CHAPTER 2

METHODS: DEVELOPMENT OF A HIERARCHICAL SPATIAL MODEL TO ASSESS VARIATIONS IN UNGULATE ABUNDANCE
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SUMMARY

1. Most studies investigating animal abundance and its environmental drivers typically rely on animal count data that are produced by interactions between ecological and spatial processes of interest. However, these counts are also biased by imperfect detections induced by the observation process itself. Reliable models of animal abundance patterns, which can deal with all these important sources of variation integrally are, however, rare. I address this issue by developing a hierarchical model of animal abundance that can rigorously investigate ungulate abundance patterns with due consideration for ecological, spatial and observation processes.

2. I use a hierarchical formulation with two model components: one describing the ecological/spatial processes that determines ungulate abundance and the other addressing the imperfect observation process involved in the field survey. I used a Bayesian Poisson regression model to establish the effects of a set of habitat-related factors (predictor variables) on ungulate species abundance (response variable). I augmented this model with a Gaussian Conditional Autoregressive (CAR) prior to include spatial interaction effects. The hierarchical model permitted specification of covariate effects on
abundances at local as well as landscape levels. Standard half-normal detection function was used to model the observation process. The observation model also included cluster size as an individual covariate affecting the detectability of animal-clusters. This model was implemented in freeware WinBUGS.

3. I illustrate the application of this hierarchical spatial model to describe the variation in the local abundance of chital deer (*Axis axis*) in Nagarahole-Bandipur, using Distance sampling data obtained from six temporally replicated surveys conducted on foot from 77 line transect samplers placed across a 1400 km² study area. The resulting count data were used to estimate chital abundance within each cell of a 1-km² grid superimposed over the landscape. Because visual detection probabilities of clusters of chital from transect lines are positively influenced by cluster size I used a zero-truncated Poisson distribution for modeling variations in cluster size.

4. Forest vegetation type, forage availability, distance to water sources, flatness of terrain, habitat-disturbance and effectiveness of protection (patrols) were considered as important predictors of local chital abundance. The model fitted the survey data well and predicted correctly that chital densities were highest at sites located on flat terrain, in moist deciduous forests with ready access to water. Results also confirmed the positive association between chital abundance and effectiveness of protection. The model was found useful to reliably
predict and map chital abundance across the landscape as well as to identify ‘hotspots’ of high local densities for informing management actions.

5. *Synthesis and applications:* The flexible structure of the above hierarchical spatial model is useful for reliably understanding ungulates-habitat relations, particularly in the context of typically sparse count data. The model is of utility for investigating the spatio-temporal dynamics of ungulate populations in a wide variety of sampling situations, where the observed count data follow a multinomial distribution and imperfect detections pose a major problem.
2.1 Introduction

Most studies investigating patterns of animal abundance and their associated drivers typically rely on count data (Williams *et al.* 2002). Variations in the count data (numbers of animals or animal-clusters) are typically induced by three primary sources: (1) the ecological process where animals respond differently to various habitat conditions (Brown *et al.* 1995), (2) the observation process where detectability of the animals is affected by several factors including animal cluster size, observer’s efficiency, screening effect of vegetation, etc (Buckland *et al.* 2001), and, (3) the spatial process where counts from any two neighboring points in space are more similar due to auto-correlation in bio-physical factors and their associated animal densities (Legendre 1993). Thus, the count data used to investigate species-habitat relations are a combined product of these sources of variations. There are well developed tools to model each one of these processes individually (McCullagh and Nelder 1989; Legendre 1993; Buckland *et al.* 2001, 2004; Pollock *et al.* 2002; Dormann *et al.* 2007; Thomas *et al.* 2010).

Ungulate densities typically tend to be low because of large body size and hence substantially high energy requirements (Eisenberg 1980; Hudson 1984). Therefore, ungulate count data are typically sparse at the level of individual sampling unit, say, a transect line (Buckland *et al.* 2001). Imperfect detection further reduces sample sizes. Such sparse data
make it difficult to draw strong inferences about ungulate abundance at local scale.

One way to resolve this problem is to pool observations across the sampling units for modeling detectability to correct the aggregated total count. However, such pooling of spatially indexed data results in loss of information on the variation in count data arising from ecological and spatial processes. Thus the resultant abundance estimate is simply an adjusted overall count corrected for imperfect detection (Royle and Dorazio 2008). Conversely, methods that effectively investigate the influence of ecological and spatial factors on animal density often use ‘naïve’ estimators, which ignore the partial detectability of animals (Royle et al. 2007). Such practices yield a biased representation of factors that influence animal density, which may even lead to false conclusions about the underlying ecological relationships between animal density and environment variables (Gu and Swihart 2004; Royle et al. 2004).

Recent methodological approaches (Royle 2004; Royle et al. 2004; Royle and Dorazio, 2005, 2008; Joseph et al. 2009) permit these different sources of variation in animal count data to be incorporated into a single hierarchical modeling framework to draw more reliable inferences about species-habitat associations. A hierarchical model is an ordered series of models that explicitly build relationships between the biological process
and observation or other sampling processes. In this modeling framework, information obtained at the level of individual sampling unit is used to specify models of abundance and detectability, and, to describe variation in abundance and detectability among sample sites. The abundance and detectability parameters are then linked to produce a model-based aggregation of the data to draw inferences about animal density as well as factors influencing its spatial variation. Such hierarchical models are being increasingly used to estimate abundance from simple binomial count data (Royle 2004), point transect data (Royle et al. 2004), removal sampling data (Royle and Dorazio 2005; Dorazio et al. 2005), presence-absence data (Royle et al. 2007), aerial waterfowl census data (Royle 2008) and capture-recapture data (Royle et al. 2009a, 2009b). These approaches can also explore influence of local habitat factors and management interventions.

In this chapter, I use these innovative statistical tools to develop a hierarchical model to estimate ungulate densities from line transect data. I first provide a brief overview of the hierarchical modeling approach highlighting its advantages over other potential approaches. I then identify various components that are required for modeling ungulate density using line transect data and describe model formulation in detail. I use Bayesian inferential approach (Gelman et al. 2004; Banerjee et al. 2004; Link and Barker 2010) and implement the hierarchical spatial
model in WinBUGS, freely available and widely used software for Bayesian analysis. I demonstrate how a simple and yet flexible structure of hierarchical models can effectively deal with all the complexities involved in modeling the spatial variation of ungulate density. This chapter also discusses the applicability of the model developed here for a variety of other sampling situations that typically yield multinomial data. I finally illustrate the application of this model by assessing habitat relationships of chital deer *Axis axis*, based on line transect survey data for the Nagarahole-Bandipur landscape in India.

### 2.2 Model philosophy

#### 2.2.1 Overview of Distance sampling method

Distance sampling is a class of methods to estimate population density of animals (see Buckland *et al.* 1994; Williams *et al.* 2002 for reviews). Line transect sampling is a specific Distance sampling formulation which is particularly useful for assessing the abundance of diurnal ungulates (Thomas and Karanth 2002). Under this method, observers typically survey the area of interest by traversing several spatially replicated lines called ‘transects’ to detect, identify and count animals usually in clusters of one or more individuals which are visually detected from the line. They will also record distances from the point of observation on transect to animal-clusters detected on either side. In a standard line transect survey the data consists of a set of such radial distances and sighting angles,
which are thereafter used to compute perpendicular distances ($x_i$) to observed animal-clusters. These distance data are then used to model and estimate the detection probability to adjust the counts and derive density of animal clusters (Buckland et al. 2001). The classical derivation of the density estimator in Distance sampling is based on the probability that a detected animal-cluster is directly on the transect line and this conditional probability is estimated from the probability density function of observed perpendicular distances (Buckland et al. 2001). The Distance sampling method uses partial likelihood approaches (Burnham et al. 1980; Buckland et al. 2001) to estimate perpendicular distance distribution function and the value of this function when the perpendicular distance is 0 (i.e., when the observed animal-cluster is directly on the transect line). The Distance sampling method also provides several options to reduce bias and improve precision of this estimate (Buckland et al. 2001; Buckland et al. 2004). For example, design-based solutions are provided to ensure random placement of transects (Strindberg et al. 2004). Another example is to include several covariates (e.g. survey season, cluster size, habitat type etc) to model multiple sources of heterogeneity on the detection process (Marques et al. 2007).

Thus, the conventional Distance sampling method using conditional likelihood approaches (Burnham et al. 1980; Buckland et al. 2001) assumes that the sampling process itself is the source of all uncertainties.
Hence, the strategy is focused on modeling the distance component of the count data, emphasizing the choice of sampled sites (i.e., transects), which need to be randomly and independently placed with reference to the sampled animal population. This approach avoids the prior specification of a probability model for the distribution of animals, which has an influence on the count statistic obtained (Buckland et al. 2001). While pointing out the advantages of this conditional likelihood (design-based) approach for estimating density, however, Buckland et al. (2001) note the difficulties involved in developing a fully model-based inferential approach. Such an approach involves a full likelihood analysis based on the joint distribution of the observed distances and animal-clusters. However, some recent advances can now deal with this problem (Hedley and Buckland 2004; Royle et al. 2004).

2.2.2 Model-based inferential approaches

Instead of just obtaining a single estimate of overall animal density from an area, ecologists and managers are more often interested in the spatial variation of animal density within that area (Brown et al. 1995). Such variations in animal densities might be induced systematically by several different environmental factors as well as by stochastic processes (Royle and Dorazio 2005). We may also be interested in predicting animal densities at un-sampled locations using just data from sampled locations and their relationship to relevant habitat covariates. Conventional
Distance sampling approaches, however, are inadequate to investigate such responses of animal populations to habitat factors because of their inability to probabilistically model the underlying spatial distribution of animals or variations in abundance within the surveyed regions. In contrast, fully model-based inference (Link and Barker 2010) proceeds with the assumption that the distribution of all possible realizations of the value of the sample counts can be described by a stochastic model with or without covariates (Royle and Dorazio 2005, 2008). Further, unlike in conventional approaches that treat local density estimates and effects of habitat on them as fixed quantities, the fully model-based approaches can build uncertainty into the estimation of all these model parameters by specifying underlying probability distributions (Ellison 2004). This can truthfully represent that only the observed data are fixed and all the model parameters are random outcomes, thus leading to unbiased predictions. However, such complex models involve unconditional likelihood formulation, which are computationally intensive and often intractable. This hindered wide-spread implementation of these complex models until recently. The advent of faster computers with powerful processors coupled with availability of new modeling and estimation software tools have changed this situation. Consequently use of fully model-based analysis of ecological problems has been increasing.
2.2.3 Hierarchical models

Hierarchical models provide a powerful framework for implementation of fully model-based inferential approaches in ecology. Instead of focusing entirely on either the observation process (disregarding the ecological process) or the ecological process (disregarding the observation and other sampling processes), hierarchical models follow a “conceptual middle ground” to describe explicitly the relationship between observations and biological processes in a single cohesive framework (Royle and Dorazio 2008). Hierarchical models typically have two or more linked constituent models describing the variation in data due to variation in the biological process of interest as well as variations induced by imperfect observation of this process. In the following sections, I describe the formulation of a hierarchical model to describe the variation in ungulate densities arising from variation in its habitat attributes (quantitative representation of the ecological process influencing ungulate densities) as well as from imperfect observation of the state variable (abundance).

2.3 Model development

2.3.1 Motives and considerations

Forest ungulate species in the study area typically occur in clusters consisting of one or more individuals (see Chapter 1 for details). They are typically diurnal and relatively easily detected visually. Ungulate densities are influenced by a variety of environment factors including
overall forest vegetation type, proximity to water availability, human impacts on habitat etc (see Chapter 1 for a detailed discussion). Some of these factors may have influences that extend over the entire landscape (e.g. forest type of the study area), whereas others may have very localized influence (such as a forage patch). Hence, exploration and quantification of these ungulate-habitat relations at different spatial scales together with plausible prediction about animal density at individual locations will be useful for planning and assessing specific management actions.

I considered count data from spatially explicit transect lines that adequately cover the entire study region for modeling ungulate-habitat relations. Following Levin (1992), I defined each of the transect lines as a “site” and the study region as the “landscape” for the purposes of investigating influence of covariates on ungulate abundances at two distinct spatial scales. I interchangeably use the terms “site-level” with “local scale”, and, “landscape-level” with “broad scale”, respectively, depending on the context. Several potential explanatory variables were identified a priori at these two spatial scales. Site-level (local scale) covariate data were collected from each transect line, while the landscape-level (broad scale) covariate data were collected for each of the 1-km grid square laid across the study region. My primary objective was to use both site-level and landscape-level covariate data to explain variations in
ungulate abundance manifested through transect-specific (site-level) ungulate count data. However, I recognized that the ungulate counts were an outcome of a combined process that included observation and spatial processes in addition to the ecological process of my interest. These were my primary motives for developing a hierarchical model of abundance for the study species.

2.3.2 The Model formulation

The process component of the hierarchical model of animal abundance consists of an abundance model that specifies the ecological process underlying the distribution of animals in space. The second component is the observation model describing the sampling process. Line transect sampling is a widely used method for counting ungulates while effectively accounting for the partial observability of the ungulates. Hence, I used the basic modeling structure described by Royle et al. (2004) to model spatial variations in abundance values derived from line transect data.

I used cluster size as the detection-related covariate in addition to the perpendicular distance to describe the observation process. The abundance model consisted of several variations of the Royle et al. (2004) basic model, in order to describe effects of ecological factors on ungulate abundance at different spatial scales. This model is further updated to
incorporate effects of spatial interactions and to account for variation in sampling efforts. I show here how the model structure is flexible and accommodates additional structures to build a realistic spatial model of animal abundance that can be implemented in freely available WinBUGS software package (Spiegelhalter et al. 2007).

I will first introduce the notations used to describe the hierarchical spatial model and then present detailed formulation of the model itself.

NOTATIONS USED

$N =$ Abundance of animal-clusters in the study region

$n =$ Abundance of animal-clusters in transect $i$

$y_i =$ Count of animal-clusters detected out of $n$ animal-clusters present in transect $i$

$x_i =$ Perpendicular distance derived for each of the detected $y_i$ animal-clusters

$l_i =$ Total distance walked in transect $i$

$g(x) =$ Probability of observing an animal-cluster given it is at distance $x$ from a transect

$gs(k) =$ Probability of the cluster size of the animal-cluster in cluster size category $k$

$p_{ijk} =$ Probability of observing an animal-cluster in distance class $j$ under cluster-size category $k$ in transect $i$
\( \lambda_i \) = Expected abundance of animal-clusters \((n)\) in transect \(i\)

\( s_{ij} \) = Value of a transect-level (site-level) covariate \(j\) measured at transect \(i\)

\( \alpha_j \) = Regression coefficient of transect-level covariate \(j\)

\( w_{ai} \) = Indicator variable for each of the transect-level covariate effect

\( z_k \) = Expected abundance of animal-clusters \((N)\) in grid-cell \(k\)

\( g_{jk} \) = Value of a grid-cell level (landscape-level) covariate \(j\) at measured at grid-cell \(k\)

\( \beta_0 \) = Value of regression slope (intercept)

\( \beta_j \) = Regression coefficient of grid-cell level covariate \(j\)

\( b_k \) = Value of random spatial effects for grid-cell \(k\)

\( w_i \) = Indicator variable for each of the grid-cell level covariate effect

### 2.3.3 Observation model

Let \( N \) represent the abundance of animal-clusters in the study region and \( n \) to the transect-level (site-level) abundance of animal-clusters. The basic data resulting from a line transect survey is a set of \( x \) distances recorded on \( y \) animal-clusters ‘detected’ out of \( n \) animal-clusters present along a set of transect lines. Each transect line is typically walked a number of times in Distance sampling surveys and the observed counts \((y)\) resulting from all temporal replicates under each transect are pooled (Buckland et al. 2001). Let \( i = 1, 2, ..., M \) index the number of sites (transect lines) that
were sampled within the survey area and let $j = 1, 2, \ldots, J$ index the distance classes in which distances to the ‘detected’ animal-clusters were recorded. Note that the distance measured is often exact and hence a continuous variable, but it can be assigned to discreet distance classes for computational ease. Also, ‘binning’ of exact distances into a large number of distance classes with a narrow class interval is a good approximation of the continuous distance function, which is in contrast to many applications where data are collected into very coarse bins. Thus, the outcome from a transect survey $y_{ij}$ is the observed counts of animal-clusters in distance class $j$ for site $i$ and this data typically follows a multinomial distribution. The following data table illustrates the data structure:

<table>
<thead>
<tr>
<th></th>
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<th></th>
</tr>
</thead>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
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<td>3</td>
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<td>0</td>
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<td>0</td>
</tr>
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<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>T[4]</td>
<td>15</td>
<td>4</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>T[5]</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
</tbody>
</table>

In the above example, there are 10 distance classes (say with a class interval of 15 m) represented by columns X[1] to X[10] and 5 transect lines represented by rows T[1] to T[5]. Each cell represents observed counts of animal-clusters in each transect line under each distance class. The multinomial probability of observing animal-clusters is a function of various parameters that describe the observation process.
Following Royle et al. (2004), the distribution of observed counts and its dependence on detection probability \(p\), transect-level abundance \(n\), and landscape-level abundance \(N\) can be expressed as follows:

\[
[y \mid n, p] = \text{Multinomial}(y \mid n, p)
\]

and

\[
[n \mid N, p] = \text{Binomial}(n \mid N, p)
\]

Distance from transect line and cluster size are the two important parameters that influence detectability of animal clusters (Thomas and Karanth 2002) and I assume that both are independent random variables. The multinomial cell probability \(p\) is a product of these two variables. In this section, I describe modeling of detectability as a function of distance from line transect and in the next section, I deal with the cluster size component.

One of the most widely used detection functions to model the relationship between detection probability and distance observed is the “half-normal” detection function (Buckland et al. 2001). The half-normal detection function uses the probability density function of perpendicular distances \(x\) to estimate detection probability \(g(x)\), which is given by the expression:

\[
g(x) = \exp\left(-\frac{x^2}{\sigma^2}\right), \quad \text{following Buckland et al. (2001).}
\]
detection probability is a declining function of distance from the transect line.

2.3.4 Modeling the effects of cluster size on detectability models

Ungulates cluster size influences their detectability from the transect line (Buckland et al. 2001; Royle 2008). Although exact cluster sizes observed were recorded in the field survey I classified them into discrete categories, because the construction of a large multinomial data matrix (the number of animals observed in each cluster size in each distance category) would be unwieldy (Royle 2008), especially for gregarious species like chital, in which cluster size can range up to 100 individuals (Karanth and Sunquist 1992). I assumed these cluster sizes to follow zero-truncated Poisson distribution, because all cluster sizes must necessarily be \( \geq 1 \). The probability of the cluster size \( gs(k) \) in a cluster size category \( k \) is given by the statistical expectation of the truncated Poisson distribution:

\[
gs(k) = \frac{1}{1 - e^{-\lambda}} \cdot \frac{\lambda^k \cdot e^{-\lambda}}{k!}
\]

The data table now is a three-dimensional matrix that provides observed counts of animal-clusters in each distance class under each cluster size category for each transect. I illustrate the data structure for the combined detection function using the example of observed counts from one of the transect lines given earlier for distance function.
In the above example, rows gs[1] to gs[4] represent cluster size categories and 10 distance classes are represented by columns X[1] to X[10], as earlier. Each cell now represents observed counts of animal-clusters in each distance class under each cluster size category for transect line T[4]. Such cluster size count data will follow for all the transect lines. The multinomial probability of observing animal-clusters in any transect line is now a function of both distance class and cluster size category.

I now modeled the $\sigma$ (sigma) parameter in half-normal detection function such that detectability is an increasing function of cluster size and a decreasing function of distance from the transect line. The multinomial probability ($p_{ijk}$) is now the detection probability of an observed animal-cluster in distance class $j$ in cluster size category $k$ for transect line $i$.

2.3.5 Abundance Model

Unlike the conditional likelihood of observations that is conventionally used to estimate abundance in Distance sampling, I used the approach developed by Royle et al. (2004), which is based on the joint distribution
of observations and detection parameters, as my primary interest is in modeling the spatial variations of $N$ due to habitat-related covariates. This unconditional likelihood approach also enables establishment of explicit linkages between abundance and covariates that induce variation in it at both local and landscape-level scales (Royle et al. 2004; Royle and Dorazio 2008). The modeling structure for the ungulate abundance model is described below.

Count data are typically discrete and positively valued. They show strong mean-variance relationships, which are useful statistical properties (Royle et al. 2002). I used the Poisson distribution to model local abundance and assumed $[N_i|\lambda_i] = \text{Poisson}(\lambda_i)$, where $\lambda_i$ is the expected abundance of animals that are available for detection in site (transect) $i$. In the simplest model, one can assume a constant expected abundance over all sampled sites (transects) such that $\lambda_i = \lambda$. This model describing an unvarying abundance across transect lines (sites) together with the observation model (described in the preceding section) forms a basic 2-level hierarchical model and the estimator of abundance is based on the joint likelihood of observations and detection parameters. This model can be easily expanded to incorporate a set of variables, which are expected to induce variations in animal abundance.
This simple hierarchical model is similar to the conventional line transect estimator which assumes that animal-clusters are uniformly distributed with respect to their distance from transect line (Buckland et al. 2001). The only difference is that the abundance estimator in line transect sampling is based on the conditional likelihood of detection distances to the observed animal-clusters, while the model formulated here estimates abundance based on the unconditional likelihood of observations and detection parameters.

2.3.6 Modeling effects of site-level covariates on abundance

In reality however, ungulates (or most other animals) are not uniformly distributed in space. Variation in their densities is likely to be induced by habitat-related covariates that influence densities at both local (transect level) and broad-scale (regional) levels. I will first consider the effect of site-level covariates (e.g. forage quantity) that affect abundance locally at the level of sample sites (transects). Site-specific expected abundance $\lambda_i$ can be modeled as a function of a set of $s$ covariates and I use a Poisson regression formulation to describe variation in local abundance among sample sites (transects). The Poisson intensities will now take the form of $\lambda_i = \exp(\sum_{j=1}^{J} \alpha_j s_{ij})$, where $s_{ij}$ is a matrix of site-specific covariates and $\alpha_j$ is the corresponding vector of $J$ regression coefficients.
2.3.7 Modeling effects of landscape-level covariates on abundance

While the above model specifies $\lambda_i$ (a set of site-specific expected abundances over $i$ sample sites) as a function of site-specific covariates, my main interest is to estimate ungulate abundance (response variable) over the survey area, and explain its variation as resulting from a set of broad-scale habitat factors. To address this problem, I will first consider the population of animals over the area of interest as an aggregate of the populations drawn from each of the sites. If $k$ equal sized grid-cells can be super-imposed covering the entire survey region, the total population $N$ can be thought of as a collection of local populations from each of the $k$ grid-cells ($N=N_1+N_2+...+N_k$). Typically, a sample site (individual transect line) cuts through several grid-cells of 1 km$^2$ size. Thus, the site-specific expected abundance $\lambda_i$ is itself an aggregate of these cell-specific abundances covered by transect $i$.

Several factors including physical (e.g. water availability), environmental (e.g. forest vegetation type) and management attributes (e.g. protection effectiveness) vary across space and are thus likely to influence local ungulate abundances. These, grid cell-specific abundances can be assumed to follow a probability distribution conditioned by some landscape-level (grid-cell specific) covariates which induce variations across the survey region. I used a Poisson regression formulation (under the class of generalized linear models) in the form of
log(\(z_k\)) = \(\beta_0 + \sum_{j=1}^{l} \beta_j g_{jk}\) as a reasonable way to model this effect of landscape variables on the expected number of animals in each grid-cell. Here, \(z_k\) is the expected abundance of animals in the \(k\) grid-cell, \(g_{jk}\) is the value of the \(j\) landscape covariate measured at grid-cell \(k\), \(\beta_0\) is the intercept and \(\beta_j\) is the regression coefficient of the \(j\) covariate. Note here that the notation used for the Poisson intensities for each grid-cell \((\lambda_k)\) is different from the Poisson parameter for each site \((\lambda_i)\) and that \(z_k\) has been log-transformed to ensure that the abundance parameter is positive valued.

2.3.8 Modeling spatial effects

The abundance model described above accounts for the structured variation in count data expected due to local (site-level) and landscape (grid-cell specific) covariates. However, the response variable (i.e., grid-cell specific animal abundances) will be spatially autocorrelated (Cressie 1993, Haining 2003) because of a suite of both known (e.g. autocorrelated environment features) and unknown (unobserved or random spatial effects) reasons (Legendre 1993). Spatial regressive models effectively deal with spatial autocorrelation (Besag 1974) and are increasingly used by ecologists to specify spatial relations. Conditional Autoregressive models (CAR) are particularly recommended (Cressie 1993), as they provide a useful framework to model the response variable not only as a
function of predictor variables but also conditional on the value of response variables in neighboring locations (Cressie 1993, Haining 2003). Thus, in a CAR model, if a grid-cell \( k \) is surrounded by neighbors whose abundance values are high based on \( j \) habitat covariates, then the abundance at \( k \) grid-cell will be higher than what is expected based on the covariate effect alone, when there is positive spatial autocorrelation. Neighborhood is usually identified by the adjacency of cells in the grid map and the neighborhood structure is expressed in the form of an \( n \times n \) matrix of spatial weights with its elements representing the neighborhood relation. Typically, this will be a binary matrix where \( n_{ij} = 1 \) when \( j \) is a neighbor of \( i \) grid-cell and 0 when it is not a neighbor. Since the immediate neighbors are more likely to have greater influence than the distant ones, weights can be specified such that distant neighbors get a lesser weight than the nearest ones (Cressie 1993).

I used a Gaussian CAR model to describe spatial variation in local abundance (Banerjee et al. 2004). The grid-cell specific expected abundance parameter is now in the form of \( \log(z_k) = \beta_0 + \sum_{j=1}^{J} \beta_j g_{jk} + b_k \) where \( b_k \) accounts for the ‘unobserved’ spatial effects. This spatial autoregressive term \( (b_k) \) is parameterized by a Gaussian CAR prior with mean zero and a variance matrix (Banerjee et al. 2004), which can be expressed as:
\[ [b_1, b_2, ..., b_k] \sim Normal(0, \sigma^2 (I - \tau W)^{-1}) \]

where \( \sigma^2 (I - \tau W)^{-1} \) is the variance-covariance matrix. Here, \( \sigma^2 \) is the variance matrix consisting of conditional variances along its diagonals, which is constant across each point in space. \( I \) is the identity matrix (with ones on the diagonals and zeros elsewhere), \( \tau \) is a measure of the direction and magnitude of the spatial neighborhood effect and \( W \) is the binary neighborhood matrix consisting of zeros on the diagonal and ones on the off-diagonal positions. Thus \( W \) is the adjacency matrix of first-order neighbors with weights set to 1 for the grid-cells sharing the common boundary and 0 otherwise (Besag et al. 1991).

Note that the abundance model now is in the form of a generalized linear mixed model that deals with both intra-cell (fixed effects due to grid-cell specific covariates) and inter-cell (random spatial interaction effects between grid-cells) effects in a combined form (Banerjee et al. 2004).

2.3.9 Modeling the variation in sampling efforts

Often due to logistic constraints (weather, terrain, detours etc), the actual distance walked along transect is not similar across sites in spatially and temporally replicated surveys. This uneven sampling effort might induce some biases, since longer distances and larger area sampled exposes a larger number of animal-clusters to detection. Hence I used the total distance walked in each transect as a factor covariate influencing local
abundance ($\lambda_i$). The effect of this fixed factor is over and above the effects of site-specific covariates on $\lambda_i$ and is multiplicative in nature. The model is now expressed as $\lambda_i = l_i \times \exp\left(\sum_{j=1}^{J} \alpha_j s_{ij}\right)$ where $l_i$ is the distance walked variable that can be viewed as an offset term or a variable with known coefficient value (Gelman et al. 2004).

2. 4 Bayesian inference

Even though the hierarchical model formulated above is fairly simple to describe, there is a complex relationship between observations and a whole suite of latent (unobserved) variables including local abundance of animal-clusters, cluster-size variable, spatial effects etc. and it is not straightforward to express the unconditional likelihood. The Bayesian approach permits these computational complexities using Markov chain Monte Carlo (MCMC) simulations with relevant sampling algorithms (Banerjee et al. 2004; Gelman et al. 2004; Link and Barker 2010). Further, the predictions of random effects of spatially correlated data are a natural product of the Bayesian analysis by MCMC (Gelman et al. 2004; Banerjee et al. 2004). Specifically MCMC simulations are implemented in well-developed statistical package WinBUGS 1.4.2 (Spiegelhalter et al. 2007) that uses the Gibbs Sampler method. I used this widely available free software to implement the hierarchical spatial model and the model specification code in WinBUGS is presented in Appendix 1.
One of the pre-requisites of Bayesian analysis is the specification of prior distributions for the model parameters. I used non-informative uniform priors to specify the prior probability distribution of the model parameters that governed observation and abundance processes. The model specification code was run for > 30,000 iterations after specifying an initial burn-in and thinning. I used three parallel Markovian chains with random starting values to ensure full coverage of the sample space of the parameters and to improve assessment of sampler convergence (Gelman et al. 2004). All burn-in simulation results were discarded and subsequent samples were ‘thinned’ (Gelman et al. 2004) to reduce spatial autocorrelation between MCMC samples. The posterior distributions of the parameters were assessed by examining kernel density plots and histograms. MCMC convergence was assessed using standard model convergence diagnostic procedures as prescribed by Gelman and Rubin (1996).

2.5 Model Assessment

There are many Bayesian approaches for determining suitable predictor variables and assessing their relative importance in multiple regressions (Bayesian Information Criterion, Schwarz 1978; Deviation Information Criterion, Spiegelhalter et al. 2002; Bayes factor, Link and Barker 2006; Bayesian stochastic search variable selection procedures, George and
McCulloch 1993; Kuo and Mallick 1998). I used a simple modeling structure developed by Kuo and Mallick (1998, see also Congdon 2006) to assess the relative importance of predictor variables wherein binary indicator variables are embedded within the regression equation that contains all regression coefficients.

I specified a set of \( w \) indicator variables, one for each covariate effect (both for site-specific and grid-cell specific covariates), and assumed them to be mutually independent. The Poisson regression model is now in the form of \( \lambda_i = \exp \left( \sum_{j=1}^{J} w_{ai} \alpha_j s_{ij} \right) \) for the site-specific covariate effects and \( \log(z_i) = \beta_0 + \sum_{j=1}^{J} w_{ij} \beta_j g_{jk} + b_i \) for the grid-cell specific covariate effects. Here, \( w_{ai} \) and \( w_{ij} \) are the indicator variables for each of the site-specific and grid-cell specific covariate effects respectively.

These indicator variables are Bernoulli random variables that assume the value of either 1 or 0, and a regressor is included in the model set only when its indicator variable takes the value of 1. I assigned a Bernoulli distribution for these indicator variables with a 0.5 prior probability such that each abundance predictor had an equal probability of its inclusion or otherwise in the regression equation. The posterior model weights of the indicator variables will represent their inclusion probability.
in the regression equation, which could be used to identify the most useful predictors of abundance, as well as to rank their relative importance. This modeling approach also allows identification of subset models with predictors that have a high frequency of occurrence in the regression equation, essentially serving as a tool to select the most credible model to explain animal abundance patterns.

2.6 Application of the Hierarchical Spatial Model: An Example

2.6.1 Chital Distance sampling data

I illustrate the application of the hierarchical spatial model using the count data of chital deer (*Axis axis*) from line transect surveys conducted during 2005-2006 in Nagarahole-Bandipur study area. The goal was to estimate \( z \), the expected abundance of chital in each 1 km\(^2\) cell in the grid draped over study area using counts obtained on a set of 77 transects, with length varying from 0.8 to 3.2 km. Each transect was walked 6-7 times within a short period of < 30 days. The field protocols of the survey are more fully described in Karanth *et al.* (2002). The count data consisted of 559 encounters of chital clusters together with associated cluster size and perpendicular distance measurements during walks that covered a total distance of 1404 km.

To explain patterns of spatial variation in chital abundance, I used prior ecological knowledge and species biology (Schaller 1967;
Dinerstein 1979, 1980; Mishra 1982; Mishra and Wemmer 1987; Karanth and Sunquist 1992; Madhusudan and Karanth 2000) to identify habitat covariates most likely to affect chital abundance at local as well as landscape levels (see chapter 1 for detailed rationale for covariate selection). Two site-level covariates (forage index and human-impact) measured at each transect and four landscape-level covariates (protection ineffectiveness, eco-climatic distance, terrain flatness and distance to water) measured at each 1-km² grid-cell were used to explain variation in chital abundance across study area (see chapter 3 for details on covariate data collection protocols). I assumed expected chital abundance (the response variable) to follow a Poisson distribution. In addition to these abundance effects at different spatial scales, I included purely spatial effects in my model through a Gaussian-CAR model specification for the response variable (described more fully in preceding sections). I used an indicator variable for each regressor to derive posterior model weights to assess relative contribution of different explanatory variables in shaping the observed spatial patterns of chital abundance. All covariates were scaled and centered (zero mean and unit variance) to improve MCMC convergence (Gelman et al. 2004). Details of survey design, rationale for covariates selected and field protocols followed to collect animal count data and covariate data, are more fully described in chapter 3 and other literature cited therein.
The WinBUGS code was run for 30,000 iterations and initial burn-in of 5,000 iterations were discarded. Subsequent samples from three chains were thinned at every 20\textsuperscript{th} iterations to obtain 3750 samples for the purposes of inference. I followed standard model diagnostics procedures prescribed by Gelman and Rubin (1996) to assess model convergence.

2.7 Results

2.7.1 Detection function

The detectability of an individual chital cluster was a decreasing function of its distance from the transect line and an increasing function of its cluster-size category. The detection function for various cluster-sizes of chital is shown in Figure 2.1. The plot shows a rapid drop in the detection probability of smaller cluster-sizes when perpendicular distance is > 60 m. The detectability of chital beyond 40-60 m is seen to be severely limited by density of undergrowth.
**Figure 2.1:** Plot of detection function of 12 chital cluster-size groups (each depicted in different colors) in Nagarahole-Bandipur region in India. Each cluster-size group consists of 5 individual chital. The X-axis is the perpendicular distance in 19 categories and the Y-axis is the estimated detection probability that ranges between 0 and 1. Each distance category depicts 20 m and the maximum observed distance is 380 m.
2.7.2 Chital abundance

A total of 559 clusters of chital were observed during the survey and the mean observed cluster size was 5.2 deer / cluster. The posterior distributions of detection probability for cluster size categories (Table 2.1) were used to derive a posterior mean cluster-size of 4.7 chital/cluster.

Table – 2.1: Posterior distributions of cluster-size group specific probabilities (gs) for chital in Nagarahole-Bandipur region. (Number of cluster-size classes: 12, Number of individuals in each class: 5).

<table>
<thead>
<tr>
<th>Node</th>
<th>mean</th>
<th>sd</th>
<th>2.5%</th>
<th>median</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>gs[1]</td>
<td>0.6053</td>
<td>0.01825</td>
<td>0.5703</td>
<td>0.6052</td>
<td>0.6423</td>
</tr>
<tr>
<td>gs[2]</td>
<td>0.2818</td>
<td>0.007331</td>
<td>0.2661</td>
<td>0.2822</td>
<td>0.2951</td>
</tr>
<tr>
<td>gs[3]</td>
<td>0.08774</td>
<td>0.007182</td>
<td>0.07347</td>
<td>0.0877</td>
<td>0.1018</td>
</tr>
<tr>
<td>gs[4]</td>
<td>0.02055</td>
<td>0.002831</td>
<td>0.01522</td>
<td>0.02044</td>
<td>0.0263</td>
</tr>
<tr>
<td>gs[5]</td>
<td>0.003863</td>
<td>7.494E-4</td>
<td>0.002521</td>
<td>0.003812</td>
<td>0.0055</td>
</tr>
<tr>
<td>gs[7]</td>
<td>8.2E-5</td>
<td>2.529E-5</td>
<td>4.12E-5</td>
<td>7.892E-5</td>
<td>1.4E-4</td>
</tr>
<tr>
<td>gs[12]</td>
<td>6.83E-10</td>
<td>4.34E-10</td>
<td>1.69E-10</td>
<td>5.85E-10</td>
<td>1.7E-9</td>
</tr>
</tbody>
</table>
The expected cluster size is a summation of the product of mid-value of the cluster-size class and its mean posterior probability over all cluster size categories.

Figure 2.2 shows the clumped spatial distribution of chital abundance in Nagarahole-Bandipur region. The highest abundance of chital is observed in south-west and south central parts of Nagarahole-Bandipur area. This corroborates results of a long term study that documented high chital densities in southwestern Nagarahole (Karanth and Sunquist 1992; Gangadharan 2005). The posterior mean chital abundance in each 1-km² grid-cell is 3.4 clusters. This translates to a density of 16 individual chital per km². This estimate matches the chital densities derived from conventional line transect surveys (Karanth et al. 2008).

2.7.3 Effects of predictor variables

The posterior distributions of the chital abundance covariates are presented in Table 2.2. The predicted responses of chital abundance to all the explanatory covariates are in the expected direction. However, human impact index (a site-level covariate), showed a weak positive relationship with chital abundance. This covariate is a combined measure of various impacts of human forest-use. I speculate that some of these impacts resulting in opening up of the forest canopy may indirectly benefit chital.
Figure 2.2: Spatial variation of chital abundance showing ‘hot-spots’ of locally high abundance in Nagarhole-Bandipur region in India.

Table – 2.2: Summary of posterior distributions of covariates affecting chital abundance in Nagarhole-Bandipur region.

<table>
<thead>
<tr>
<th>Abundance Covariate</th>
<th>Mean</th>
<th>SD</th>
<th>2.5%</th>
<th>Median</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forage index</td>
<td>0.295</td>
<td>0.146</td>
<td>0.015</td>
<td>0.294</td>
<td>0.578</td>
</tr>
<tr>
<td>Human impact index</td>
<td>0.102</td>
<td>0.126</td>
<td>-0.148</td>
<td>0.105</td>
<td>0.346</td>
</tr>
<tr>
<td>Regression intercept</td>
<td>-0.036</td>
<td>0.236</td>
<td>-0.551</td>
<td>-0.025</td>
<td>0.387</td>
</tr>
<tr>
<td>Variance in slope</td>
<td>-0.802</td>
<td>0.643</td>
<td>-2.244</td>
<td>-0.739</td>
<td>0.262</td>
</tr>
<tr>
<td>Distance to water</td>
<td>-0.170</td>
<td>0.153</td>
<td>-0.478</td>
<td>-0.171</td>
<td>0.129</td>
</tr>
<tr>
<td>Eco-climatic distance</td>
<td>-0.929</td>
<td>0.444</td>
<td>-1.797</td>
<td>-0.931</td>
<td>-0.063</td>
</tr>
<tr>
<td>Protection ineffectiveness</td>
<td>-0.213</td>
<td>0.172</td>
<td>-0.545</td>
<td>-0.213</td>
<td>0.129</td>
</tr>
</tbody>
</table>
However, the support for this hypothesis is weak (Posterior Mean 0.1, SD 0.13) as discussed in chapter 3. The other site-level predictor of chital abundance (forage abundance) positively influenced chital abundance (Posterior Mean 0.3, SD 0.15). All the grid-cell specific abundance predictor variables induced a strong negative effect on chital abundance supporting my *a priori* hypotheses. *(see* the Kernel density plots of explanatory variables, trace plots of MCMC convergence and other model diagnostic plots in Appendix 2.2).

2.7.4 Relative importance of predictor variables

The posterior distributions of indicator variables for each of the predictor variable effects used for modeling chital abundance are in Table 2.3. Posterior model weights clearly indicate that five out of the six proposed covariates have strong individual effects on chital abundance, and in combination they explain the observed abundance patterns in the study area well. Forest vegetation type, forage availability, distance to water and protection (patrol) effectiveness are seen to be the most important predictors of chital abundance.
**Table – 2.3:** Mean posterior weights and their standard deviation of indicator variables for each covariate effect (wa1=Forage index, wa2=Human impact index, w1=Variance in slope, w2=Distance to water, w3=Eco-climatic distance, w4=Protection ineffectiveness) included in chital abundance model.

<table>
<thead>
<tr>
<th>Node</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>wa1</td>
<td>1.0</td>
<td>0</td>
</tr>
<tr>
<td>wa2</td>
<td>0.04</td>
<td>0.20</td>
</tr>
<tr>
<td>w1</td>
<td>0.66</td>
<td>0.47</td>
</tr>
<tr>
<td>w2</td>
<td>0.98</td>
<td>0.15</td>
</tr>
<tr>
<td>w3</td>
<td>1.0</td>
<td>0.0</td>
</tr>
<tr>
<td>w4</td>
<td>0.90</td>
<td>0.29</td>
</tr>
</tbody>
</table>

**2.8 Discussion**

In this section, I discuss the usefulness of hierarchical modeling approach proposed here to understand species-habitat associations. Ecological and management implications of the results from the study of chital-habitat relations are more fully discussed in chapters 3 and 4.

Although study of the relationship of a species to its environment is a fundamental goal of ecology, the challenges posed by imperfect observation processes and complexities of spatial relationships pose
major challenges to understanding of these relationships. Most research efforts have focused individually on these ‘nuisance’ parameters, thereby often blurring ecological parameters affecting animal abundance. However, animal count data, which provide the basis for studies of species-habitat relations, are generated by simultaneous interaction of three processes involving observation, spatial relationships and ecological processes driving abundance. Although ecological literature that dwells on each of these three distinct mechanisms ‘independently’ is common, models of animal abundance simultaneously dealing with all the three important influences on variation in abundance are uncommon (Joseph et al. 2009). The hierarchical spatial model described here tries to address these challenges to build an ecologically realistic model of ungulate abundance in a tropical forest region.

Although I have used a half-normal detection function (Buckland et al. 2001) to model the observation process, it is easy to specify any other plausible function under this model. Furthermore, this model includes effects of cluster size on detectability (size bias, Buckland et al. 2001) by modeling the scale (sigma) parameter within the detection function. Another key feature is that the cluster size is modeled as an individual covariate, which is unobserved for the animal-clusters that did not appear in the sample and the hierarchical formulation enables specification of an
appropriate probability distribution for the cluster size variable (Royle 2008).

The Generalized Linear Mixed Model (GLMM) used in this study to describe the spatial variation in abundance accounts for both ‘deterministic’ and ‘stochastic effects’ (McCullagh and Nelder 1989; Bolker 2008). Thus the model permits inclusion of mechanistic process components (abundance covariates) that reflect local site-level ecological characteristics as well as broad-scale habitat features, which together shape animal abundance and define its habitat. The model structure also allows these site-level and grid-cell level covariates to be treated differently where necessary. The model can also accommodate variables with ‘known’ coefficient values, such as variable sampling effort covariate included in chital model, thus addressing a common sampling problem in animal surveys. Another positive feature of this model is its flexibility to incorporate random spatial effects (local random variation in abundance due to spatial interactions between neighboring locations) at the grid-cell level (e.g. 1-km grid square in chital model). Another noteworthy feature of this model is the treatment of spatially misaligned sampling units (e.g. line transects in chital model) (Bannerjee et al. 2004) to account for spatial coverage bias induced by them. For example, a transect line used in chital model (a sampling unit to collect count data) cuts across several grid-cells resulting in the spatial misalignment of
sampling units and the inferential units for which chital abundance is interpolated. This model effectively deals with such thorny field survey issues.

The Bayesian variable selection approach (Kuo and Mallick 1998) incorporated in this model provides an elegant framework to assess relative contribution of different ecological factors in determining local animal abundance. Furthermore, it also serves as a model selection tool to choose the most credible subset model from among several competing models that contain all plausible combinations of explanatory variables under consideration. The posterior model probabilities reflect the degree of belief that a particular hypothesis is “true”, given the sample data and prior belief (in this study, although no prior information was assumed) about the model (Ellison 2004; Link and Barker 2010).

The chital abundance model illustrated here demonstrates that the proposed hierarchical model works well when confronted by carefully gathered survey data from the real world. The statistically rigorous model yielded ecologically sensible explanations for the relations between chital abundance and several predictor variables, while correcting for observation bias and spatial effects. More importantly, the model was able to efficiently infer from sparse animal count data, a typical feature of most ecological studies of large mammals. Despite small samples of data
the model could predict abundance at un-sampled locations or at any subset area of particular interest. It also reliably assesses species-habitat relations at site level as well as at wider spatial scale of a larger landscape.

From a practical perspective this model is implemented in readily accessible software (WinBUGS). The model may be applicable for a wider variety of sampling situations, wherever the observed count data follow a multinomial sampling distribution. The model can also be potentially extended to investigate temporal dynamics of animal populations in response to changing environmental conditions. I believe its many advantages result from a strong foundation resting on the conceptual and philosophic approach of doing science using hierarchical, model-based, Bayesian inferential framework (see Royle and Dorazio 2008; Link and Barker 2010 for detailed treatment), that can deal with ecological complexities, which are intractable under most other inferential paradigms.

2.8.1 Management implications

The map (Figure 2.2) shows “local hot spots” of high chital abundance. Such a map enables managers to clearly focus their interventions on sub regions of higher quality and highlight need for prioritization of appropriate interventions at sub-optimal habitats. The model is also helpful to predict responses of chital abundance to changing levels of
environmental factors, thus providing objective targets for various management interventions in an adaptive framework. The monitoring methods built into this model can facilitate evaluation of results of management interventions (see chapter 4 for a detailed discussion). The model also can potentially specify limits of chital carrying capacity for a given set of habitat conditions thus being useful to conservation of not just ungulate species but also potentially of large carnivores that prey on these animals.

APPENDICES

Appendix – 2.1: WinBUGS model specification code for fitting the hierarchical spatial abundance model for chital line transect data from Nagarahole-Bandipur region, India.

Appendix – 2.2: Model diagnostics, MCMC convergence plots and detailed summary results of Bayesian analysis of chital data using hierarchical spatial model.
APPENDIX – 2.1

Model specification in WinBUGS (Spiegelhalter et al. 2007) used for fitting the hierarchical spatial abundance model to chital line transect survey data from Nagarahole-Bandipur region, India.

### observed distance from transect, cluster size are detection covariates
### alpha1 and alpha2 are site-level abundance covariates
### beta1, beta2, beta3, beta4 are 1km-grid level abundance covariates

model {
  beta0 ~ dnorm(0,.001)
  sigma0 ~ dunif(0,10)
  p ~ dunif(0,10)
  # modeling sigma parameter for cluster size effects
  for(k in 1:ngs) {
    log(sigma[k]) <- sigma0 + p*(k-1)
    sigma2[k] <- sigma[k]*sigma[k]
  }
  for(k in 1:ngs){
    totmass[k] <- sum(pdf[,k])
    totmasscomp[k] <- sum(comppdf[,k])
  }
  # modeling detection function using half-normal function
  for(j in 1:ndistcat){

for(k in 1:ngs) {
    log(pdf[j,k])<- -1*(j*j)/sigma2[k]
    comppdf[j,k]<- 1-pdf[j,k]
    mncell[j,k]<-pdf[j,k]/(totmass[k] + totmasscomp[k])
}

# modeling cluster-size variable using zero-truncated Poisson distribution
for (k in 1:ngs) {
    gs[k]<- exp(-lams)*pow(lams,k)/(fack[k]*(1-exp(-lams)))
}
lams~dunif(0,50)

# modeling site-level covariate effects, variable sampling efforts and
spatial mis-alignment
for(i in 1:ntrans){
    lam[i]<- ndistwalk[i]*(bigM[i,7]*Z[bigM[i,2]] + 
                        bigM[i,8]*Z[bigM[i,3]] + 
                        bigM[i,9]*Z[bigM[i,4]]+bigM[i,10]*Z[bigM[i,5]] + 
                        bigM[i,11]*Z[bigM[i,6]]) * exp(alpha1*covsites[i,2] + 
                        alpha2*covsites[i,3])
    for (j in 1:ndistcat) {
        for(k in 1:ngs) {
            mu[k,j,i]<- lam[i]*mncell[j,k]*gs[k]
            newy[k,j,i]~dpois(mu[k,j,i])
        }
    }
}
# modeling landscape-level covariate effects and random spatial effects

for(k in 1:Ngrid){
  log(Z[k])<-beta0 + b[k] + beta1*cov1km[k,3] + beta2*cov1km[k,4] + beta3*cov1km[k,5] + beta4*cov1km[k,6]
}

# specification of Guassian CAR prior

b[1:Ngrid] ~ car.normal(adj[], weights[], num[], tau)

for(k in 1:sumNumNeigh) {
  weights[k] <- 1
}

# assigning prior distributions

alpha1~dunif(-5,5)
alpha2~dunif(-5,5)
beta1~dunif(-5,5)
beta2~dunif(-5,5)
beta3~dunif(-5,5)
beta4~dunif(-5,5)
sigs~dunif(0,5)
tau<-1/(sigs*sigs)
Appendix – 2.2: MCMC convergence plots, kernel density plots and other model diagnostics plots of model parameters estimated in the Bayesian analysis of chital data using hierarchical spatial model. (beta 0 = Regression intercept; alpha 1 = Forage index; alpha 2 = Human impact index; beta 1 = Slope variance; beta 2 = Distance from water; beta 3 = Degree of deciduousness; beta 4 = Protection ineffectiveness index).
beta2 chains 1:3

beta3 chains 1:3

beta4 chains 1:3

deviance chains 1:3

sigs chains 1:3
beta4 chains 1:3 sample: 3750

deviance chains 1:3 sample: 3750

sigs chains 1:3 sample: 3750

Gelman Rubin statistic

alpha1 chains: 1:3

alpha2 chains: 1:3
Autocorrelation function