Estimating population trends in elusive species using dynamic occupancy modelling; the Critically Endangered Alaotran gentle lemur

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“A thesis submitted in partial fulfilment of the requirements for the degree of Master of Science and the Diploma of Imperial College London”
“If a tree falls in the forest, but there is no-one there to hear it, does it make any noise?” - Zen Koan

“If a bird sings in the forest, but the investigator fails to detect it, is the forest occupied?” - Evan Cooch
Contents

1. Introduction ......................................................................................................................... 1
   1.1 Monitoring of elusive species ......................................................................................... 1
   1.2 Aims and objectives ....................................................................................................... 3

2. Background .......................................................................................................................... 5
   2.1 Remote sensing .............................................................................................................. 5
       2.1.1 Remote sensing derived vegetation indices .............................................................. 5
   2.2 Imperfect detection in occupancy studies ...................................................................... 6
   2.3 Multi-season occupancy models .................................................................................. 7
       2.3.1 Occupancy model assumptions .............................................................................. 8
   2.4 Distance analysis ......................................................................................................... 8
   2.5 Lac Alaotra; the habitat .............................................................................................. 9
   2.6 The Alaotran gentle lemur ......................................................................................... 11
       2.6.1 Alaotran gentle lemur population estimates .......................................................... 12
       2.6.2 Occupancy and suitability studies on the Alaotran gentle lemur ......................... 13

3. Methods ................................................................................................................................ 14
   3.1 Data Collection ............................................................................................................. 14
   3.2 Population trend estimation; a framework ..................................................................... 15
   3.3 Analysis of detection / non-detection data ................................................................... 17
   3.4 Occupancy models inclusive of covariates .................................................................. 20
   3.5 Model Covariates .......................................................................................................... 22
       3.5.1 Occupancy, colonisation and local extinction covariates ..................................... 23
       3.5.2 Detectability covariates .......................................................................................... 23
   3.6 Remote sensing data ..................................................................................................... 25
       3.6.1 Burn History ......................................................................................................... 25
       3.6.2 Lake height ............................................................................................................. 27
   3.7 Analysis of DISTANCE data ......................................................................................... 27

4. Results ..................................................................................................................................... 29
   4.1 Summary of observations ............................................................................................. 29
   4.2 Occupancy ..................................................................................................................... 32
4.2.1 Fixed model ........................................................................................................... 32
4.2.2 Covariate inclusive models .................................................................................. 33
4.2.3 Top model ............................................................................................................ 35
4.3 Estimating density .................................................................................................... 42
4.4 Estimating population size ...................................................................................... 43

5. Discussion ................................................................................................................. 45
  5.1 Overview ................................................................................................................. 45
  5.2 Distribution of occupied habitat ............................................................................ 46
  5.3 Occupancy model findings ...................................................................................... 47
    5.3.1 Initial occupancy covariates ............................................................................ 47
    5.3.2 Colonisation and local extinction covariates ................................................... 47
  5.4 Limitations ............................................................................................................... 49
    5.4.1 Lack of a probabilistic sampling scheme ......................................................... 49
    5.4.2 Unmodelled heterogeneity .............................................................................. 50
    5.4.3 Covariate accuracy ........................................................................................ 50
  5.5 Implications for management ................................................................................. 51
  5.6 Recommendations for monitoring ........................................................................ 52
    5.6.1 Improving density estimates .......................................................................... 54
  5.7 Future work ............................................................................................................. 54
    5.7.1 Integrated modelling of suitability and occupancy ........................................... 54
  5.8 Transferability ........................................................................................................ 55

References .................................................................................................................. 56

Appendices .................................................................................................................. 67
  Appendix 1 Distance from nearest settlement map ...................................................... 67
  Appendix 2 MODIS burned area map combined with FIRMS active fire map for the 12
  months preceding March of the year shown ............................................................... 68
  Appendix 3 NDVI map for March of 2004-2007 ......................................................... 69
  Appendix 4 Map of village management zones ............................................................ 70
  Appendix 5 NASA FTP servers used to download the MODIS data and further processing
  notes using the MODIS reprojection tool ................................................................. 71
Appendix 6 Map of predicted occupancy for 2004 overlaid by the protected area boundary and the no take zone .......................................................... 72

Appendix 7 The global detection function produced by pooling the Distance data across the four years of the study.................................................................................................................. 73

Appendix 8 Alaotran gentle lemur habitat suitability map fit to the study area used in this study, adapted from Lahoz-Monfort et al, 2010 ........................................................................................................ 74
List of Acronyms

95% CI - 95% Confidence Interval
AIC - Akaike’s Information Criterion
FIRMS - Fire Information for Resource Management System
FTP - File Transfer Protocol
IUCN - World Conservation Union
MODIS - Moderate Resolution Imaging Spectroradiometer
MRT - MODIS Reprojection Tool
NDVI - Normalised Difference Vegetation Index
NSIDC - National Snow and Ice Data Centre
RMSE - Root Mean Square Error
UTM - Universal Transverse Mercator coordinate system

Symbols in Equations

\( \psi \) - Probability of occupancy
\( p \) - Probability of detection
\( \gamma \) - Probability of colonisation
\( \varepsilon \) - Probability of local extinction
\( \beta \) - Logit regression coefficient (beta value)
\( h \) – Detection history
\( \Sigma \) - (Sigma) sum the following
\( \prod \) - (Pi) product of the following

Sigma and pi will normally have \( i=n \) below where \( n \) = the first number in the series and another number on top showing the total number of numbers in the series.
Abstract
Monitoring provides an essential feedback loop in the implementation of conservation projects, ensuring that impacts of management actions are measured. Monitoring of elusive mammal species can be difficult as they are imperfectly detected and their distribution is hard to predict. This study aimed to develop a novel monitoring method which integrates occupancy modelling and Distance analysis to accurately estimate the population trend of the Alaotran gentle lemur, an elusive species in a highly dynamic system that does not allow for a probabilistic sampling scheme. Data was collected from existing marsh channels and lake edges by Durrell Madagascar staff in canoes between February and March from 2004 to 2007. As access to the marsh was limited a probabilistic sampling scheme could not be used. Habitat and disturbance covariate data for occupancy models was derived entirely from remotely sensed data. This study found that although remote sensing data effectively described habitat data, it was unable to account for the lack of occasion specific disturbance data recorded during the study. Fire, habitat quality (NDVI) and a proxy for hunting pressure were shown to be important drivers of occupancy, colonisation and local extinction throughout the marsh. The study generated population estimates across the four seasons ranging from 2053 +/- 1339 to 6106 +/- 2504, a magnitude of which represents similar estimates to those previously generated. Patterns in the distribution of occupancy are investigated in relation to current protected area positions, showing that while partial coverage of the occupied lemur habitat is achieved, coverage is not focussed on the most important areas for the lemur. Methods for refining this monitoring method and its potential for use in similar systems are discussed.

Word Count 13435
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1. Introduction
1.1 Monitoring of elusive species

Monitoring provides an essential feedback loop in the implementation of conservation projects, ensuring that impacts of management actions are measured and can be adapted to maximise effectiveness (Possingham et al., 2001). Monitoring can also provide the data necessary for the development of models that can be used to make predictions about the impacts of potential future management interventions (Kendall, 2001; Nichols, 2001).

Although they play a vital role in conservation, many monitoring programmes are poorly designed and the resulting conclusions can be flawed (Yoccoz et al., 2001; Field et al., 2007; Lindenmayer and Likens, 2010). This is especially the case when studying rare or elusive species which often live in low density populations, with low and variable detectabilities and are difficult to predict leading to small sample sizes (Thompson, 2004). Monitoring programmes are often created with the simple objective of gaining more information about a system rather than defining the objectives sufficiently clearly to ensure they are designed adequately (Yoccoz et al., 2001).

Most populations span very large areas and so it is often not possible to survey the entire distribution. For this reason the design of most monitoring studies should include a probabilistic sampling scheme with which decide on which sites to survey (Thompson, 2004). If the data from the survey are then used to estimate population parameters which are representative of the sampled population, it is essential ensure that sufficient sample data are collected (Williams et al., 2001). The monitoring of habitat variables or other drivers of the state variable is also essential in order to robustly describe the system. It is otherwise possible that large amounts of the variation observed will remain unmodelled and any inferences flawed. Remote sensing provides a successful method for describing such variation, even when the system is very small and lacks topographic and climatic variation across its range (e.g. Lahoz-Monfort et al., 2010).

The choice of state variable is also an essential part of designing a monitoring programme. A common conundrum is whether to use data intensive abundance estimates such as Mark recapture (White and Burnham, 1999) or simply to track changes in occupancy (defined as the proportion of sites occupied) or distribution with presence–absence data (Mackenzie
and Nichols, 2004). Although abundance data have commonly been assumed to be more informative on a per site basis, presence-absence data allows more sites to be visited meaning inferences of patterns across a much larger study site are available. The decision on which state variable to monitor is also influenced by the detectability of the study species (Royle et al., 2005). When monitoring a more elusive species, fewer data can be collected on the individuals in the site and so presence-absence data represents a cost-effective method of data collection. It has also been shown that presence-absence surveys in studies with small budgets or those targeting elusive species are most useful in an attempt to successfully assign IUCN red list categories of threat (Joseph et al., 2006) and can accurately represent trends in population size (Gaston et al., 2000).

Many monitoring studies also fail to account for imperfect detection of their study species as is common in elusive species (Yoccoz et al., 2001; Thompson, 2004). Variation in detectability in space and time is one of the main sources of error in many monitoring studies (Yoccoz et al., 2001; Mackenzie et al., 2002). In studies where species are not detected in sites in which they do occur, incorrect inferences about the system properties and species-habitat relationships may be made (Tyre et al., 2003; Field et al., 2005; Mackenzie et al., 2006). Many abundance estimation techniques have mechanisms that can be employed to reduce the prevalence of these “false absences” including distance sampling and mark-recapture as well as occupancy studies (White and Burnham, 1999; Buckland et al., 2001; Mackenzie et al., 2002; Pollock et al., 2002). In occupancy studies, the problem of imperfect detection is dealt with through repeated visits (Mackenzie et al., 2006). Repeated surveys allow formation of a detection history of detections and non-detections. These detection histories can then be directly included into a maximum-likelihood framework (Mackenzie et al., 2002; Tyre et al., 2003) in which a probability distribution is generated and the point at which the values of the parameters maximise the function is used as the estimator.

Although occupancy alone is a useful state variable, understanding the dynamic processes that drive changes in occupancy (colonisation and local extinction) can provide a greater understanding of the system and allow stronger inferences on the patterns observed. For this reason occupancy is the state variable in many metapopulation studies (e.g. Levins,
1970; Hanski and Gilpin, 1997; Hanski, 1998, 1999) and in studies investigating extinction thresholds (e.g. Lande, 1987). The relationship between occupancy and characteristics of occupied patches, can inform future management actions and define areas of importance throughout a habitat. Occupancy maps have therefore been described as “the fundamental unit of analysis in community ecology and biogeography” (Gotelli, 2000). By employing management actions that reduce the most common causes of local extinction of sites, conservation can be focussed and so increasingly effective.

Occupancy estimates also present an opportunity for improving population estimates produced using density estimation techniques such as Distance (Thomas et al, 2010; Buckland et al, 2001) which has been argued to provide a robust estimate for density in elusive species (Thompson, 2004). By applying the density estimate to only occupied areas rather than all potential habitat, the uncertainty with which predictions are associated can be reduced. By combining Distance and occupancy, a monitoring programme will not only generate data on population trends which have obvious implications for threat designation, but also how the population dynamics are impacted by the landscape structure, something that has been seen as having increasing importance in biodiversity conservation (Wiens et al, 1993; Fahrig and Mirriam, 1994).

1.2 Aims and objectives
Aim
This study aimed to develop a novel monitoring method which integrates occupancy modelling and Distance analysis to accurately estimate the population trend of the Alaotran gentle lemur, an elusive species in a highly dynamic system that does not allow for a probabilistic sampling scheme. Data from surveys of the lemur carried out along a selection of routes in the marshes of Lac Alaotra between 2004 and 2007 were used along with remotely sensed data sources.
Objectives

1. Create a maximum likelihood of occupancy, colonisation and local extinction explicitly accounting for detectability to predict occupancy of the lemur across the surveyed site and apply this model to the entire marsh

2. Map the distribution of site occupancy across the marsh surround Lac Alaotra

3. Combine the occupancy estimates with a density estimates from a Distance model across the same site to generate estimates for population size in all years for which data are available

4. Assess the ability of this technique to generate population trends across a four year study period

5. Assess the use of remote sensing variables as the only source of predictor variables for a dynamic occupancy model which incorporates detection probability

6. Provide recommendations for the development of a robust monitoring programme for the Alaotran gentle lemur and assess its potential for other similar systems.
2. Background
2.1 Remote sensing

Remote sensing is the “acquisition of information about an object or phenomenon, without making physical contact with the object” (Schowengerdt, 2007). Remote sensing generally refers to the use of aerial sensors to map or detect objects on the earth’s surface. This technology provides the possibility of a cheap form of predictor variables for spatial ecology studies. Many remote sensing data is available freely to those with the technical knowledge necessary to utilise it which means it has the capacity to contribute greatly to studies in organisations that cannot afford an expansive ground staff. It also means it can be applied to large area studies without the requirement for extended ground surveys. It also allows collection of habitat data for habitats that are largely inaccessible (e.g. Lahoz-Monfort et al, 2010). Remote sensing data do however require sufficient technical knowledge to ensure correct interpretation (Roughgarden et al, 1991).

2.1.1 Remote sensing derived vegetation indices

Commonly used remotely sensed data include vegetation indices. Green vegetation absorbs visible blue and red light through the large amounts of chlorophyll and other pigments in its leaves and reflects near infrared wavelengths as a result of the cell structure. This pattern can be used to differentiate active vegetation from other habitat types using remote aerial sensors, for example bare ground has similar reflectance from both bands and open water reflects more near infrared than visible light (Lillesand et al, 2008).

These reflectance properties have been used as the basis for several vegetation indices derived from the remote sensing data (for a review see Gong et al, 2003 and Lu et al, 2004). A commonly used index is the Normalised Difference Vegetation Index (NDVI) which is simply a ratio of the amount of near infrared light scattered by the leaf cell structure to the amount of red light absorbed by the chlorophyll. For each pixel, the index produces a value for greenness ranging between -1 and 1 with the common range for green vegetation of 0.2 to 0.8. NDVI has weaknesses in that it is known to be sensitive to some atmospheric conditions for example sun position and background reflectance (Ramsey et al, 2002).
2.2. Imperfect detection in occupancy studies

There is a large volume of literature on the subject of imperfect detection (e.g. Moilanen, 2002; Anderson, 2003; Mackenzie et al, 2003; Tyre et al, 2003; Bailey et al, 2004). In occupancy studies, detection histories rather than presence-absence data are directly included into a maximum-likelihood framework (Mackenzie et al, 2002; Tyre et al, 2003). The likelihood function for a multiple-season model is a composite of the likelihood functions for the individual seasons. An equation (2.1) can be formed for the Likelihood (L) of the observed detection histories (h) in a single season (t) in terms of occupancy probability (ψ) and detectability (p), assuming independence between sites (MacKenzie et al, 2003).

Equation 2.1

\[ L_t(\psi_t, p_t|h_{11}, h_{12}, \ldots, h_{1s}) = \prod_{i=1}^{s} \Pr(h_{ij}), \]

where \( \psi_t \) is the probability of site \( t \) being occupied by the species of interest, and \( p_t \) is the conditional probability of detecting the species in site \( t \) given that the species is present.

Within each season the occupancy state is assumed constant and so a detection history of 001 would have a probability of

\[ \psi (1 - p_1) (1 - p_2) p_3 \]

However with a detection history of 000 it could be the result of either an unoccupied site or the non-detection the species at the site and so the probability becomes

\[ \psi (1 - p_1) (1 - p_2) (1 - p_3) + (1 - \psi) \]

Where for the third occasion the possibilities of occurs but is not detected \((1 - p_3)\) and species does not occur \((1 - \psi)\) are both included.

This likelihood equation can be easily adapted to include missing data by effectively ignoring survey information for that site on that occasion. This means that a detection history of 0-1 where, - indicates a missing observation, becomes:

\[ \psi (1 - p_1) p_3 \]

The ability to include missing observations allows for unequal sampling effort at different sites, meaning all data can be used despite a different number of visits to all of the transects. The full likelihood equation for all \( T \) seasons is calculated as the product of the individual seasonal likelihoods as shown in Equation 2.
2.3 Multi-season occupancy models

Information on the dynamic processes (colonisation and local extinction) that drive changes in occupancy can provide information on what management actions will have the greatest conservation impact. Many studies have focussed on these dynamic processes that drive occupancy patterns which can then be described using meta-population dynamics (Hanski, 1998). Some examples of studies that have used presence-absence on which to base dynamic occupancy models are shown in Table 2.1.

Table 2.1 A selection of studies that have used presence/absence data to draw inferences on patch occupancy and dynamic population processes

<table>
<thead>
<tr>
<th>Author(s)</th>
<th>Target species and location</th>
<th>Technique used to collect presence/absence data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peltonen and Hanski, 1991</td>
<td>Sorex spp. On islands in Northern Finland</td>
<td>Mark-recapture</td>
</tr>
<tr>
<td>Betts et al, 2008</td>
<td>Black-throated blue warbler (<em>Dendroica caerulescens</em>) in North America</td>
<td>Direct observations</td>
</tr>
<tr>
<td>Kery, 2004</td>
<td>Various plant species in Europe and North America</td>
<td>Mark-recapture</td>
</tr>
<tr>
<td>Franken and Hik, 2004</td>
<td>Collared pikas (<em>Ochotona collaris</em>) in the Yukon</td>
<td>Mark-recapture</td>
</tr>
<tr>
<td>Verboom et al, 1991</td>
<td>European nuthatch (<em>Sitta europaea</em>) in Western Europe</td>
<td>Direct observations</td>
</tr>
<tr>
<td>Araujo et al, 2002</td>
<td>78 species of breeding passerine birds in Britain</td>
<td>Occurrence records</td>
</tr>
<tr>
<td>Hames et al, 2001</td>
<td>Four species of tanagers in the genus <em>Piranga</em> across North America</td>
<td>Point counts</td>
</tr>
<tr>
<td>Hecnar and M’Closkey, 1996</td>
<td>11 amphibian species in Ontario, Canada</td>
<td>Direct observations</td>
</tr>
<tr>
<td>Moore et al, 2008</td>
<td>Glaucous-winged gulls (<em>Larus glaucescens</em>), Washington</td>
<td>Direct observations</td>
</tr>
<tr>
<td>Lawes et al, 2001</td>
<td>Blue duiker (<em>Philantomba monticola</em>), tree hyrax (<em>Dendrohyrax arboreus</em>), and samango monkey (<em>Cercopithecus mitis labiatus</em>), South Africa</td>
<td>Direct observations</td>
</tr>
</tbody>
</table>
2.3.1 Occupancy model assumptions

There are five main assumptions involved in the description of occupancy models (MacKenzie et al., 2006):

1. Another species is never wrongly identified as the target species (i.e. no false positives)
2. Occupancy status at each site does not change during the survey season, meaning the site is closed to changes in occupancy (however this can be relaxed in certain scenarios; see Kendall, 1999)
3. Occupancy is either constant across sites or differences are modelled using covariates
4. Detectability is either constant across sites and surveys or differences are modelled using covariates and
5. Detection histories at each location are independent

If these assumptions are broken, resulting estimators may be biased and the model flawed. These techniques have been made available to science within program PRESENCE 3.1 (Hines, 2011), incorporated to the program MARK (White and Burnham, 1999) and can now be used in Unmarked in Program R (Fiske and Chandler, 2011).

2.4 Distance analysis

Distance analysis is a common method for estimating abundance and density of animal populations (Thomas et al., 2010). In distance analysis, detection probability is modelled as decreasing with increasing distance between observer and study species (Thomas et al., 2010). Selecting the key function is the first step in building this model and Distance uses three models that have been shown to create robust models with the correct shape criterion (Buckland et al., 2001). The key functions are Uniform, Half-normal and Hazard-rate and are used in conjunction with a series expansion that can adjust the key function, to improve the fit of the model to the data (Buckland et al., 2001).

There are two main engines through which it is possible to perform distance analysis. Firstly; conventional distance sampling in which detection probability is modelled only as a function of distance from the observer and assumes perfect detection at zero distance. Secondly and more recently developed is multi-covariate distance analysis (Buckland et al., 2004) in which
detection probability can be modelled not only as a function of distance but also of covariates.

Distance analysis relies on three assumptions (Buckland et al, 2001): (1) that species on a line are detected with certainty, (2) animals do not move; distance analysis measures a single point in time and movement of animals may result in re-observation. This is also a problem if animals attempt to avoid the observer and move further away before they are detected as animals are assumed to be distributed independently to the position of the observer (Fewster et al, 2008). (3) Measurements are exact; observers with little experience will often make poor estimates of distance (Alldredge et al, 2007).

2.5 Lac Alaotra; the habitat

Lac Alaotra is the largest lake in Madagascar and is situated in the Alaotra-Mangoro Region of North-East Madagascar (17°2’ to 17°6’S, and 48°1’ to 48°4’E). The lake has over 20,000ha of open water alone and is surrounded by a large wetland containing both marsh areas and rice fields (Andrianandrasana et al, 2005). The lake is shallow, ranging from 1 metre in depth in the dry season to 4 metres in the wet season (Ramanampamonjy et al, 2003). Seasonality dominates the climate in the region with a wet and hot season between December and April and a dry season with lower temperatures between May and November (Mutschler et al, 1998). The marsh area is estimated at around 25,000 hectares (coloured green in Figure 2.1) and the dominant vegetation is and reeds (*Phragmites communis*) and papyrus (*Cyperus madagascariensis*). The area is considered an important area for biodiversity (Pidgeon, 1996) supporting eight endemic waterbird and five endemic fish species (IUCN, 2011a; Andrianandrasana et al, 2005) as well as the subject of this study; the critically endangered Alaotran gentle lemur (*Hapalemur alaotrensis*; Rumpler, 1975). Due to this biodiversity value, Lac Alaotra was designated a wetland of international importance under the RAMSAR convention in 2003 (Ramanampamonjy et al, 2003). In 2007, the lake was also designated a protected area including a large area in which no extraction is permitted (IUCN category VI) (Ranarijaona, 2007).
Figure 2.1 Lac Alaotra study area and its location within Madagascar. Five villages responsible for management of small parts of the marsh are marked on this map.

The rice fields surrounding the marsh occupy an area of around 120,000ha and produce and estimated one third of the countries rice (Pidgeon, 1996) earning the area the name ‘The Granary of Madagascar’. The lake is also the largest inland fishery in Madagascar (Pidgeon, 1996).

The Lac Alaotra watershed is also home to over 550,000 people (PRD, 2003), a population that is thought to have grown rapidly from an estimated 106,000 in 1960 (Pidgeon, 1996). This population is highly dependent on rice cultivation and fishing (Ranarijaona, 2007; Blanc-Pamard, 1987), however subsistence crop growth, livestock rearing and textile manufacture are also known in the area (Jarosz, 1994).

Despite conservation efforts, burning of the wetland is a significant threat to biodiversity in Lac Alaotra and the surrounding marshes (Ranarijaona, 2007). The marsh has consistently declined in recent years and is currently less than half of its original 60,000-80,000ha (Bakoariniaina et al, 2006). In 2004 the area of wetland was reduced by c.50% through
burning during the dry season (Durrell, 2006). Conversion of lake to areas for rice cultivation has been recorded as one of the main reasons for burning (Ralainasolo et al, 2006; Copsey et al, 2009). Many channels cut by fishermen to gain access to new areas of the lake have also been recolonised by invasive plants such as water hyacinth (*Eichhornia crassipes*) and *Salvinia spp.*, which now cover an estimated 70% of the waterways and lakes (Andrianandasana et al, 2005).

2.6 The Alaotran gentle lemur

The Alaotran gentle lemur, previously known as the Alaotran bamboo lemur and known locally as the bandro, is a small primate that exclusively inhabits the papyrus and reed beds surrounding Lac Alaotra (Garbutt, 2007). This species is the only primate known to live in marsh habitat (IUCN, 2011b) and is regarded as a flagship species for its marsh habitat. The lemur occurs in two sub-populations; a small one in the North around the Belempo peninsula and a larger population in the South of the marsh (Mutschler et al, 2001). The Alaotran gentle lemur was classified a separate species recently having previously been regarded a sub-species of the lesser bamboo lemur; *Hapalemur griseus* (Mittermeier et al, 2006; Groves, 2005). The lemur feeds mainly on papyrus, reeds and two grasses (*Echinochloa crusgalli* and *Leersia hexandra*) (Mutschler, 1999).

The lemur is highly territorial and observations have been made of it defending its home range against other nearby lemur groups (Nievergelt et al, 1998) even across channels (Guillerain-Arroita et al, 2010a). The lemur lives in groups of between 2 and 9 individuals with an average group size of 4.33 with each group thought to occupy a home range of 0.6-8 hectares (Mutschler and Tan, 2003; Mutschler et al, 1994). Groups of the lemur have been found to have an even sex ratio as is common in the Hapalemur family (Nievergelt, 2002). The lemur displays cathemeral activity with peaks in activity at the beginning (6:00-9:00) and end (15:00-18:30) of day light hours, however some activity has been noted during the night (Mutschler et al, 1998; Tattersall, 2006).

The Alaotran gentle lemur is classified as Critically Endangered on the IUCN Red List as it triggers criteria A2c,d and B1+2c (Ganzhorn, 2000). The Alaotran gentle lemur has therefore gained the highest conservation priority in the Lemur Action Plan (Mittermeier et al, 1992). The lemur action plan lists the main threats as habitat destruction and poaching (Mutschler

Despite laws against hunting the lemur, it remains common in several villages surrounding Lac Alaotra for both food and for pets. Hunting is thought to occur at significant levels in Anororo and Ambodivoara with one village in 2004 reportedly hunting upwards of 500 lemurs (Ralainasolo et al, 2004; Andrianandrasana et al, 2005).

2.6.1 Alaotran gentle lemur population estimates
Since 2001, annual surveys have been carried out during the rainy season between February and March (Ralainsolo, 2004; Mutschler and Fiestner, 1995). Five sites are surveyed: Anororo and Andilana-Sud in the South-West of the marsh and Andreba and Ambodivoara in the South-East (Figure 2.1) and a reference site; Andreba-Gare in which exhaustive survey effort is used to produce a reference density of relatively high confidence (Nievergelt, 1999). Estimates of population size are then calculated for each of the other sites using group encounter rates, calculated by dividing the number of lemur groups encountered by the amount of time spent surveying (Mutschler et al, 1994; Mutschler et al, 2001). The mean encounter rate is then calculated for each location and compared to the reference density to calculate a relative group density for each site. This relative density is then multiplied by the area of that site to generate four estimates which are combined to calculate an overall population size.

This technique produced estimates of between 7500 and 11000 from Mutschler and Feistner (1995) and 2840 from Ralainsolo (2006). Although this technique accounts at least partially for low detectability through thoroughly studying one area therefore gaining an understanding of how many are detected and how many actually exist, it does assume that detectability is consistent across the marsh, something that more recent studies have shown to be false (Guillera-Arroita et al, 2010b). The studies between 1994 and 1999 were also carried out by a different team to the study in 2002 and heterogeneity in observer skill is not included in the analysis making the comparability of these studies questionable.
2.6.2 Occupancy and suitability studies on the Alaotran gentle lemur

Guillera-Arroita et al (2010a, 2010b) carried out a single-season occupancy study on the lemur in 2008. This study has shown that occupancy can be used successfully as a state variable when monitoring the Alaotran gentle lemur. They also showed that detectability was not only very low (6.4%) but also lacked uniformity across the lake and so confirmed the requirement for a robust description of detectability in any future monitoring of the lemur. Around 20% of the marsh area surveyed was predicted to be occupied by the lemur which was supported by Andrianandrasana (2009) using Landsat classification of suitable habitat to produce an estimate of 25% (6000ha) in 2007. Habitat suitability maps have also been created by Lahoz-Monfort et al (2010) producing predictions that around 23% of the marsh is highly suitable habitat. Lahoz-Monfort et al also showed that using remotely sensed data as the single predictor variable for producing these estimates maintained the integrity of the results.

Habitat suitability studies have however, not accurately accounted for hunting pressure and other non-habitat related variables that have been shown to be a major threat to the lemur. Guillera-Arroita et al (2010b) is also a snap-shot study only 1 month in length. Drawing conclusions from a single study period can generation spurious consequences, as it is possible that the state of the system at the time of the study may not be a good representation of the normal state, especially in such a dynamic system. If, for example there had been a large burn in that year, the occupancy state of the marsh would likely have been different than the occupancy state in a year with less burning.

No study has yet combined habitat variables and disturbance variables over a multiple year study period in order to generate estimates of population trend in the lemur. Although Andrianandrasana (2009) shows a downwards trend in area of suitable habitat, there is no evidence for its impact on the lemur. It is possible that as the lemur has survived in this dynamic system for so long, that it is robust to these sporadic declines in habitat availability.
3. Methods
3.1 Data Collection

In the data collection phase of this study a number of survey routes were chosen along natural borders (e.g. around lake edges) and along channels that had been cut or burned by fishermen. These sites were visited multiple times in order to generate a detection history for the lemur (see Table 3.1 for number of repeats per route). It was not possible to carry out systematic sampling as the marsh is too dense to travel through without causing considerable damage to an already delicate ecosystem through the facilitation of spread of invasive plants. The study was carried out mainly in the southern section of the marsh which contains the largest population (Mutschler et al, 2001) although two survey routes were used in the north of the marsh in 2007 (See Figure 3.1).

Data collection was carried out annually by staff from Durrell Madagascar between 2004 and 2007. A team consisting of one fisherman, one local guide, one researcher and one paddler travelled along survey routes by canoe, recording the presence of the lemur by direct observation. The day was divided into two sampling sessions (5:00-11:00 and 15:00-19:00) coinciding with two peaks in lemur activity (Mutschler et al, 1998) which would increase the likelihood of detection but ensure detectability was constant between sessions. For each observation, the GPS location of the canoe at time of sighting, distance and angle to the centre of the group of the lemurs at point of first sighting was recorded. The GPS was also used to map out the survey routes to provide an understanding of the area covered by the study.

The surveys were conducted throughout March in each year. These periods were assumed closed to changes in occupancy. It is assumed that animals may move in and out of the study units as the units may not encompass the entirety of a group’s territory; however these movements were assumed random in order for the occupancy estimator to remain unbiased (Kendall et al, 1997; Kendall, 1999). By carrying the study out at the same time each year, it is assumed that environmental conditions will be similar and so provide no source of bias in the study.

The length of survey routes and number of repetitions for each route was largely similar across the four years as shown in table 3.1. This allows investigation into whether the
results for each year are comparable and prevents the dynamic model being flawed through biased sampling.

Table 3.1 A summary of the total length of routes surveyed across the 4 years of study including the number of repetitions of the routes

<table>
<thead>
<tr>
<th>Year</th>
<th>Overall survey route length (km)</th>
<th>Range of repetitions</th>
<th>Mean no. of repetitions</th>
<th>Total length surveyed (km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>102</td>
<td>2-5</td>
<td>4</td>
<td>266</td>
</tr>
<tr>
<td>2005</td>
<td>78</td>
<td>2-5</td>
<td>3</td>
<td>232</td>
</tr>
<tr>
<td>2006</td>
<td>94</td>
<td>2-5</td>
<td>2</td>
<td>308</td>
</tr>
<tr>
<td>2007</td>
<td>109</td>
<td>2-5</td>
<td>3.3</td>
<td>364</td>
</tr>
</tbody>
</table>

3.2 Population trend estimation; a framework

This study combined annual density estimates using Distance analysis (Thomas et al, 2004; Buckland et al, 2001) of lemur density with estimates of the total area occupied, estimated using a multi-season occupancy model (Mackenzie et al, 2006), to generate a population estimate for the years 2004-2007. Occupancy probability was averaged for all cells in the grid to generate an estimate of percentage occupancy for the marsh for each year and then multiplied by the total area of marsh studied (25,000 ha) in order to generate an estimate for occupied area. These annual area estimates were multiplied by the density of lemurs in each year to generate a population estimate. The error for the population estimates was calculated using the root mean squared error (RMSE) method, in which the standard error of the occupied area (scaled down to a per hectare value) and the density estimate error were both squared and summed and the square root taken. This error was then multiplied by the area estimate to generate the error for the total population estimate for that year.

In order to assess whether or not the relative lemur abundance (lemurs / km route surveyed) observed by the Durrell Madagascar staff displayed any evidence of a trend, a route regression was used (Geissler and Sauer, 1990). Using this method, regional trends are estimated as a weighted average of trends on individual routes (Link and Sauer, 1997a, 1997b).
Figure 3.1 The routes surveyed across the 4 years. The study was concentrated in the southern section of the marsh which contains the largest population (Mutschler et al, 2001) although two routes were used in the north of the marsh in 2007.
3.3 Analysis of detection / non-detection data

Occupancy of the lemur was modelled using a multi-season single-species model developed by Mackenzie et al (2006) that explicitly accounts for detectability (Mackenzie et al, 2002) and estimated using the maximum likelihood approach as per Mackenzie et al (2006) as an extension of the single season model for the lemur created by Guillera-Arroita (2010b). Covariates were examined to explore the factors that were most important in influencing where the lemur occurs, when a site is recolonised, when a site becomes locally extinct and when lemurs are detected.

The marsh area was delineated into units that could be assessed for occupancy by imposing a 250m x 250m grid over the map (See Figure 3.2). A 250 metre grid was chosen as this represented a square with equal area to the theoretical maximum H. alaotrensis territory size (Mutschler and Tan, 2003) thus preventing ‘grid saturation’ (Kunin et al, 2000) and was identified as the largest size for the optimal pixel size of predictor variables when mapping H. alaotrensis habitat (Lahoz-Monfort et al, 2010). Although using an arbitrary grid approach did ignore that often lemur territories are separated by channels (Nievergelt et al, 1998) it would not otherwise have possible to divide the marsh into meaningful units and derive a marsh wide estimate of occupancy.

A detection history was created for each grid cell that had been surveyed in at least one the surveys. GPS records of each individual spotted were used to generate a map of lemur sightings. Grid squares in which more than one lemur had been spotted in one sampling occasion were identified and these duplicates were then removed and a detection history formulated.
The occupancy likelihood equation in background section 2.2.1.1 in terms of occupancy ($\psi$) and detectability ($p$) can be expanded to investigate the effects of colonisation ($\gamma$) and local extinction ($\varepsilon$) where $\gamma_i$ is the probability that a site is colonised between occasions, $\varepsilon_i$ is the

Figure 3.2 The study area was delineated into 250m$^2$ grid squares. A 250m$^2$ grid was chosen as this represented a square with equal area to the theoretical maximum *H. alaotrensis* territory size (Mutschler and Tan, 2003) and was identified as the largest size for the optimal pixel size of predictor variables when mapping *H. alaotrensis* habitat (Lahoz-Monfort *et al.*, 2010)
probability that the site became locally extinct at this site between occasions. This resultant dynamic process is visualised in Figure 3.3 (Adapted from Mackenzie et al, 2006).

This likelihood model, generates an estimate for initial occupancy only, it then incorporates potential changes in the occupancy of a site using the dynamic parameters of colonisation and local extinction (Mackenzie et al, 2003). Now a multiple year detection history is used (e.g. 010 000 110). From this detection history we can derive that the species was present in the first and third seasons however the second season has one of two possible explanations: either the species went locally extinct between occasion one and two and re-colonised between seasons two and three, or it did not go locally extinct between any of the years but remained undetected in the second year. Mathematically this can be represented as:

\[ (1 - \varepsilon_1) \prod_{i=1}^{3} (1 - p_{2,i}) (1 - \varepsilon_2) + \varepsilon_1 \gamma_2, \]

Where \((\varepsilon_1 + \gamma_2)\) represents the local extinction followed by colonisation and the preceding part of the equation represents non-detection in the second season

The model can then used to derive occupancy in subsequent seasons using Equation 3.1 in which sites occupied in season 2 are a combination of those sites occupied in season 1 that did not go locally extinct between seasons \((1 - \varepsilon(t))\) and those not occupied in season 1 that were colonised between seasons \((1 - \psi(t)) \gamma(t)\).

Equation 3.1 \[ \psi(t+1) = \psi(t) (1 - \varepsilon(t)) + (1 - \psi(t)) \gamma(t) \]
Using program PRESENCE 3.1 (Hines, 2011) the probabilities for each site were combined to build a likelihood function of these variables. The likelihood function was then maximised to estimate the parameter values for which the observed detection histories were most likely.

3.4 Occupancy models inclusive of covariates

The first model created was the fixed model; in which the $\psi$, $\gamma$, $\epsilon$ and $p$ parameters were assumed constant. The model was then extended to include covariates (MacKenzie et al., 2002, MacKenzie et al., 2006) for each of the parameters. This allowed investigation into the relationships between the covariates chosen and the model variables and develop a model of the factors most important for predicting the dynamic process of occupancy. The model covariates were normalised to ensure that each covariate had equal predictive power to ensure that the beta values (logit regression coefficients produced using Equation 3.2) were not skewed by unevenly large ranges in the data (Mackenzie et al., 2006). The covariates were added to the model using a logit link function (as per Mackenzie et al., 2006) in which a linear combination of the covariate values (which may take any value) are converted to the scale of probability and used to create an extension of the linear regression model which when combined to the original model is able to account for imperfect detection. Occupancy, colonisation, extinction and detectability were expressed in terms of the chosen covariates and the logit regression coefficients ($\beta$ values) as shown in Equation 3.2 which shows the probability of a site being occupied as a function of the covariate values at that site. All covariates were site specific as no remote sensing data was available at a temporal resolution great enough to validate its use in predicting occasion specific values.

Equation 3.2

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \ldots + \beta_U x_{iU},$$

Where $U$ is the maximum number of covariates associated with site $i$. An extra $\beta$ value is required ($\beta_0$) to calculate the intercept of the regression meaning $U + 1 \beta$ values are estimated.

The likelihood maximization was then performed with respect to the $\beta$ parameters from which individual estimates of the model variables were generated for each site.

In order to assess which combination of covariates best explained the detection histories observed it was decided it was not suitable to run all possible models (there were 250000
possible models) and so each model parameter was run against every combination of its covariates whilst fixing the remaining three parameters. The highest ranked 20% of each of these covariate combinations were run against the highest ranked 20% of each of the other parameters covariate combinations based on the assumption that combining the best explanatory covariates for each variable would generate the majority of the top overall models. Within a multi-model inference framework, Akaike’s Information Criterion (AIC) was used to rank and identify the most parsimonious models for the observed data (Burnham & Anderson, 2002). A set of candidate models was generated by selecting those that had a summed AIC weight of at least 0.95 indicating there was 95% confidence that these models best explained the data. The lower the AIC weight, the less predictive power the model is said to have (Burnham and Anderson, 2002).

For the models in the subset overall estimates of occupancy, colonisation, local extinction and detectability (the average of the results for each season), including their corresponding standard errors (MacKenzie et al., 2006), were calculated as shown in Equation 3.3.

\[
\hat{\theta}_{overall} = \frac{\sum_i s_i \hat{\theta}_i}{\sum_i s_i}, \quad var(\hat{\theta}_{overall}) = \frac{\sum_i s_i^2 var(\hat{\theta}_i)}{\sum_i s_i^2}
\]

Where \( s_i \): number of sites of type i, \( \hat{\theta} \): occupancy / colonisation / local extinction / detectability

The models in the subset had similar AIC weights and as there was no justification for choosing between them, a model averaging technique (Burnham & Anderson, 2002) was applied to estimate the average occupancy, colonisation, local extinction and detectability probabilities described by these models (Equation 3.4 which includes standard error).

\[
\hat{\theta}_A = \sum_{j=1}^m w_j \hat{\theta}_j, \quad SE(\hat{\theta}_A) = \sum_{j=1}^m w_j \sqrt{var(\theta_j | m_j) + (\hat{\theta}_j - \hat{\theta}_A)^2}
\]

Where \( w_j \): AIC weight for model \( j \), \( \theta_j \): overall occupancy/colonisation/local extinction/detectability for model \( j \), \( \theta_A \): overall occupancy/colonisation/local extinction/detectability for the averaged model

3.4.1 Estimating and mapping occupancy across the marsh

Once this model had been created, the parameters were applied to all grid squares on the marsh again using program PRESENCE. Depending on its covariate values, a probability of occupancy was generated for each of the grid cells. All AIC weights were identical for both
the model area alone and the entire marsh as the same detection histories were used with which to build the model.

The parameter estimates from the averaged model were then used to map occupancy across the four years for the entire study area. The occupancy probability for each cell was predicted based on the covariate values in that cell as in equation 3.4. This map represents the probability of occupancy for each grid cell rather than each cell simply being occupied or unoccupied.

3.5 Model Covariates

Factors suggested as most likely to impact occupancy have been identified in previous studies (e.g. Guillera-Arroita et al, 2010b; Lahoz-Monfort et al, 2010) and are detailed in Figure 3.4. This study aims to use only covariates generated from remotely sensed sources to enable the application of any models to the entire marsh. For this reason a new selection of possible covariates had to be developed.

<table>
<thead>
<tr>
<th>Covariate Category</th>
<th>Variable</th>
<th>Category</th>
<th>Covariate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupancy / colonisation / local extinction</td>
<td>Habitat type</td>
<td>NDVI</td>
<td>Patch size</td>
</tr>
<tr>
<td></td>
<td>Disturbance</td>
<td>Lake shore or marsh channel</td>
<td>Distance to nearest human settlement</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Burn history</td>
<td>Hunting pressure (village management zone as proxy)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Distance from nearest fire</td>
<td></td>
</tr>
</tbody>
</table>

Fig 3.4 Factors identified in previous studies of *Hapalemur alaotrensis* occupancy in Lac Alaotra (Guillera-Arroita et al, 2010) (light grey) and factors included in the model in this study (dark grey). Black outlines indicate a covariate that was unique to this study.
3.5.1 Occupancy, colonisation and local extinction covariates

Firstly covariates for modelling occupancy, colonisation and extinction were examined. These factors have previously been divided into two groups; (1) habitat quality, required as it is thought that lemurs preferentially inhabit areas of good reed structure for locomotion (Mustchler and Tan, 2003; Garbutt, 2007) and (2) disturbance (Guillera-Arroita et al, 2010).

There are several factors that in combination have a dramatic effect on the habitat type; firstly the vegetation, both in type and in quality and secondly the history of fires and flooding in the area (Guillera-Arroita et al, 2010b). It was decided that both of these factors could be modelled simply using remotely sensed data in the form of a burn history and a vegetation index. It was also assumed that proximity of nearby quality habitat would therefore have an effect on the colonisation rates and local extinction rates of the lemur and whether there was access to the nearby habitat, which would not be true on the edge of a lake or in isolated patches of habitat. The second group of factors; disturbance can be described through the proximity and scale of anthropogenic impacts on the lemur. The covariates of disturbance would not only impact where the lemur occurred but also how easy it was to detect as disturbance would interrupt the normal activity pattern of the lemur and so these covariates are discussed in more detail in the following section.

3.5.2 Detectability covariates

It was hypothesised that the activity level of lemurs would impact detectability as it is easier to spot a moving object than a stationary one. However, this was accounted in the study design which targeted periods of known activity in the lemur (see section 3.1). Secondly the level of anthropogenic disturbance would certainly have an impact on the behaviour of the lemurs as has been shown in previous studies (Guillera-Arroita et al, 2010). The Durrell data collection team did not record data on human traffic and so a retrospective estimate was used. An expert in local fishing pressure was contacted prior to the study to investigate patterns of fishing pressure within the marsh however it was deemed too variable to classify retrospectively (Wallace, pers. comm.) and so it was decided that a proxy for fishing / hunting pressure should be used.

Two variables were used for this firstly distance from nearest human settlement as it was assumed that there would be higher levels of traffic near villages. This was derived from a
point shapefile of human settlements surrounding the lake (see Appendix 1). Secondly four large villages that manage zones of the marsh were used to classify hunting pressure as it is known that lemurs are hunted more readily in some villagers over others (Andrianandrasana et al., 2005; Guillera-Arroita et al., 2010b). This variable was derived through the creation of Thiessen polygons to delineate the marsh into sections classified by the nearest of the four villages (See Appendix 4).

Ability to detect the lemur was also thought to be affected by whether the survey route was one or two sided, meaning whether it was along a lake edge or a marsh channel. It was also thought that weather would affect the movement of the reeds and therefore the ability to pick out a lemur from its habitat however, again, no data had been collected and so this remained a source of unmodelled heterogeneity. Another covariate for which no data was collected was observer name as observers would have differed in their ability to detect lemurs. Finally lake height was assumed to have an effect in allowing the observer to see varying distances over the marsh and so was included as a covariate. A full description of how these variables were included in the model is provided in Table 3.2.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Data type</th>
<th>Initial occupancy</th>
<th>Colonisation</th>
<th>Local extinction</th>
<th>Detectability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time since last burn</td>
<td>Ordinal 0-4 years (capped at 4</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td></td>
<td>as this was the total of available data for the first year of the study</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NDVI</td>
<td>Continuous naturally constrained to the range -1 to 1</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Village management zone</td>
<td>4 dummy binary variables (one for each village as is necessary in presence)</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Distance to nearest village</td>
<td>normalised continuous (-1 to +1)</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Lake edge or marsh channel</td>
<td>binary variable (lake edge =1,</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>marsh channel = 0)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake height</td>
<td>relative lake height ordinal (-1, 0, +1)</td>
<td></td>
<td>x</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
3.6 Remote sensing data

Geotiff files for each of the MODIS products were downloaded and windowed to the Lac Alaotra region (UTM coordinates: min X = 843000, max X = 885000, min Y = 8033000, max Y = 8084000). NASA FTP servers from which the data were downloaded and further processing notes for MODIS data using the MODIS reprojection tool (MRT) and Idrisi Kilamanjaro (Eastman, 2002) are listed in Appendix 5.

In order to generate a remote-sensed estimate for habitat quality, two proxies were examined; normalised differential vegetation index (NDVI) with a 250 resolution (Huete et al., 1999) and tasselled cap greenness with only a 500m resolution (Zhang et al., 2002). After comparison of both NDVI and tasselled cap greenness maps with Landsat images of the same years from previous studies (e.g. Andrianandrasana, 2009) it was decided that NDVI was the most accurate reflection of the vegetation across the years. Habitat quality was derived from the high resolution 250m x 250m normalised difference vegetation index (NDVI) product (Huete et al., 1999).

3.6.1 Burn History

A burn history for each grid cell was derived from the MODIS burned area product (Justice et al., 2006) combined with the FIRMS active fire data (Giglio, 2010). The burned area product data is only available at a 500m resolution meaning 4 grid squares would share the same burn history. For each cell, a value of 1 or 0 was generated, recording a 1 if it was burned in either the burned area image or had at least one active fire for that year from the FIRMS data. Attempts have been made to make field observations of burned areas in the marsh with limited success (Young and Long, pers. comm.). The covariate generated ‘time since last burn’ for which there was a large range of values from (0-4 years) capped at 4 as this was the extent of data availability for 2004.

Appendix 2 contains the maps of burned areas combined with active fire data from the FIRMS database for the four years of this study and Figure 3.5 shows the resulting maps of time since last burn used as a covariate in this study. Any grid square containing either a burned area point or an active fire point is assumed entirely burned. Using these assumptions a total area burned was calculated and is presented in Table 3.3, including data.
for 2001-2003 that was used to create the time since last burned covariate. As can be seen for the years 2003-2004, 2004-2005 and 2006-2007 have abnormally large burned areas, with 6, 12 and 14 percent of the marsh burned respectively.

Figure 3.5 Maps of time since last burned for 2004-2007. The values were capped to 4 years as this was the maximum available for 2004 and so was required to avoid biasing data in later years.
Table 3.3 A summary of the total number of cells burned as observed by the MODIS burned area dataset and the FIRMS active fire database. The number of cells is then extrapolated to generate a total area burned and the percentage of the marsh this presents. This table includes years 2000-2003 as these years were used to generate the time since last burned covariate.

<table>
<thead>
<tr>
<th>Period</th>
<th>No. of cells burned</th>
<th>Area burned (ha)</th>
<th>Percentage marsh burned (of 24000ha total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mar 2000 – Mar 2001</td>
<td>33</td>
<td>206.25</td>
<td>0.86</td>
</tr>
<tr>
<td>Mar 2001 – Mar 2002</td>
<td>51</td>
<td>318.75</td>
<td>1.33</td>
</tr>
<tr>
<td>Mar 2002 – Mar 2003</td>
<td>13</td>
<td>81.25</td>
<td>0.34</td>
</tr>
<tr>
<td>Mar 2003 – Mar 2004</td>
<td>254</td>
<td>1587.5</td>
<td>6.61</td>
</tr>
<tr>
<td>Mar 2005 – Mar 2006</td>
<td>20</td>
<td>125</td>
<td>0.52</td>
</tr>
<tr>
<td>Mar 2006 – Mar 2007</td>
<td>556</td>
<td>3475</td>
<td>14.48</td>
</tr>
</tbody>
</table>

3.6.2 Lake height

Lake height was downloaded from the National Snow and Ice Data Centre (NSIDC) archive in the form of IceSAT surface elevation data granules (GLAS06 version 31 (Zwally et al, 2011)) from orbits that intersected the Lac Alaotra region during the entire lifetime of the satellite (2003-2010) of which there was only 5 instances. For years when an estimate of lake height was not recorded, the mean of all other available years was used as was the case in 2005. The results are shown in Table 3.4 and are accurate to within 10cm (Zwally et al, 2011). The relative lake height fluctuates significantly between years with 2004 and 2006 having low water levels and years 2007 and 2009 having high water levels relative to the mean.

Table 3.4 Lake height estimates from IceSAT (GLAS06 version 31) accurate to within 10cm for all available years

<table>
<thead>
<tr>
<th>Date</th>
<th>Lake elevation from GLAS (m)</th>
<th>Lake elevation on date minus mean lake elevation (m)</th>
<th>Relative water level on date</th>
</tr>
</thead>
<tbody>
<tr>
<td>6th Jan 2004</td>
<td>743.89</td>
<td>-0.98</td>
<td>low</td>
</tr>
<tr>
<td>18th Oct 2004</td>
<td>744.30</td>
<td>-0.57</td>
<td>low</td>
</tr>
<tr>
<td>11th Aug 2006</td>
<td>744.34</td>
<td>-0.53</td>
<td>low</td>
</tr>
<tr>
<td>26th Mar 2007</td>
<td>745.83</td>
<td>0.96</td>
<td>high</td>
</tr>
<tr>
<td>23rd Mar 2009</td>
<td>746.00</td>
<td>1.13</td>
<td>high</td>
</tr>
<tr>
<td>Mean</td>
<td>744.87</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Covariate maps were generated for all the variables in ArcMap ver. 9.3.1 (ESRI, 2009) and are displayed in Appendices 1-5.

3.7 Analysis of DISTANCE data

Density estimates (individuals/hectare) were calculated using Distance v6.0 Release 2 (Thomas et al, 2010), with individual survey routes assigned as sampling units. Route length
was used to estimate survey effort, being multiplied by two when it passed through areas of marsh that made it possible to survey from both sides of the canoe.

Analysis was carried out on lemur clusters rather than individuals and group size was recorded. In order to fulfill the requirement that detection probability is one on the transect, distance to group was estimated from the edge of the reeds (Thomas et al, 2010). Distance was recorded in intervals as recommended by Thomas et al (2010). The intervals used are shown in Table 3.5. This technique prevents rounding by surveyors and therefore provides more accurate data for analysis. The maximum distance was truncated by 5% to remove any obvious outliers which contain little information used for density estimation (Buckland et al, 2001).

Analysis was run using the following combinations of key functions and series expansions as recommended by Buckland et al (2001); uniform function with cosine/simple polynomial adjustment, half-normal function with cosine/hermite polynomial adjustment, and hazard-rate function with cosine/simple polynomial adjustment.

<table>
<thead>
<tr>
<th>Interval name</th>
<th>Interval (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Int1</td>
<td>0-2</td>
</tr>
<tr>
<td>Int2</td>
<td>3-4</td>
</tr>
<tr>
<td>Int3</td>
<td>5-6</td>
</tr>
<tr>
<td>Int4</td>
<td>7-10</td>
</tr>
<tr>
<td>Int5</td>
<td>11-13</td>
</tr>
<tr>
<td>Int6</td>
<td>14+</td>
</tr>
</tbody>
</table>

The estimates were then post stratified year to generate an estimate of density for all four years using a global detection function as there were insufficient data points in each year individually to calculate accurate separate detection functions. Lake height was used as part of a multi-covariate distance analysis that allowed the detection function to be altered dependent on the water height in the year as it was thought that with higher water height the ability to detect lemurs further into the marsh would be increased.
4. Results
4.1 Summary of observations

During the study, 596 lemurs were observed in 199 groups. More detailed observation data with a break down for the individual years is shown in Table 4.1. As can be seen there is a large fluctuation in relative abundance and the number of sites in which these individuals occurred. Years 2004 and 2006 had relatively low lemur observations and sites whilst 2005 and 2007 are relatively high. The group sizes encountered ranged from 1 to 10 and the mean group size recorded was 3.1103 with a ratio of 4:1 adults to juveniles. Group size frequencies are displayed in Figure 4.1. A map of the observations is also displayed in Figure 4.2.

Table 4.1 A summary of the observations made across the four study seasons

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of lemurs observed</th>
<th>No. Sites in which observed</th>
<th>Average group size</th>
<th>Relative abundance (lemurs / km of survey)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>105</td>
<td>23</td>
<td>3.17</td>
<td>0.40</td>
</tr>
<tr>
<td>2005</td>
<td>202</td>
<td>48</td>
<td>3.14</td>
<td>0.87</td>
</tr>
<tr>
<td>2006</td>
<td>102</td>
<td>26</td>
<td>2.76</td>
<td>0.33</td>
</tr>
<tr>
<td>2007</td>
<td>193</td>
<td>43</td>
<td>2.89</td>
<td>0.53</td>
</tr>
</tbody>
</table>

A route regression provided no support for a significant trend in relative abundance across the four study seasons (df= 53, t=-0.8014590, p=0.4264).

Figure 4.1 Frequency group sizes observed during the study
Figure 4.2 A map of observations made across the 4 years. Only the southern part of the marsh is shown as although there were two transects in the north in 2007, no lemurs were observed.

As can be seen in Figure 4.2, the location of observation remains similar between years however frequency varies greatly. Figure 4.3 is a map showing all observations made in relation to the protected area boundary and no take zones. As can be seen few observations are made within the no take zones. Zone D is consistently occupied by a high abundance of lemurs.
Figure 4.3 A map of all observations made during the study overlaid with the protected area boundary and no take zones.
4.2 Occupancy

4.2.1 Fixed model
This model assumes that occupancy, colonisation, local extinction and detection probabilities are constant across sites and surveys and is denoted here with a dot to indicate that no parameter is to be estimated. Program Presence first calculates the occupancy without accounting for detectability known as the ‘naive occupancy’. The estimation consists simply of calculating the proportion of sites for which there is at least one observed lemur in the detection history across the four seasons. This study generated naive occupancy estimates of 5.46% in 2004, 13.52% in 2005, 6.91% in 2006 and 13.19% in 2007. The fixed model accounting for colonisation, local extinction and detectability was then computed. The AIC obtained for this model was 1544.4 and the model parameters estimated are shown in Table 4.5. Occupancy increased across the four year period from 10% in 2004 to 21.5% in 2007 (Figure 4.4). Detectability across the four seasons was estimated at 19.6% suggesting that many of the lemurs in the marsh remained undetected during the surveys. The average estimate of occupancy generated by the fixed model (18%) is therefore inflated in comparison to the naive estimate to reflect this low detection probability.

Figure 4.4 The trend in total percentage occupancy (average occupancy probability for whole study site) (+/- 1 Std. error) generated by the fixed model
4.2.2 Covariate inclusive models

The models were ranked based on AIC value and as can be seen in Table 4.2, the covariates for initial occupancy (time since last burn and NDVI) remain largely unchanged in the top models suggesting there is a large amount of support for their inclusion. Village management zone has little support for its inclusion as there is few data in 2004 (only 23 sites containing a detection) for which to provide support for a four level covariate. It was able to be fit to colonisation and local extinction as estimates of the parameters are derived from the pooled data from 2005-2007.

When modelling colonisation there is similar support for time since last burn, marsh channel or lake edge and village management zone suggesting they have important roles to play in the dynamics of the system. The results are similar for local extinction with NDVI replacing time since last burn. Here village management zone was supported in all models in the top set as the estimates for colonisation and extinction are based on three years worth of data which seems to provide overwhelming support for its inclusion. All models for which village management zone was not included as a parameter for both colonisation and local extinction could not be fit as there was too large an element of unmodelled heterogeneity all sites had 95% confidence intervals of 0-1 probability of occupancy and errors could not be calculated).

Covariates of detectability were more varied, although village management zone and distance from nearest village have a very high level of support whilst lake height has less of an impact than expected. More detail on covariate support is displayed in Table 4.3.
Table 4.2 shows the top ten models based on AIC value together with the averaged model. T= Time since last burned, N= NDVI, V= Village management zone, L= Lake edge or marsh channel, D= Distance to nearest village, H= Lake height

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>AIC Weight</th>
<th>Delta AIC</th>
<th>No. Parameters</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \psi(T,N) \gamma(T,V,L,D) \varepsilon(V,L,N,D) p(V,D) )</td>
<td>1475.85</td>
<td>0.5352</td>
<td>0.00</td>
<td>25</td>
</tr>
<tr>
<td>( \psi(T,N) \gamma(T,V,L,D) \varepsilon(V,L,N,D) p(V,L,D) )</td>
<td>1477.42</td>
<td>0.2441</td>
<td>1.57</td>
<td>26</td>
</tr>
<tr>
<td>( \psi(N,L) \gamma(T,V,L,D) \varepsilon(T,V,D) p(V,L,D) )</td>
<td>1479.30</td>
<td>0.0954</td>
<td>3.45</td>
<td>25</td>
</tr>
<tr>
<td>( \psi(T,N) \gamma(T,V,L,D) \varepsilon(T,V,L,N) p(V,D,H) )</td>
<td>1479.65</td>
<td>0.0800</td>
<td>3.8</td>
<td>26</td>
</tr>
<tr>
<td>( \psi(T,N) \gamma(T,V,L) \varepsilon(T,V,L,N) p(V,D) )</td>
<td>1480.86</td>
<td>0.0438</td>
<td>5.01</td>
<td>25</td>
</tr>
<tr>
<td>( \psi(T,N) \gamma(T,V,L) \varepsilon(T,V,L,N) p(V,D) )</td>
<td>1488.45</td>
<td>0.0010</td>
<td>12.6</td>
<td>25</td>
</tr>
<tr>
<td>( \psi(T,N) \gamma(T,V,L,D) \varepsilon(L,N,D) p(V,L,N,H) )</td>
<td>1492.07</td>
<td>0.0002</td>
<td>16.22</td>
<td>23</td>
</tr>
<tr>
<td>( \psi(V,L) \gamma(T,N,V) \varepsilon(T,V,L,N) p(V,L,D) )</td>
<td>1492.28</td>
<td>0.0001</td>
<td>16.43</td>
<td>24</td>
</tr>
<tr>
<td>( \psi(T,N) \gamma(T,V,L) \varepsilon(V,L,N) p(V,D) )</td>
<td>1493.48</td>
<td>0.0001</td>
<td>17.63</td>
<td>23</td>
</tr>
<tr>
<td>( \psi(V,L,N,D) \gamma(V,L,D) \varepsilon(V,L,N) p(V,D) )</td>
<td>1493.51</td>
<td>0.0001</td>
<td>17.66</td>
<td>25</td>
</tr>
<tr>
<td>( \psi(.) \gamma(.) \varepsilon(.) p(.) )</td>
<td>1543.44</td>
<td>0.0000</td>
<td>69.59</td>
<td>4</td>
</tr>
</tbody>
</table>

Table 4.3 Support for each covariate in the top 100 models and the model set used in model averaging (summed AIC weight of 0.95). T= Time since last burned, N= NDVI, V= Village management zone, L= Lake edge or marsh channel, D= Distance to nearest village, H= Lake height

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Top Set</th>
<th>Top 100 Models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial occupancy</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>75%</td>
<td>84%</td>
</tr>
<tr>
<td>N</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>V</td>
<td>0%</td>
<td>44%</td>
</tr>
<tr>
<td>L</td>
<td>25%</td>
<td>43%</td>
</tr>
<tr>
<td>D</td>
<td>0%</td>
<td>53%</td>
</tr>
<tr>
<td>Colonisation</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>100%</td>
<td>43%</td>
</tr>
<tr>
<td>N</td>
<td>0%</td>
<td>41%</td>
</tr>
<tr>
<td>V</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>L</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>D</td>
<td>100%</td>
<td>57%</td>
</tr>
<tr>
<td>Local extinction</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>50%</td>
<td>49%</td>
</tr>
<tr>
<td>N</td>
<td>50%</td>
<td>57%</td>
</tr>
<tr>
<td>V</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>L</td>
<td>75%</td>
<td>100%</td>
</tr>
<tr>
<td>D</td>
<td>75%</td>
<td>47%</td>
</tr>
<tr>
<td>Detectability</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>0%</td>
<td>44%</td>
</tr>
<tr>
<td>V</td>
<td>100%</td>
<td>100%</td>
</tr>
<tr>
<td>L</td>
<td>50%</td>
<td>67%</td>
</tr>
<tr>
<td>D</td>
<td>100%</td>
<td>84%</td>
</tr>
<tr>
<td>H</td>
<td>25%</td>
<td>59%</td>
</tr>
</tbody>
</table>

Only the top four models were selected to create an averaged model as this encapsulated 95% of the AIC weight meaning there was 95% confidence that the averaged model was the best estimate possible from the data. A summary of the parameter estimates generated are
shown in Table 4.6. The occupancy probability fluctuates between years reflecting the pattern in the collected data with occupancy of between 19% in 2004 and 21% in 2007 as shown in the graph in Figure 4.5. Detectability is also lower for all years than in the fixed model as expected, resulting in these higher occupancy estimates. The estimates from the averaged model suggests that local extinction levels remain fairly constant through the years only dipping by 3% in one year whilst colonisation seems more variable building across the years from 7% in 2005 to 11% in 2007. One problem with this model is that detectability is constant across occasions as there were no occasion specific covariates in the averaged model.

![Figure 4.5 Percentage occupancy (+/- 1 std. error) as predicted using the averaged occupancy model across the four years of this study when applied to the entire study area](image)

4.2.3 Top model

The top model \( \psi(T,N) \gamma(T,V,L,D) \epsilon(V,L,N,D) \beta(V,D) \) was examined in further detail and beta estimates for the covariates that were used to model each parameter were generated as shown in Table 4.4.

4.2.3.1 Initial occupancy covariates

When examining the beta estimates for initial occupancy (Table 4.4), it can be seen that both time since last burn and NDVI have a positive relationship with occupancy, meaning
occupancy increases in concert with both covariates. The inverse logit of the burn history and NDVI slopes can then be graphed using equation 3.4 to provide an estimate for $\psi$. A graph in which varying time since last burn is plotted with five constant values for NDVI(-1, -0.5, 0, 0.5, 1) has been plotted (Figure 4.6). It is worth noting that these are theoretical combinations as the two variables graphed co-vary meaning an NDVI of 1 and a time since last burned value of 0 would not occur in the same cell.

Table 4.4 Logit regression coefficient (beta) estimates of each of the model covariates. A positive number suggests a positive relationship between the covariate and the model parameter it is a predictor of and vice versa

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Covariate</th>
<th>Beta estimate</th>
<th>Std. Error</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupancy</td>
<td>intercept</td>
<td>-1.960</td>
<td>0.346</td>
</tr>
<tr>
<td></td>
<td>Time since last burn</td>
<td>0.476</td>
<td>1.871</td>
</tr>
<tr>
<td></td>
<td>NDVI</td>
<td>1.124</td>
<td>0.297</td>
</tr>
<tr>
<td>Colonisation</td>
<td>intercept</td>
<td>-8.279</td>
<td>2.884</td>
</tr>
<tr>
<td></td>
<td>Time since last burn</td>
<td>6.170</td>
<td>1.907</td>
</tr>
<tr>
<td></td>
<td>Ambodivoara vmz</td>
<td>3.249</td>
<td>1.938</td>
</tr>
<tr>
<td></td>
<td>Andilana-Sud vmz</td>
<td>5.403</td>
<td>3.475</td>
</tr>
<tr>
<td></td>
<td>Andreba vmz</td>
<td>4.283</td>
<td>2.842</td>
</tr>
<tr>
<td></td>
<td>Anororo vmz</td>
<td>-17.563</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>Lake or marsh</td>
<td>-0.692</td>
<td>3.385</td>
</tr>
<tr>
<td></td>
<td>Distance to settlement</td>
<td>0.203</td>
<td>3.700</td>
</tr>
<tr>
<td>Local extinction</td>
<td>Intercept</td>
<td>-0.894</td>
<td>2.140</td>
</tr>
<tr>
<td></td>
<td>Ambodivoara vmz</td>
<td>-2.402</td>
<td>0.615</td>
</tr>
<tr>
<td></td>
<td>Andilana-Sud vmz</td>
<td>0.143</td>
<td>1.438</td>
</tr>
<tr>
<td></td>
<td>Andreba vmz</td>
<td>1.037</td>
<td>1.246</td>
</tr>
<tr>
<td></td>
<td>Anororo vmz</td>
<td>0.364</td>
<td>0.761</td>
</tr>
<tr>
<td></td>
<td>Lake or marsh</td>
<td>1.724</td>
<td>1.500</td>
</tr>
<tr>
<td></td>
<td>NDVI</td>
<td>-0.028</td>
<td>2.283</td>
</tr>
<tr>
<td></td>
<td>Distance to settlement</td>
<td>3.702</td>
<td>1.146</td>
</tr>
<tr>
<td>Detectability</td>
<td>Intercept 2004</td>
<td>-0.813</td>
<td>0.406</td>
</tr>
<tr>
<td></td>
<td>Intercept 2005</td>
<td>1.423</td>
<td>0.607</td>
</tr>
<tr>
<td></td>
<td>Intercept 2006</td>
<td>-1.157</td>
<td>0.538</td>
</tr>
<tr>
<td></td>
<td>Intercept 2007</td>
<td>0.579</td>
<td>0.633</td>
</tr>
<tr>
<td></td>
<td>Ambodivoara vmz</td>
<td>-1.011</td>
<td>1.431</td>
</tr>
<tr>
<td></td>
<td>Andilana-Sud vmz</td>
<td>-0.834</td>
<td>1.069</td>
</tr>
<tr>
<td></td>
<td>Andreba vmz</td>
<td>0.059</td>
<td>1.724</td>
</tr>
<tr>
<td></td>
<td>Anororo vmz</td>
<td>-1.688</td>
<td>1.162</td>
</tr>
<tr>
<td></td>
<td>Distance to settlement</td>
<td>-0.235</td>
<td>1.404</td>
</tr>
</tbody>
</table>
### Table 4.5 Model parameter estimates (probabilities) for the fixed model across the four seasons after applying the model to the entire marsh area

<table>
<thead>
<tr>
<th>Probabilities</th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>Std. error</td>
<td>95% CI</td>
<td>Estimate</td>
</tr>
<tr>
<td>Initial occupancy</td>
<td>0.1005</td>
<td>0.0214</td>
<td>0.0657-0.1509</td>
<td>0.1585</td>
</tr>
<tr>
<td>Colonisation</td>
<td></td>
<td></td>
<td></td>
<td>0.0974</td>
</tr>
<tr>
<td>Local extinction</td>
<td></td>
<td></td>
<td></td>
<td>0.2943</td>
</tr>
<tr>
<td>Detectability</td>
<td>0.1958</td>
<td>0.0202</td>
<td>0.1592-0.2385</td>
<td>0.1958</td>
</tr>
</tbody>
</table>

### Table 4.6 Model parameter estimates (probabilities) for the averaged model across the four seasons after applying the model to the entire marsh area

<table>
<thead>
<tr>
<th>Probabilities</th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Estimate</td>
<td>Std. error</td>
<td>95% CI</td>
<td>Estimate</td>
</tr>
<tr>
<td>Initial occupancy</td>
<td>0.1910</td>
<td>0.0609</td>
<td></td>
<td>0.1781</td>
</tr>
<tr>
<td>Colonisation</td>
<td>0.0727</td>
<td>0.0203</td>
<td></td>
<td>0.0889</td>
</tr>
<tr>
<td>Local extinction</td>
<td>0.3712</td>
<td>0.1050</td>
<td></td>
<td>0.3409</td>
</tr>
<tr>
<td>Detectability</td>
<td>0.1170</td>
<td>0.0301</td>
<td></td>
<td>0.1777</td>
</tr>
</tbody>
</table>
4.2.3.2 Colonisation and local extinction and detection covariates

As shown in Table 4.4 Lake edge or marsh channel has a negative relationship with colonisation suggesting that colonisation probability is lower for lake edges than for marsh channels, it also has a positive relationship with extinction meaning the probability of local extinction was higher for lake edges than for marsh channels. Surprisingly NDVI also has a marginal positive relationship with local extinction suggesting that risk of extinction increased with marginally higher NDVIls a result that will be discussed later in this study. Another unexpected result was the increased chance of extinction with distance from village away from what is thought to be higher anthropogenic pressures. There is some support for NDVI as a proxy for habitat type as a source of variation in detectability however it was not represented in the top models predicted in this study. This meant there was a lack of occasion (or survey) specific variables with which to model detectability and so it was allowed to vary across the years in an attempt to capture some of the temporal heterogeneity. As a result, detectability is lower in 2004 and 2006 than in 2005 and 2007 reflecting the relative abundances in Table 4.1.

4.2.3.3 Village management zone results

Village management zone should be examined in more detail as although colonisation is more likely in the Ambodivoara, Andilana-Sud and Andreba zones, there is also a positive
relationship with chance of local extinction in Andilana-Sud and Andreba suggesting these are very dynamic zones. Ambodivoara is the only zone in which colonisation is high and extinction low. Anororo has a negative relationship with colonisation and a positive relationship with local extinction suggesting lemur numbers are declining in that zone particularly.

4.2.3.4 Occupancy maps

The maps of occupancy were created using the occupancy estimates from the averaged model and are shown in Figure 4.7. In 2004 there was no effect of village management zone as a covariate and so there is a clear pattern of low occupancy in low NDVI and time since last burn areas. In 2005-2007 as occupancy is derived from colonisation and extinction, village management zone becomes an important predictor of occupancy as is clear from the straight edges in the centre of the maps. There is obvious grouping of areas of high occupancy close to areas of low occupancy on these maps suggesting that displacement of the lemurs may be occurring. There are high levels of occupancy on the south east edge of the marsh and the south west as was found in the observations showing that the model has accurately captured this data. Figure 4.8 shows the map of occupancy in 2007 overlaid with the national park and no take zone boundaries. 2007 was chosen as it is representative of the distribution across the years (excluding 2004) and the distribution of fire is clear across the South West of the marsh. A similar figure for 2004 is shown in Appendix 6.

Figure 4.8 shows that there are large portions of the no take zones (e.g. E and large parts of A) that contain no habitat that is predicted to be occupied. Zones A and B contain large areas of burnt marsh suggesting that designation as a no take zone has little impact on the treatment the marsh receives from the local people. Both zone A and B do however contain patches of habitat that are predicted to have a very high probability of occupancy (>70%).
Figure 4.7 Occupancy maps showing the predicted probability of occupancy of each grid cell based on the estimates generated by the averaged occupancy model.
Figure 4.8 Map of 2007 predicted occupancy based on the averaged model, overlaid with the protected area boundary and no take zones
4.3 Estimating density

The density model selected was Half normal – Cosine on which a chi-squared goodness of fit test was performed showing no evidence for a lack of fit (DF=2, Chi-Sq =0.2532, p=0.8811). A global detection function is shown in Appendix 7. This detection function was then re-estimated using distance from mean lake elevation as a covariate, resulting in a separate detection function for each lake height as shown in Figure 4.9.

![Figure 4.9 detection functions resulting from the multi-covariate distance analysis for 3 relative lake elevations](image)

This shows that in 2007 even though the lake height was higher than in previous years there is a weaker detection curve suggesting that the ability to detect lemurs dropped off more quickly in years of higher water level, contrary to initial hypotheses, however this is likely to have been compounded by small sample sizes in the year of low water level. Table 4.7 contains the estimates of density calculated by this density model with coefficient of variation and 95% confidence intervals.
Table 4.7 Density estimates for each year produced by multicovariate distance analysis using lake height as a covariate

<table>
<thead>
<tr>
<th>Year</th>
<th>Density (lemurs/ha)</th>
<th>Std. error</th>
<th>% Coefficient of variation</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>2004</td>
<td>0.359</td>
<td>0.113</td>
<td>32.03</td>
<td>0.185</td>
<td>0.675</td>
</tr>
<tr>
<td>2005</td>
<td>0.671</td>
<td>0.211</td>
<td>31.23</td>
<td>0.360</td>
<td>1.270</td>
</tr>
<tr>
<td>2006</td>
<td>0.294</td>
<td>0.129</td>
<td>43.45</td>
<td>0.124</td>
<td>0.706</td>
</tr>
<tr>
<td>2007</td>
<td>0.726</td>
<td>0.268</td>
<td>36.66</td>
<td>0.349</td>
<td>1.533</td>
</tr>
</tbody>
</table>

The coefficients of variation on these estimates mean that the results produced should be used with caution and have large associated errors. 92.9% of the variation was due to variation in encounter rate which is expected when studying a species with patchy distribution (Buckland et al, 2004). Estimates fluctuate between years; 2004 and 2006 have relatively low and 2005 and 2007 relatively high densities.

4.4 Estimating population size

The estimate of percentage occupancy multiplied by the total area surveyed provided an estimate of area of occupancy which was then multiplied by density estimate for that year generated an estimate of population size. A population range estimate can be generated for the 4 years of the study of between 2053 +/- 1662 and 6105 +/- 2504 with a mean of 3766. It is clear that according to this model area of occupancy does not vary greatly with year, whilst the density estimates vary by over 100% and have error of a magnitude that unreliable. These results are summarised in Table 4.8 and a graph of the population estimates over time is presented (Figure 4.10).

Table 4.8 Population estimates for the four years of the study, together with estimates of area of occupancy and density estimates for each year of the study. The error for the area occupied is the standard error of the 4 estimates used to create the averaged model

<table>
<thead>
<tr>
<th></th>
<th>2004</th>
<th>2005</th>
<th>2006</th>
<th>2007</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage occupancy</td>
<td>19.1 +/- 6.09</td>
<td>17.8 +/- 2.25</td>
<td>19 +/- 4.13</td>
<td>22.9 +/- 4.56</td>
</tr>
<tr>
<td>Area occupied (ha)</td>
<td>7009 +/- 1461</td>
<td>6535 +/- 540</td>
<td>6977 +/- 991</td>
<td>8405 +/- 1094</td>
</tr>
<tr>
<td>Density estimate (per ha)</td>
<td>0.359 +/- 0.113</td>
<td>0.671 +/- 0.211</td>
<td>0.294 +/- 0.129</td>
<td>0.726 +/- 0.268</td>
</tr>
<tr>
<td>Estimated no. of lemurs</td>
<td>2517 +/- 1662</td>
<td>4389 +/- 1481</td>
<td>2053 +/- 1339</td>
<td>6106 +/- 2504</td>
</tr>
</tbody>
</table>
Figure 4.10 A graph of population estimates of the Alaotran gentle lemur generated through the combination of occupancy estimates and density estimates using DISTANCE. Results are shown +/- 1 RMSE.
5. Discussion
5.1 Overview

The population estimates generated by the averaged model in this study ranged between 2053 +/- 1339 and 6106 +/- 2504 (+/- 1 RMSE). The fluctuations in these estimates are not biologically possible and the associated errors are relatively large meaning their reliability must be examined. The mean (3766) and total range of the estimates are of a similar magnitude to estimates of the lemur population size that have been calculated between 1994 (7500) and 2002 (2840) (Mutschler and Feistner, 1995; Ralainasolo, 2006). Although this technique has allowed the generation of an estimate of reasonable magnitude, no patterns can be inferred as the variation is too large.

The study has also confirmed the feasibility of using detection-non detection data to describe occupancy for the Alaotran gentle lemur. Overall occupancy estimates are comparable to those generated by Guillera-Arroita et al (2010b) of 20.29% in comparison to a range of 17.81% to 22.91% in this study. There is however, a difference in detection probability between this and the previous study. Guillera-Arroita et al produced an estimate of 6.4% compared to the average estimate of 14.9% in this study. It is thought the difference in detection is likely a combination of the lack of occasion specific detection data collected in this study and an artefact of the different data collected in the studies. For example, Guillera-Arroita et al carried out their study in 2008, a year with little burning and as can be seen in Table 4.6, detectability was lower in 2004 and 2006; years with less area burned.

Density estimates also fluctuate greatly between years (Table 4.7) ranging from 0.294 +/- 0.129 to 0.726 +/- 0.268 lemurs/ha in 2006 and 2007 respectively. The years predicted to have the largest density (and population size) estimates are the years with the largest areas of burning. It is hypothesised that the increased density estimates were the result of crowding or clumping of lemurs that were displaced by the fire. The same effect is noted in the detectability predicted in the averaged occupancy model with an increased estimate of 17.7% in 2005 compared with 11.7% in 2004. It was thought that the area occupied would decrease and therefore account for the inflated density estimates, however there were no such significant declines. This lack of a decline may be an intrinsic effect of the lack of a probabilistic sampling design. Guillera-Arroita et al (2010b) suggest that the lemurs
preferentially inhabit areas further from edges to avoid weather conditions and other edge effects. During a year of large burns, lemurs may be displaced from interior areas where they would normally remain undetected to edges where the surveys pick them up and so artificially inflate occupancy estimates.

5.2 Distribution of occupied habitat

Although the estimates of occupancy fluctuate between years, the distribution of the population is predicted to remain relatively similar (excluding 2004). The predicted distribution is similar to that of the suitable habitat predicted by Lahoz-Monfort et al. (2010) as shown in Appendix 8 suggesting that the integrity of the occupancy model has been maintained when applying it to the entire marsh. Large areas of marsh in the South-West and the South-East of marsh are predicted to be both suitable and occupied. Lahoz-Monfort et al. predict there to be some suitable habitat in the centre of the marsh, although this study predicts a low probability of occupancy for the same areas (Figure 4.7).

The lack of a decline in abundance in 2007 despite large burns, could also be explained spatially. It appears that burns in 2007 took place in similar areas to those burnt in 2005 which remain unoccupied throughout 2006. Fire also occurs in the centre of the marsh, again an area that is predicted to be unoccupied in 2006 meaning there are very few occupied sites that are affected by the burn.

Occupancy maps (Figure 4.7) also provide a potential mechanism for the survival of the lemurs in large burn years. It seems that the lemur population is displaced to new areas within the marsh as was suggested by the detectability estimates of both the occupancy and distance models. Areas of fire in the South West of the marsh are surrounded by areas that are predicted to have a very high level of occupancy. This suggests that when areas were burnt, lemurs migrated to new habitat nearby.

The predictions on the drivers of changes in occupancy through the processes of colonisation and local extinction are one of the significant results from this study. Understanding the mechanisms of these processes is an important part of conservation action on a rare species such as the lemur (Yuttam et al., 2003; Akcakaya et al., 2007) as they can direct management objectives such as need for maintenance of corridors for the
hypothesised displacement of the lemurs to occur. It is also clear that there is a need for a continuation for the community education work that has been carried out by Durrell in previous years aimed at reducing the prevalence of fires across the marsh.

5.3 Occupancy model findings

5.3.1 Initial occupancy covariates

As expected, NDVI; a proxy for habitat type, and time since last burn of each grid cell were important predictors of occupancy in 2004. However as Figure 4.6 shows, no combination of these two covariates can provide 100% probability of occupancy for a patch which suggests that there is at least some unmodelled heterogeneity in this parameter. This was expected due to the inability to fit village management zone to this model parameter. It is thought the management zone covariate could not be fitted as the number of cells in which lemurs were present in 2004 was only 23 which was unable to provide support for the 4 levels of the covariate. For this reason the occupancy map in 2004 is thought not to represent the lemur distribution as certainly but does provide an insight into the effect of habitat type and fire on the lemur.

5.3.2 Colonisation and local extinction covariates

As shown in Table 4.4, time since last burn, village management zone, lake edge or marsh channel and distance to settlement are important predictors of colonisation. Similar predictors are important in predicting local extinction with time since last burn and lake or marsh replaced by NDVI. As time since last burn is an important predictor of colonisation, it can be hypothesised that lemurs prefer habitat with a uniform history or suitability as is supported by negative relationship between NDVI and local extinction. It is also clear that as hypothesised areas bordered by lakes are less likely to be colonised as the lakes provide a barrier to movement.

As distance from settlement increases, both colonisation and extinction increase. This provides yet further evidence that the marsh is a very dynamic system suggesting that areas in the centre of the marsh are both colonised and go locally extinct on a regular basis. This may be the result of migrants that are looking for new habitat and so move through the grid squares or possibly an area of high hunting which creates a “sink” area that is colonised by
“source” areas toward the edge of the marsh (Pulliam, 1988). Unfortunately the correlation does not indicate causation and as yet the reasons for this pattern can only be speculated upon.

The pattern of colonisation and extinction in the different management zones seems to provide support for the observed pattern of hunting being common in the village of Anororo (Andrianandrasana et al, 2005) exhibiting a positive relationship with local extinction and a negative relationship with colonisation. This pattern is not observed for Ambodivoara which is also suspected of carrying out lemur hunts, although manual assessment of the results show that very few lemurs were observed close to Ambodivoara (Figure 4.2) and so there is little chance for extinction to be recorded. Although there is some local extinction observed in the Andreba and Andilana-Sud management zones, this is expected as a part of normal population dynamics (Hanski, 1998).

The willingness of fishermen to travel large distances across the marsh to catch the best fish (Wallace, pers. comm.) means responsibility for hunting in a particular zone cannot be assigned to the people living in that zone with any certainty. Travelling elsewhere to hunt is likely to occur as there is law prohibiting lemur hunting and so people may travel away from their village in order to minimise the chances of being caught.

It is worth noting that village management zone is a very crude proxy for hunting pressure and although there is a great deal of support for the covariate, it is possible that it encapsulates some other variation that is otherwise not included in the model and so the results should be used with caution.

### 5.3.3 Detection covariates

The covariates that best represent detectability according to both the best and averaged models are village management zone, lake edge or marsh channel and distance from human settlements. All these variables are site specific rather than occasion specific, meaning that any heterogeneity between study occasions is not captured in these models. Detectability does vary inversely with relative abundance, although not sufficiently to account for this variation. Guillera-Arroita et al (2010b) showed that an important predictor of detectability is fishing traffic on the survey routes. If a fishing canoe travels down a channel and scares
away any lemurs, and soon after the survey is carried out, detectability will be significantly reduced. Unfortunately, traffic data were not collected during the study and there was no method for deriving a proxy for this variable using remote sensing. The importance of disturbance is demonstrated within the models in this study in the form of distance from nearest settlement, with detectability increasing toward the centre of the marsh. There are several possible explanations for this result; firstly it is thought that the lemur is unlikely to occupy the centre of the marsh as the habitat is more uniform and lacks the diversity required for the lemur to survive (Mutschler and Feistner, 1995). Secondly it is likely there are fewer fishermen in the centre of the marsh and so detectability may increase as less human contact occurs. Without occasion specific disturbance variables, the resulting models are not able to account for a variation in detectability that is likely to occur and so may underestimate occupancy in some situations. This variable is a necessity should further occupancy studies be carried out on the lemur. Detection is also higher in Andreba, a village that has not been recorded as carrying out any significant levels of lemur hunting (Andrianandrasana et al., 2005) and is home to a small ecological tours company (Young, pers. comm.).

5.4 Limitations
The limitations of this study can be categorised into four groups; (1) lack of a probabilistic sampling scheme (2) unmodelled heterogeneity (3) accuracy of MODIS derived covariates and (4) lack of occasion specific detectability covariates e.g. traffic on route surveys as discussed in section 5.3.3,

5.4.1 Lack of a probabilistic sampling scheme
One of the main limitations in this study was the lack of a probabilistic sampling scheme. It presents a problem because although this study can make generalisations to other areas of lake edge or marsh channels, it is unable to predict successfully the occupancy probability for the lemur in habitat for which there are fewer edge effects. There is no other method for surveying the marsh from the canoes without opening new channels which would facilitate the proliferation of invasive species and so this problem will remain without significant investment in, for example, infra-red aerial surveys which have been demonstrated to produce feasible density estimates (Tappe et al., 2003). By running canoe based surveys
alongside aerial studies, accuracy of the canoe surveys could be assessed by modelling against the true estimates.

5.4.2 Unmodelled heterogeneity
It is clear that it is not possible for a model based on a small sample to perfectly represent a complex distribution (McPherson *et al*, 2004), however having unmodelled heterogeneity can seriously flaw models (Mackenzie *et al*, 2006). In this study only one notable covariate that is assumed to be important in predicting lemur occupancy was not used. An example is the lack of patch size data. This data was not available for MODIS data on which this study was based, due to a lack of endmembers (or pixel values for pure pixels of a specific habitat) for the different habitat types. The greenness of the reeds and invasive plants such as *Eichhornia crassipes* and *Salvinia spp.* were too similar to use the available LandSat endmembers from previous Alaotra studies.

5.4.3 Covariate accuracy
Contrary to the findings of previous studies (e.g. Ramsey *et al*, 2002), NDVI seems to have performed well when describing greenness of vegetation that has grown on open water areas, which was thought would cause incorrect reflectance descriptors. This success is thought to be a result of the red and near-infrared reflectances, which are used to derive NDVI, being measured to 11 bit precision by the MODIS instrument. This is in contrast to NDVI as derived from other sensors, for example LandSat, which have a lower radiometric resolution and have been criticised for their failure over open water. Although there has been success in the use of NDVI, several other covariates require further assessment before their subsequent use.

5.4.3.1 Burned area accuracy
The total burned area calculated using the MODIS burned area product and FIRMS active fire database is significantly smaller in some years (e.g. 2981ha vs. 9566ha in 2005) than has calculated in previous studies (Andrianandrasana, 2009) using unsupervised classification of LandSat images. Manual examination of LandSat images indicate that the MODIS sensor does correctly identify recently burnt black areas, but may not correctly identify brown partially burned reeds as burnt. It is thought that through the inclusion of the NDVI
covariate, areas of browned reeds are picked up and incorporated in the model. The occupancy maps seem to confirm this suggestion (e.g. across the centre of the southern marsh in 2004 - see Figure 4.6).

A more sophisticated method for monitoring burnt areas of reeds would be the creation of a dense time series of MODIS-LandSat fused images to calculate a time series of delta-normalised burn ration (Miller and Thode, 2007; Brewer et al, 2005) which could be used to generate a covariate for severity of historical burning, or time since last burn using a burn after setting a threshold intensity.

5.4.3.2 Lake height accuracy
The lake height data is also flawed in that there is no estimate for 2005, a year in which the long term mean was used as a replacement in the models. If the water height was significantly different in 2005 than the mean, this covariate would be skewed and the results inaccurate. There is sufficient support for lake height as a covariate of detectability in this study to warrant further investigation into methods of its collection, an idea for doing so is discussed in section 5.6.1.

Another method that was thought feasible was the use of radar altimetry from TOPEX or SSM; however this was not possible as these sensors have a 10km resolution meaning the height variations in lake height would not contribute sufficiently to the land-water mixed signal to generate any usable variation (Long, pers. comm.). A simple solution to the lack of lake height data in future studies is the use of a simple water height measure at some point in the lake such as a large ruler which can be checked annually.

5.5 Implications for management
This study has shown that in years with large amounts of fire, the lemurs are more likely to be observable on marsh channels and lake edges. This suggests that fire causes more damage than simply destroying habitat; it may also confound the risk of hunting and other disturbances such as poor weather. For this reason the focus on reducing burning the marsh has to be seen as a priority and work with the communities by Durrell in recent years must continue (Andrianandrasana et al, 2005).
The protected area boundary does appear to surround most of the occupied habitat with exception of a small part of the south west of the marsh (Figure 4.8). The designated no take zones have variable levels of success in their coverage of occupied lemur habitat. Zone A for example, covers a large area of the centre of the marsh which is not predicted to be occupied at any point during the study suggesting its role in lemur conservation is limited. Zones A and B also contain large areas of burnt habitat possibly the result of uncontrolled burns by fishermen attempting to gain access to fish (Copsey et al, 2009). In a dynamic system such as Lac Alaotra with uncontrolled burns, it is very difficult to designate and provide adequate protection to certain areas. However, as can be seen in Figure 4.3 very few observations are made within no take zones A and B. This is a result of there being no access channels in these areas. It is possible then, that the local people do respect the protected area boundaries and do not cut fishing channels into these areas. As much of the population around the lake rely on it for their living (Ranarijaona, 2007). Designation of large areas close to settlements where much of lemur population is predicted to occur as no take zones is unrealistic. The current protected areas then, do appear to provide good coverage of the marsh considering the restrictions within which they must operate although there are areas of significant lemur occupancy that are not within these zones and designation of some important corridor areas could be assessed.

Local extinction estimates suggest that conservation action with local people should be focussed in the Village of Anororo as despite legal protection for the lemur (Ralainasolo et al, 2006) there is still evidence of hunting and large fires that saturate some of the no take zones in the area.

5.6 Recommendations for monitoring

This section has great importance in its impact on a study that is due to commence at the end of 2011. Further monitoring is taking place on the Alaotran gentle lemur funded by the MacArthur fund (Long, pers. comm.). This study has the advantage of collecting data weekly rather than annually and so the ability to detect trends should be increased through the creation of a longer time series. It would then be possible to use a general additive model rather than a general linear model as used here to model a trend which would allow a more
The larger time series of estimates for population size will also provide greater power with which to detect trends (Gerrardette, 1987). This study is also likely to detect seasonal changes in the lemur population which may be an important factor that this study is unable to investigate. However, the recommendations from this study could have important impacts on the data collection methods used in the new program.

As detection non-detection data is simple to collect, it is a candidate for use in participatory monitoring programmes (Danielson et al, 2005). As the new monitoring programme will run over an extended period of time, at times participatory monitoring could be run alongside professional monitoring in order to assess differences in the quality of data produced. This could easily be built upon the existing Durrell scheme that uses the lemur as a predictor of marsh health (Andrianandrasana et al, 2005).

Rhodes et al (2006) suggests that there are two ways of using occupancy surveys to best detect trends. If the aim of the study is to detect a decline in occupancy then the study should focus on habitat that is known to be occupied and if the study is attempting to detect an incline in occupancy, it should aim to survey areas of semi-high quality that the species may expand into during a period of population growth. Using these suggestions, monitoring could be focussed on areas that this study has estimated have a high or medium probability of occupancy and exclude sites that have a low probability of occupancy as these have little or no part to play in describing trends in the species.

The new monitoring programme should attempt to focus some survey effort on the North of the marsh as this study has shown an area in the North West that has a relatively high probability of occupancy (up to 70% in 2007). Ralainsolo (2004) failed to detect any lemurs in the area but suggested there was some evidence for their existence. Confirmation that a lemur population still occurs in this area is essential. If the population has gone locally extinct it would demonstrate the fragility of the lemur population but would also justify a focus on conservation of the South of the marsh. If the population still exists, some investigation into the genetic quality could be required as it is possible that the population is
genetically isolated and may suffer from some level of inbreeding depression (Frankham et al, 2002; Keller and Waller, 2002).

5.6.1 Improving density estimates
In order to reduce the coefficient of variation that results from encounter rate, surveys that are found to pass though habitat that is found to be unoccupied could be removed from the analysis. The density estimate for occupied and unoccupied habitat is otherwise being applied to only occupied habitat resulting in an underestimation. This was not attempted in this study as a map was not generated with 0 and 1 values for occupancy, but is recommended in future studies. Multi-covariate distance analysis could be expanded to generate a density estimate for each village management zone in order to capture some of the variation observed across the marsh.

During the MacArthur funded study, it is recommended that full time “lemur spotters” are employed in order to build the skills with which to successfully spot the lemurs. Experienced spotters in Distance surveys have been shown to miss less individuals and record distances more accurately (Alldredge et al, 2007).

5.7 Future work
5.7.1 Integrated modelling of suitability and occupancy
Although the model created by this study uses habitat descriptors for each site to model occupancy, it models usage of habitat rather than suitability. By combining habitat suitability and occupancy in the same model as suggested in Mackenzie et al (2006, p. 272), the occupancy estimates produced are likely to be more sensitive to the reductions in area of suitable habitat caused by the burns across the marsh. In such a study, a history of suitability would also be formed and included in the likelihood model. If no individual was detected in a grid square this could then be explained through lack of suitability. It is thought this may show a reduction in occupancy in large burn years to account for the hypothesised clumping that is thought to have occurred. It would also allow investigation into the lowest suitability of habitat that is required to maintain a group and so allow estimation of extinction thresholds (Lande, 1988; Merila and Kotze, 2003).
5.8 Transferability

There is potential to use this technique not only for cryptic species but also for species that occur over a large area for which exhaustive sampling is unfeasible. This technique would however work best in studies in which habitat use can be described using remotely sensed data which has been shown to be possible for species ranging from lizards (e.g. Herkt, 2007), to large mammalian herbivores (e.g. Heitkonig et al, 1998; Heitkonig et al, 2003) (reviewed in Leyequien, 2006). This technique is especially applicable in other wetland areas where surveys are often limited to being boat based. Both Distance and occupancy data can be collected by boat unlike many other abundance estimation techniques. Mangrove forests present an example of where this technique has potential as limited access and low detectability may limit the amount of data available. Another example is the Pantanal in Latin America which spans an area of a size that would unfeasible to survey exhaustively. Areas such as the Pantanal and Lac Alaotra are of particular interest as freshwater habitats and the species therein have been shown to be among the most threatened around the world (Jenkins, 2003; Revenga et al, 2005).

The technique could also be applied to nest counts or burrows such as for the giant jumping rat (*Hypogeomys antimena*) in Madagascar for which Distance studies have been shown to produce good baseline population estimates (Young et al, 2008), but the occupancy of the species within its theorised extent remains unknown, something that this method could rectify and so improve the accuracy of the population estimates.

**Concluding remarks**

This study has suggested that combination of accurate density models with maps of occupancy corrected for detectability have the potential to be used to generate estimates of population sizes for elusive species in habitats that prevent extensive surveying especially in wetland areas. Distance density estimates used must be stratified by habitat or region as the variation in encounter rate observed when monitoring an elusive species can be prohibitive to producing a precise estimate of density. Combining detection histories and habitat suitability also has the potential for increasing the accuracy of this technique.
References


Appendices
Appendix 1 Distance from nearest settlement map
Appendix 2 MODIS burned area map combined with FIRMS active fire map for the 12 months preceding March of the year shown.
Appendix 3 NDVI map for March of 2004-2007
Appendix 4 Map of village management zones
Appendix 5 NASA FTP servers used to download the MODIS data and further processing notes using the MODIS reprojection tool

The MODIS reprojection tool (MRT) was used to convert all 'bands' of each HDF scientific data set to geotiff format, then project from integerised sinusoidal (ISIN) to UTM zone 38S on the WGS84 datum and then nearest-neighbour resample to 500m resolution (burned area product) or 250m resolution (NDVI). All subsequent image processing used Idrisi Kilimanjaro (Eastman, 2002).

MODIS collection 5 data granules from MODIS tile h22v10 (North Madagascar) in EOS-HDF format were obtained from the following NASA FTP servers:

- Burned areas product
  ftp://e4ftl01u.ecs.nasa.gov/MOTA/MCD45A1.005
  (all months from April 2000 until March 2007 except June 2001 and Feb 2009 which were not available)

- Vegetation indices product
  ftp://e4ftl01u.ecs.nasa.gov/MOLT/MOD13Q1.005
  (all 16 day periods ending on day of year 97 (usually 7th April) in years 2004-2007)

- Nadir bidirectional reflectance distribution adjusted reflectance (NBAR) product
  ftp://e4ftl01u.ecs.nasa.gov/MOTA/MCD43A4.005
  (all 16 day periods ending on day of year 97 (usually 7th April) in years 2004-2007)

Active fires data from the Fire Information for Resource Management System (FIRMS) of the University of Maryland were downloaded. Maps for the relevant tile and year were downloaded with no need for further processing. These were downloaded from the FIRMS fire archive (http://firefly.geog.umd.edu/download/).

To generate the ‘time since last burn’ covariate, the burned areas product burn date 'band' was reclassified in each month such that areas which had been burned in the month of the product took values of 1 and all other areas, including cloud and no-data fill areas, took values of 0 (0 -> 0; 1 - 366 -> 1; 367 - 11111 ->0) (Justice et al, 2009). The reclassified monthly burned areas maps from all 11 periods of the 12 months preceding March in the years 2000 - 2007 were added together to produce 4 maps of the pixels burnt in those years using Idrisi Kilimanjaro (Eastman, 2002). These maps were subsequently reclassified (as 0 or 1) to identify areas which had not been burned at all or which had been burned at least once in the previous year. This allowed the generation of a burn history for each cell (truncated at April 2000 as there are no observations prior to that date). This value was capped at four years as this was the most data available for 2004.
Appendix 6 Map of predicted occupancy for 2004 overlaid by the protected area boundary and the no take zone
Appendix 7 The global detection function produced by pooling the Distance data across the four years of the study
Appendix 8 Alaotran gentle lemur habitat suitability map fit to the study area used in this study, adapted from Lahoz-Monfort et al, 2010