672	1.504	12.322
50	2	0.075	5.371	0.836	11.996
50	2	0.02	7.711	0.125	11.001

' r ' is the number of cells, 'T' is the number of trials and ' r ' is the animal-specific detection probability.

APPENDIX C

Species captured in camera traps



Brown Pam Civet (*Paradoxurus jerdonii*)



Common Mongoose (*Herpestes edwardsii*)



Leopard Cat (*Prionailurus bengalensis*)



Sambar (*Cervus unicolor*)



Smooth-coated Otter (*Lutrogale perspicillata*)



Chital (*Axis axis*)



Tiger (*Panthera tigris*)



Leopard (*Panthera pardus*)



Elephant (*Elephas maximus*)