Testing the effects of habitat modification on the reptiles of a southern African grassland

---

Gavin P.R. Masterson

A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Doctor of Philosophy

Johannesburg, South Africa

August, 2014

DECLARATION

I declare that this thesis is my own, unaided work unless specifically acknowledged in the text. It has not been submitted before for any degree or examination in any other university, nor has it been prepared under the aegis or with the assistance of any other body or organisation or person outside the University of the Witwatersrand, Johannesburg.

Gavin Masterson, on the

19th day of August 2014

ABSTRACT

Globally, reptiles are one of the most threatened vertebrate taxa, with a higher proportion of species threatened with extinction than either birds or mammals. The primary threat to reptile species is habitat loss, habitat change or habitat degradation associated with human population growth. Reptiles are relatively sedentary and many are habitat specialists which can be negatively affected by small changes in land-use or habitat quality. Many species have restricted distributions and many exist in low-density populations in which the deaths of a small number of individuals can lead to population-level declines. Unfortunately, our understanding of the responses of reptile species to habitat change or modification is currently limited. Despite numerous studies on individual species or assemblages, the literature is still geographically biased in favour of the New World and Australia, with more studies conducted in temperate areas than in the tropics. To date, little research regarding the responses of reptiles to habitat modification has been conducted in southern Africa, which was the motivation for this project.

The grasslands of southern Africa have been heavily impacted by humans, primarily due to their suitability for agriculture. Reptiles occurring in these grasslands are therefore under immense pressure as the extent and quality of their habitat decreases. I tested the effects of various types of habitat modification on the reptile species in the grassland reserve Suikerbosrand Nature Reserve (SNR), Gauteng, South Africa. Using passive trapping, I surveyed reptiles in southern SNR in 2005-2006, and in northern SNR in 2009-2010. I investigated the efficacy of pitfall and funnel traps for sampling reptiles and show that the two trap types are complementary and that the use of both trap types should be considered when surveying reptiles. I compared the estimates of two species richness estimation techniques and their consequent utility when making decisions which must consider the distribution of reptiles within a managed, conservation landscape. I show that a hierarchical site-occupancy approach to species richness estimation is preferable for its ability to quantify uncertainty, link important variables in the decision-making process and for the richness of the information that the approach provides. Using a small-scale, experimental approach to habitat modification, I tested the effects of fire and grass cutting on reptile site occupancy during the 2005-2006 survey. Species for which sufficient data were available showed no response to habitat modification by either fire or grass cutting. Species for which insufficient data were available could not be analysed, and I recommend that a larger, landscape-level investigation is conducted to confirm or refute these findings. Lastly, I investigated the response of reptile species to a vegetation restoration programme conducted on the recently-acquired northern extension of SNR. Using data collected during the 2009-2010 survey, I compared the species richness of sites at that were previously ploughed and then restored, sites that were ploughed and left to recover unaided, and sites that were not ploughed during the period for which records exist. The results indicate that there is no difference in the species richness of sites in the three groups, but that subtle differences in the species assemblages are still evident. Species such as *Trachylepis capensis* are more frequently detected at previously-ploughed sites than unploughed sites, while other species such as *Nucras lalandii* have never been detected in any previously-ploughed area – whether the target of restoration efforts or not. The cryptic nature of reptiles makes the job of studying reptile-habitat interactions that much more challenging, and remains one of the primary causes of low confidence in model parameter estimates. While low detection probabilities do not eliminate the possibility of firm conclusions, they do result in increases in both time and costs associated with reptile surveys. The work in this thesis indicates that significantly greater levels of effort are required to survey reptiles than is typically invested for the production of Environmental Impact Assessments. Fortunately, improvements in Bayesian methods over the past decade mean that data from different surveys will in the future be able to be combined in a meta-analytical framework, thereby reducing the demand on individual surveys and leading to greater improvements in our understanding of the responses of reptiles to habitat change.

Ultimately, the work of this project demonstrates that we have much to learn regarding reptile responses to habitat change and their patterns of fine-scale distribution. One of the key, general findings of this thesis is that an explicit consideration of detection probability during the modelling of site occupancy and the derivation of species richness estimates is fundamental to studies of site occupancy within habitat mosaics. In this way, this thesis supports the growing literature on the subject, but this thesis is, to my knowledge, the first to apply these methods to southern African reptiles.

ACKNOWLEDGEMENTS

Permission for the work conducted during this project was granted by Gauteng Department of Agriculture, Conservation and Environment and by the Animal Ethics Screening Committee of the University of the Witwatersrand – Clearance numbers 2005/67/1 and 2005/67/2.

A first and big thank you goes to Professor Graham Alexander for his supervision during this project. Graham – thank you for the constant support and encouragement that you gave me during both the high and low points of the project. The road has been long and windy, potholed and bumpy at times, but we've reached the end and I hope you are as satisfied as I am with the product of our collaboration. I have learned an uncountable number of valuable skills through my conversations with you and through your example of scientific endeavour, thank you and thank you.

I also thank Professor Ed Witkowski for his support and encouragement of this project. Ed – thank you for the NRF bursary you gave me and thank you most of all for constantly encouraging me in both this project and in thoughts about my future in academia.

Thank you to Dr. Craig Whittington-Jones and his team for providing assistance with the installation of my trap arrays in August 2005. Many thanks also go to Daniel Koen and Liesl du Toit, who spent countless hours supporting my field surveys and who have carried the 'torch' for reptiles in Suikerbosrand for as long as I have known them. You both do amazing things for conservation, and my thanks is but small compensation for what you are owed.

To all the friends who helped me with fieldwork: Dax Mackay, Trevor Woollacott, Christopher Jones, Michael Geddes, Daniel Geddes and Alastair MacMurray - thank you for helping me repair drift fences and replace traps. You made the routine that much memorable.

I thank all the Suikerbosrand Nature Reserve for their help during the fieldwork of this project: Johnny Hennop and all the members of the team who helped to burn my sites, Samuel Ndlandla and Isak Molio for cutting my sites. To Neville Green – thank you for all the ways in which you supported this project and for making my time spent living at Suikerbosrand Nature Reserve so enjoyable.

Special thanks go to Bryan Maritz, who has been like a brother throughout the course of my tertiary education and who inspires me with his passion. From the 4 am fieldwork alarm call in 2004, to the 1 am quiet of this final night in 2014, you have been part of my work in Suikerbosrand. Thanks for all the ways in which you keep reminding me that learning is a rewarding pursuit.

Special thanks go to my parents, Pip and Lesley Masterson, and my brother and sister-in-law, Grant and Mary-Louise Masterson, for their unwavering support of my goal particularly at moments when I faltered. Thank you all for visiting me during fieldwork and for your love and prayers that kept me going in the (many) tough times. I hope you enjoy the results of endeavour as much as I do, for you are heroes behind its scenes.

Lastly, I thank my wife, Vanessa. For as long as you have known me I have been a PhD student. It's largely because of you that I am one no longer – thank you for your inspiration, encouragement, love, determination and never-say-die attitude. They say that behind every good man is a good woman. Well behind this PhD, there is a *spectacular* woman. Thank you.

Soli Deo gloria.

LIST OF TABLES

Table 2.1: Total detections observed and estimated daily detection probabilities (shown to two significant figures or a maximum of three decimal places) for each reptile species in funnel and pitfall traps between August 2005 and April 2006. In the case of non-overlap in the 95% credible intervals for detection probability of the two trap types, the trap type that is more effective at detecting the species is indicated using a double asterisk (**).

Table 3.1: A comparison of the number of species observed (S_{obs}) with the mean Chao2 ($\hat{S}_{Chao2}$) estimates of species richness and their 95% confidence intervals (CI) at each site and for the full survey dataset. Chao2 estimates are calculated by adjusting S_{obs} using the ratio of uniques (q_1) to duplicates (q_2) in combination with the number of sampling occasions (m). See Methods section for the specific calculations.

Table 4.2: Estimated mean detection and occurrence probabilities, with 95% credible intervals (as per the WinBUGS output) for the 20 species detected between 29 August 2005 and 19 January 2006. Estimates are shown up to three decimal places.

Table 3.3: Comparison of the number of species observed (S_{obs}) and estimated species richness according to the hierarchical model (S_{HM}) for each sample site and for all sites sampled between 29 August 2005 and 19 January 2006. Mean sample completeness is calculated as $(S_{obs} / S_{HM})*100$. The WinBUGS output for the 95% credible intervals is shown.

Table 4.1: Details of the 12 sites sampled between 29 August 2005 and 26 April 2006. The Phase 1 structural classification of each site's habitat (*sensu* Edwards 1983), the treatment applied at each site, and the mean grass height and grass cover at each site in each phase are shown.

Table 5.2: Total number of detections across all sites per phase for each of the 20 reptile species recorded between 29 August 2005 and 26 April 2006. Species selected for analysis using the dynamic occupancy model are indicated (**).

Table 4.3: Model-based parameter estimates for each of the 10 species selected for analysis. Parameters estimated by the dynamic occupancy model are: the logit-scale survival (ϕ) and colonisation (γ) probability of each species from Phase 1 to Phase 2; the logit-scale effect of treatment type ($\beta_{control}$, β_{cut}, β_{burn}) on site occupancy in Phase 2; the initial occupancy probability of occurrence in Phase 1 (ψ_1); the occupancy rate i.e. finite-sample estimates of occurrence probability (ψ^{fs}) in Phase 1 and 2, which are derived from the number of occupied sites in each phase (N_{occ}). Apart from *G. flavigularis* and *T. capensis*, the model assumed a constant detection probability (p) for each species in the two phases of sampling. For *G. flavigularis* and *T. capensis*, detection probability was allowed to vary by treatment type in each phase ($\alpha_{control}$, α_{cut}, α_{burn}; as per eqn 4.8) and estimates are shown on the logit scale. The posterior mean, standard error (posterior standard deviation) and 95% credible interval are shown for all parameters. The phase of sampling relevant to each parameter is shown in square brackets.

LIST OF FIGURES

Table of Contents

CHAPTER 1

Project Context and Conceptual Framework

1.1. Introduction

Reptiles comprise a significant portion of the vertebrate diversity of South Africa (Branch 2001). The great richness of the reptile fauna in South Africa contrasts with the little that is known about the life histories of many species (see Branch 1998), and new species are being described on a regular basis e.g. Branch *et al.* (2006). Limits in our understanding of reptile ecology and their resilience in the face of change, anthropogenic or otherwise, represent a significant obstacle in the efforts to conserve reptiles in South Africa. In 2004, I began an investigation into the effects of habitat management and the diversity of herpetofauna in Suikerbosrand Nature Reserve (hereafter referred to as SNR). The work presented in this thesis is an extension of my initial study (i.e. Masterson, Maritz & Alexander 2008), but focuses on the reptile component of the herpetofauna only and seeks to address some of the key challenges regarding their conservation in SNR, particularly in light of the reserve's landscape context.

My thesis has been structured into topical chapters that work through the relevant research issues from least to most complex. Chapter 1 deals with the background and contextual information necessary for those who are either new to the field of herpetology or wish to gain a broad understanding of the techniques used in the collection, analysis and presentation of the data. Data from the 2005-2006 survey is used in chapters 2, 3, 4 and 5. Chapter 2 assesses the benefits and challenges of using trapping to sample reptiles and presents an analysis of trap success. Chapter 3 presents a comparison between two methods of estimating species richness and their utility for inference in a decision making context. Chapter 4 examines the effects of habitat modification by burning and grass-cutting on the reptile assemblages at affected sites. Chapter 5 presents the results of a second herpetofaunal survey conducted in 2009-2010. Following on from the study of Masterson *et al.* (2009), Chapter 5 investigates the effects of a vegetation restoration project in northern SNR on the richness and similarity of reptile assemblages in previously cultivated grassland. Chapter 6 contains a summary and synthesis of the research outcomes of the data chapters and my recommendations for future studies of reptile ecology, richness and distribution.

1.2. Reptile Diversity

1.2.1. Reptiles in southern Africa

There are 421 recognised, indigenous reptile taxa (383 species and 38 subspecies) in South Africa, Lesotho and Swaziland (hereafter referred to as southern Africa), of which 190 (45%) are endemic (Bates *et al.* 2014). The structure and composition of southern Africa's reptile fauna broadly mirrors the global pattern. Lizards make up the greater portion of southern Africa's reptiles with 244 recognised species, followed by snakes with 116 species, 23 chelonian species and 1 crocodile species (Bates *et al.* 2014). The three most speciose lizard families are the Gekkonidae (70 species), Scincidae (59 species) and Cordylidae (39 species; Bates *et al.* 2014). Sixty-six of the 116 snake species are lamprophids (Lamprophiidae), a diverse family which is currently divided into five sub-families (Bates *et al.* 2014). All other snake families in southern Africa are represented by >10 species – excluding Pythonidae (1 species) and the Typhlopidae (6 species) – with the Viperidae containing the highest number of endemic snake species i.e. 5 species (Bates *et al.* 2014).

Recent work by Böhm *et al.* (2013) estimated that, globally, 19% of reptiles are Threatened i.e. listed in the Critically Endangered, Endangered or Vulnerable categories, and that another 7% are listed as Near Threatened. The proportion of reptiles in the Near Threatened and Threatened categories in southern Africa differs from the global estimates. Of the 421 taxa in southern Africa, 405 were assessed recently by Bates *et al.* (2014). Sixteen taxa were not assessed by Bates *et al.* (2014; typically due to them only entering South Africa peripherally and a deficiency of information for their distributions outside of South African), six species were assessed as Data Deficient and two species were listed as Extinct. Of the 397 extant and assessable reptile taxa, 36 (9%) were listed as Threatened and 37 (9%) were listed as Near Threatened (Bates *et al.* 2014). The two Extinct taxa are both lizards i.e. *Tetradactylus eastwoodae* (Cordylidae) and *Scelotes guentheri* (Scincidae), and are now considered to have been driven to extinction by anthropogenic habitat loss (Bates *et al.* 2014). According to Bates *et al.* (2014), the major threats to reptile species in southern Africa are (1) habitat loss, degradation or fragmentation i.e. agriculture, infrastructure development and fires, (2) intrinsic factors i.e. restricted range, limited dispersal or low densities, (3) natural disasters e.g. wildfires, (4) pollution i.e. chemicals, noises or lights that negatively impact upon species behaviour or reproduction, and (5) human disturbance. While each of these effects can be substantial in their own right, they can also interact in synergistic fashion with compounded negative impacts.

With 190 endemic reptile taxa in southern Africa, the conservation stakes are high. Many of the endemic genera or species have restricted ranges that are easily threatened by small-scale threat processes. For example, 15 of the 17 recognised species in the genus *Bradypodion* (Dwarf Chameleons) are endemic to South Africa (Bates *et al.* 2014) and none are found outside of southern Africa (Tilbury, Tolley & Branch 2006). New species of *Bradypodion* are still being discovered and described (Branch, Tolley & Tillbury 2006; Tolley & Burger 2007) although resolving the relationships between them has proven challenging (Tolley & Burger 2004). Nine of the 17 *Bradypodion* species are listed as Threatened with two additional species listed as Near Threatened by Bates *et al.* (2014). The majority of *Bradypodion* species have restricted distributions due to their habitat specialisations, and are threatened with habitat loss and transformation (Bates *et al.* 2014). The conservation of species with restricted distributions depends upon an understanding of the habitat and population characteristics that influence a species' persistence. Dedicated research attention is required if we are serious about conserving the richness and diversity of the reptile fauna of southern Africa into the future. The extinction of two reptile species to date demonstrates the consequences of complacency.

1.2.2. Reptiles in Gauteng

Gauteng is the smallest province in the Republic of South Africa (17 010 km^2) and contains only 1.4% of the country's total land area, yet contributes 34.5% of South Africa's gross domestic product (Lehohla 2012). The province is highly urbanised and has a population of 10.4 million people at an average density of 616 people per km^2 (Lehohla 2008). The needs of the population and the impacts of the province's industrial activities as well as anthropogenic changes in disturbance frequencies e.g. fire patterns constitute an obvious threat to the conservation of reptiles in the province. Continuing population growth and immigration mean that infrastructure development and habitat transformation in Gauteng are still occurring at a rapid pace. Expanding road networks and changing land-use have resulted in the fragmentation of natural habitats with impacts on local populations of fauna and flora (e.g. Masterson *et al.* 2009). Nature reserves in Gauteng, such as SNR, are growing increasingly isolated due to urban sprawl, which approaches the reserve from both north (southern Johannesburg) and south (Heidelberg). As habitat surrounding SNR is transformed, reptile populations outside of the reserve are expected to decline with implications for metapopulation dynamics (*sensu* Hanski 1998) in the landscape.

Gauteng lies on the transitional zone between the grassland and savannah biomes. In the south-west, the vegetation is predominantly high-altitude, or 'highveld', grassland, while in the north-east the lower altitude leads to a mix of treed vegetation and grassland, called 'bushveld'. Reptile distributions in Gauteng are often delineated by the changes in altitude and vegetation that occur in the north-easterly direction, with the majority of reptile species occurring in the north-east bushveld region (Bates *et al.* 2014). Gauteng is also topographically diverse with rocky outcrops, ridges, wetlands and rivers criss-crossing the province (Whittington-Jones *et al.* 2008) and has an altitudinal range of 600 metres from approximately 1300 to 1900 metres above sea level (m.a.s.l.). The presence of two biomes, the altitudinal range and the various landscape features likely play a significant role in the diversity of reptile species occurring in the province. Ninety-one reptile species (24% of the reptile species in South Africa) have been recorded within Gauteng's provincial boundary (Bates *et al.* 2014). One species is marginal to Gauteng i.e. *Smaug vandami*; the record of *Lycodonomorphus laevissimus* is considered unlikely to reflect an accurate identification; and one species has been introduced i.e. *Bradypodion ventrale* (Bates *et al.* 2014). Many of the species records are dated. Records of just 45 of the 88 reptile species that can be considered 'resident' in Gauteng were submitted to the Virtual Museum during the Southern African Reptile Conservation Assessment (SARCA), raising questions as to the status of the populations of the other 43 species in the rapidly changing landscape of Gauteng (Bates *et al.* 2014). Many of Gauteng's reptile species are generalists that inhabit numerous habitat types, but other species such as *Chamaesaura aenea* and *C. anguina* are grassland specialists that are susceptible to fire (Boycott 1990). Just two specimens of *C. aenea* were recorded at a single site in Gauteng during the 2000-2008 provincial survey (Whittington-Jones *et al.* 2008). A decline in the populations of the two *Chamaesaura* species are likely linked to urbanisation, land-use change and the modification of natural fire regimes (Bates *et al.* 2014).

In a landscape that is both diverse and highly-transformed, the formal protection of natural habitats plays an important role in the conservation of small vertebrates such as reptiles. A recent assessment of the protection afforded to reptile species in Gauteng concluded that 13 of the 88 resident reptile species (± 15%), are currently inadequately protected, either by protected areas or legislation (Whittington-Jones *et al.* 2008). The work of this thesis recognises that protected areas play a critical role in the long-term protection and conservation of reptiles in Gauteng, but also that the habitat management of the province's protected areas "has long been biased towards ungulate production [and] may not suit all taxa" (Whittington-Jones *et al.* 2008). In a future where land-use in Gauteng is transformed to meet the needs of agriculture, housing or industry, the management of protected areas may play the pivotal role in the conservation of the province's reptile diversity.

1.3. Suikerbosrand Nature Reserve

1.3.1. Selection of a Grassland Study Site

The Grassland Biome contains the most under-protected ecosystems and the greatest proportion of threatened vegetation types in South Africa (Driver *et al.* 2005). Three of the nine broad conservation priority areas of South Africa are in the Grassland Biome. In order of conservation priority, the Moist Grasslands, Bushveld-Bankenveld and Central Grasslands, rank 1st, 3rd and 4th respectively on the list of priority conservation areas identified by Driver *et al.* (2005) in the National Spatial Biodiversity Assessment. The agricultural suitability of grasslands has already resulted in 49% of the biome being ploughed (Bredenkamp 2002) and further modification can be expected as anthropogenic pressures on the biome increase, particularly in Gauteng. With only 2% of the grassland biome formally conserved (Bredenkamp 2002) and a plethora of potential and current threats to its conservation (Driver *et al.* 2005), it is clear that the Grassland Biome of South Africa requires urgent attention from both conservation organisations and research institutes alike.

1.3.2. Reptiles in Suikerbosrand Nature Reserve

Suikerbosrand Nature Reserve was proclaimed in 1973 to protect the mountain catchment of the Suikerbosrant plateau and to protect the associated biodiversity. The reserve is situated in high-altitude or 'highveld' grassland between 1545 and 1917 m.a.s.l. and receives a mean annual rainfall of 675 mm per year (Schultze 1997). In 2005, Gauteng Nature Conservation purchased a further 6 936 ha adjoining the northern border of SNR, thereby increasing the size of the reserve to 18 587 ha and making SNR the largest grassland reserve in Gauteng (Fig. 1.1). The major threats to the integrity of SNR and its conservation objectives are (1) the probability of alien plant invasion, (2) the crop potential of the grasslands in SNR, (3) the mining potential of the area and (4) habitat fragmentation (Driver *et al.* 2005). Suikerbosrand NR is considered the most important protected area in the province due to its size and the grassland habitat it protects, and will play a critical role in the conservation of grassland reptile species in Gauteng (Compaan 2006).

A total of 39 reptile species have been recorded within SNR between 1973 and 2008 (Whittington-Jones *et al.* 2008). The actual number of species present may be higher due to confusion about the species delineations in the *Leptotyphlops* (Bates *et al.* 2014). Recent surveys of SNR between 2004 and 2007 have, in total, captured 2466 individuals of 33 reptile species (Koen & du Toit 2007; Masterson, Maritz & Alexander 2008; Masterson *et al.* 2009). The effort has produced several noteworthy reptile records. For example, recent surveys of the newly acquired extension have detected the presence of a *Nucras lalandii* population (Masterson *et al.* 2009). *Nucras lalandii* is rare in Gauteng, particularly south of Johannesburg (Whittington-Jones *et al.* 2008), and has not been recorded within the 1973 boundary of SNR during several surveys, making the population in northern SNR the only confirmed population for the species in Gauteng. The survey of Koen & du Toit (2007) provided the first confirmation of the presence of *Homoroselaps lacteus* in SNR, and trapped the first individual of *H. dorsalis* within SNR in nearly 20 years. These outcomes demonstrate that intensive trapping surveys have the potential to improve the currently incomplete distribution data for many species, both in Gauteng and in South Africa. The quantity and quality of reptile data, the documented management of the reserve and the size of SNR make it an ideal location for an investigation into the effects of habitat management on reptiles. The reptile data has been used (e.g. Masterson *et al.* 2009) and

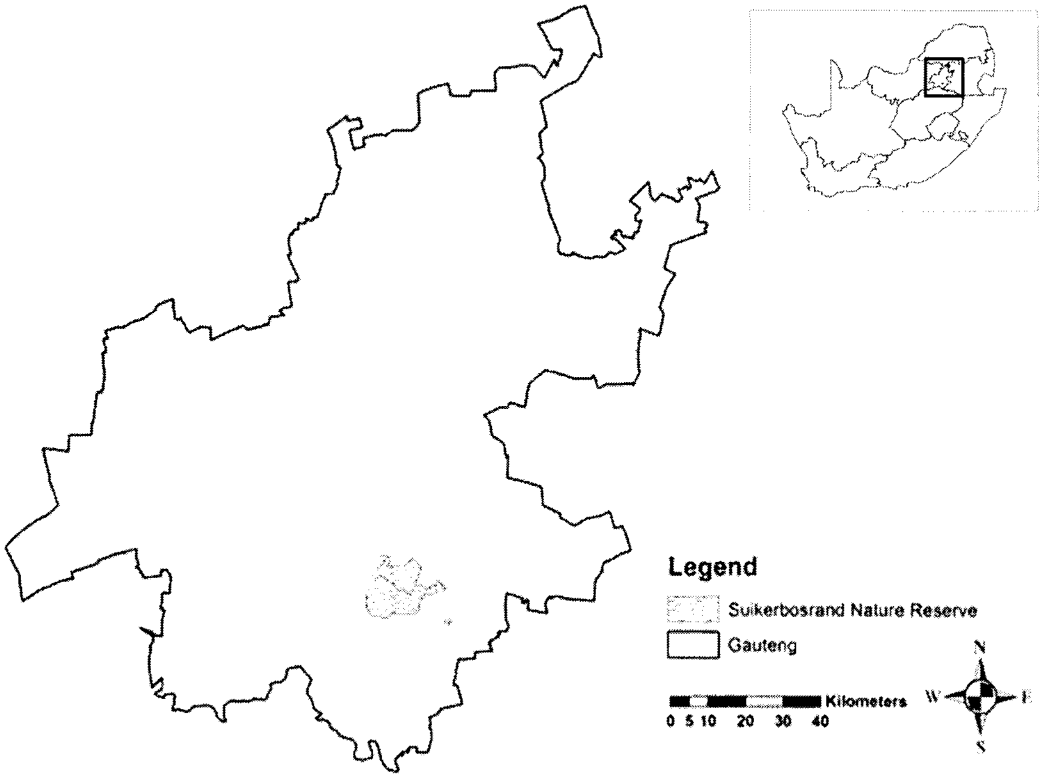

Fig. 1.1: The location of Suikerbosrand Nature Reserve (SNR) within Gauteng and South Africa (inset). The southern portion of SNR was proclaimed in 1973, while the northern portion was purchased by Gauteng Nature Conservation in 2005.

will continue to be used (e.g. in this thesis) to investigate reptile distribution within SNR as well as the sensitivity of reptile assemblages to land use change.

1.4. Reptile Conservation

1.4.1. Managing habitat change for conservation purposes

Conservation goals are achievable when protected areas or reserves are able to separate the biodiversity they protect from the processes that threaten the biodiversity (Margules & Pressey 2000). In the case of SNR, the achievement of conservation objectives is complicated by the growth of human settlements surrounding the reserve, the impacts of regional mining on the area's hydrology and the threat of climate change. Managers of protected areas are challenged in that their influence on the development of human settlements, mining concessions and global climate change are severely limited. Consequently this thesis focuses on the tools and management strategies that can be used to achieve conservation objectives within a protected area. In SNR, the two primary management tools are fire and herbivory. Fire is an invaluable management tool in that it is easy to control and can effect multi-scale changes in a landscape (Parr & Brockett 1999; Govender, Trollope & Van Wilgen 2006), while herbivory, and thus the management of ungulate populations, influences vegetation structure and composition (Sawadogo, Tiveau & Nygård 2005), which impact on vertebrates such as reptiles (Read 2002; Fabricius, Burger & Hockey 2003) and small mammals (Eccard, Walther & Milton 2000).

An analysis of the structure or composition of one or several reptile assemblage/s requires that one can reasonably accurately measure or estimate the structure and composition of said assemblage/s. Note: In this thesis, the term "assemblage" is used when referring to a group of reptile species occupying the same site as opposed to the word "community" in that the former is a restricted group of phylogenetically-related species within a larger "community" (*sensu* Fauth *et al.* 1996).

1.4.2. Method of Sampling

Reptiles are typically solitary animals with secretive habits, which avert close study (Gardner, Barlow & Peres 2007). Various methods of sampling have been employed in our attempts to study them. Examples of sampling methods and tools employed for research purposes include active searching (Jones *et al.* 2000), transect surveys (Lindenmayer *et al.* 2008), pitfall traps (Driscoll & Henderson 2008), funnel traps (Cavitt 2000), coverboards (Russell, Guynn Jr. & Hanlin 2002), and glue traps (Whiting & Alexander 2001). Each of the various methods is particularly useful in specific settings e.g. using glue traps to immobilise reptiles that would otherwise evade capture by retreating into crevices, as well as for certain study objectives e.g. using pitfall traps to sample the leaf-litter reptiles in a forest patch. Many studies have compared the efficacy of the various sampling methodologies (Gibbons & Semlitsch 1981; Greenberg, Neary & Harris 1994a; Hobbs *et al.* 1994; Webb 1999; Enge 2001; Maritz *et al.* 2007; Thompson & Thompson 2007a; Kjoss & Litvaitis 2008; Hutchens & DePerno 2009). While such studies provide useful recommendations for choosing between available methods, caution must be employed when designing a study's sampling methodology. As an example, the use of coverboards to sample reptiles across a variety of habitat types creates a potential problem if the study aims to establish the 'suitability' of the habitat types. If the absence of cover is a potential limiting factor in a habitat type (either by increasing predation or limiting thermoregulatory options), the provision of cover as part of the sampling methodology may artificially improve the habitat's 'suitability' and lead to erroneous conclusions about the species-habitat interaction.

The use of traps in faunal surveys has a long and well-established history from Fitch (1951) to the present. Basic trapping methods have undergone some notable improvements, such as the addition of drift fences to aid in the delivery of animals to the traps (Gibbons & Semlitsch 1981) and the design of novel trap types (Fitch 1951). Trap arrays i.e. structures that combine drift fences and traps, are a useful tool for sampling reptile assemblages in that they can function in most weather conditions, are able to catch terrestrial, fossorial and arboreal species of reptiles (Koen & du Toit 2007), standardise sampling effort between two locations (Maritz *et al.* 2007) and are stationary within a landscape, which can be used to control for effects of landscape features. Of course, the static nature of traps is also a disadvantage in that they are dependent on animal activity for their success. To compensate for this, traps are usually operated in periods when the activity levels of the target faunal group are at their highest. In the grasslands of SNR, the monthly trap captures of reptiles are at their highest between late spring and late summer i.e. November – February (Koen & du Toit 2007).

1.4.3. Understanding reptile sensitivity to habitat change

Many studies have reported on the effects of habitat characteristics on reptiles, although the number of reported studies is less than that for either birds or mammals (Gardner, Barlow & Peres 2007). Reptile sensitivity to habitat modification depends on microhabitat availability (Lillywhite & North 1974; James & M'Closkey 2003; Goode, Swann & Schwalbe 2004); dispersal and recolonisation following a disturbance (Twigg & Fox 1991); the type of disturbance (Jones *et al.* 2000); predation intensity following modification (Janzen 1976; Reinert 1993); and the thermal properties of the habitat (Row & Blouin-Demers 2006). Given the difficulties involved in comparing all these factors simultaneously and the range of scales at which they operate, studies on these factors tend to revolve around factor hierarchies (Fischer, Lindenmayer & Cowling 2004). For example, species distribution may be well explained by climatic variables at larger scales (Guisan & Hofer 2003), yet poorly explained by climate at smaller scales where habitat features become more important (Greenberg 2001; Ribeiro *et al.* 2009). Studies which focus on a single scale are not always ideal for the development of broader ecological theories, as there are limits to the number of factors that can be adequately controlled, the number of replicates required to adequately model factor effects, and because interactions between factors are likely (Jones *et al.* 2000). Nevertheless such studies are useful in that they focus attention on a particular subset of factors operating at the relevant scale (Hodgkison, Hero & Warnken 2006).

Recently, some authors have argued that our understanding of the effects of habitat change on reptiles remains poorly developed (Gardner, Barlow & Peres 2007). Gardner, Barlow & Peres (2007) used criteria regarding the geographic coverage of studies on habitat change and the correlation between *a priori* expectations and observed responses to habitat change to assess the status quo of scientific understanding. Currently, there is little consensus regarding the effects of many types of habitat change on reptiles species or assemblages (Gardner, Barlow & Peres 2007). This poses a challenge for researchers, who must potentially test for the effects of many ecological parameters e.g. habitat features, climate variables, edge effects etc. with a limited budget, and conservation managers, for whom incorrect assumptions regarding species can have severe consequences. The literature is currently geographically and taxonomically biased, with more studies conducted in the New World and temperate areas, and more studies conducted on amphibians than reptiles respectively (Gardner, Barlow & Peres 2007). Due to broad discrepancies in sampling method (see Section 1.5.1 below), study design and the reporting of basic statistics or patch size, Gardner, Barlow & Peres (2007) were unable to conduct a formal meta-analysis of the published literature and were limited to general comments and observations about reptile-habitat interactions. Considering that habitat change is considered the greatest threat to the survival of reptile species (Böhm *et al.* 2013), the challenges encountered by Gardner, Barlow & Peres (2007) during their review offers a clear signal that greater attention needs to be given to the study of reptile habitat requirements.

1.4.4. Natural forms of habitat change

Fire is a natural phenomenon in southern African ecosystems yet its impacts on the less vagile groups of vertebrates i.e. small mammals, reptiles and amphibians, are under-investigated and poorly understood (Parr & Chown 2003). International literature provides examples of all three possible impacts of fire on reptile species: (1) an increase in richness or abundance following fire (Mushinsky 1985; Jones *et al.* 2000 (snakes); Cunningham *et al.* 2002), (2) a decrease in richness or abundance following fire (Lunney, Eby & O'Connell 1991; Mushinsky 1992; Cavitt 2000; Jones *et al.* 2000; Woinarski, Risler & Kean 2004) and (3) no response to fire (Lunney, Eby & O'Connell 1991; Ford *et al.* 1999; Cavitt 2000). Within a single assemblage, species responses to fire may vary drastically, where some species appear impervious to the impacts of fire and others exhibit successional specialisation (Smith, Bull & Driscoll 2013). In southern Africa there are few studies that provide information on the sensitivity of reptiles to fire (e.g. Wright 1988; Masterson, Maritz & Alexander 2008). This is concerning given the widespread use of fire in the management of the region's protected areas. Additional research into fire's impacts on reptiles in southern African ecosystems is necessary for the refining of fire management in protected areas. In SNR, fire is currently used to regulate vegetation biomass and to relieve the grazing pressure on well-established grazing lawns in the reserve by drawing herbivore herds to the flush of post-fire growth in novel areas.

Herbivory, like fire, is an important part of ecosystem dynamics, as vegetation structure and composition often vary in response to the intensity, duration and type of grazing e.g. selective or non-selective (Archer 2004; Metzger *et al.* 2005). In my 2004 study, I captured fewer species of reptiles and amphibians in the heavily-grazed areas of SNR than in the lightly-grazed areas; a result which was correlated with site-specific differences in the structure of the vegetation (Masterson, Maritz & Alexander 2008). By contrast, a fence-line survey around the Greater Fish River Reserve in the Eastern Cape province of South Africa by Fabricius, Burger & Hockey (2003) trapped more reptiles in the communal grazing area bordering the southern edge of the reserve than in the reserve itself. In this instance, the more open habitat was preferred by xeric-adapted species over the more dense thicket within the reserve (Fabricius, Burger & Hockey 2003).Read (2002) investigated the impacts of overgrazing on arid-zone reptiles in Australia. His study indicated that local reptile assemblages were, on the whole, resilient to short bouts of overgrazing and that changes in species abundance were linked to changes in the vegetation cover of the grazed habitats. Woinarski & Ash (2002) studied the effect of sustained pastoralism (>100 years) on vertebrate assemblages in an Australian savannah. Their study, and that of James (2003), found that diurnal reptiles are more sensitive to sustained grazing pressure than nocturnal reptiles, as the latter were equally abundant on grazed and ungrazed sites.

1.5. Estimating species richness

Data generated from a sampling protocol follow a predictable pattern. Initially, each additional sample adds new information to the dataset regarding species richness, but in later stages of sampling, the additional samples contribute few or no additional species to the list of sampled species (Colwell & Coddington 1994; Gotelli & Colwell 2001; Magurran & Henderson 2003). The goal of many sampling scenarios is to observe/detect/capture every species present at each sample site, yet in practice this is not possible because the detection probability of the species being sampled is not perfect i.e. $p < 1$ (Colwell & Coddington 1994; MacKenzie *et al.* 2002; Mao & Colwell 2005; Royle *et al.* 2010). Detection probability (also referred to as detectability e.g. Kéry & Schmid 2004) is determined by the interaction of factors such as species identity, sampling method, timing of sampling, abundance and behaviour. A species that is very difficult to detect during certain periods of the year may be easily detected in others e.g. flowering plants or breeding amphibians (Mazerolle *et al.* 2007). In the same way, species that are hard to detect using one sampling method may be easily detected using another e.g. trapping versus active searches (Hutchens & DePerno 2009). Knowledge of the detection probability of target species provides valuable information about the type, timing and duration of sampling that will likely be required to confirm either the presence or the absence of those species at a sample site (Dorazio *et al.* 2006).

No matter how successful sampling is, it is reasonable to expect that species which are present at a site or in the study area will remain undetected after sampling has finished. Analysis of sampling data can either utilise uncorrected count/detection data for observed species (e.g. Greenberg, Neary & Harris 1994b) or corrected count/detection data, which include an estimate of the number of species not detected during sampling (e.g. Colwell & Coddington 1994; MacKenzie *et al.* 2002). Using uncorrected count/detection data to estimate state variables of interest e.g. population size, site occupancy or species richness, requires the use of strict assumptions e.g. all species present at a site are detected during sampling, which are easily violated (Mazerolle *et al.* 2007). In recent times, the use of corrected count/detection data has become standard in studies of species richness and many studies are devoted to the methods by which an accurate estimate can be achieved (e.g. Chao 1987; Soberón & Llorente 1993; Colwell & Coddington 1994; Boulinier *et al.* 1998; Walther & Martin 2001; Magurran & Henderson 2003; Thompson *et al.* 2003, 2007; Ugland, Gray & Ellingsen 2003; Chiarucci *et al.* 2003; Dorazio & Royle 2003; Colwell, Mao & Chang 2004; Chao & Shen 2004; Gelfand *et al.* 2005; Murtaugh & Birkes 2006; Dorazio *et al.* 2006; Hortal, Borges & Gaspar 2006; Thompson & Thompson 2007b; Kéry & Royle 2008; Longino, Coddington & Colwell 2009; Meyer *et al.* 2011).

1.5.1. Species accumulation curves

Species accumulation curves tend to rise steeply in the initial stages of sampling but 'plateau' or asymptote as the discovery of new species decreases in later stages of sampling (Thompson *et al.* 2003). The greater the degree of asymptote in a species accumulation curve, the greater the completeness of the sampling (Thompson *et al.* 2003). This does not mean that all species accumulation curves have the same shape when plotted from the raw data, as the shape of the curve is directly determined by order in which samples are added (Gotelli & Colwell 2001). In order to compare two species accumulation curves that are inherently variable, it is critical that they be 'normalised' (Gotelli & Colwell 2001). 'Normalisation' involves the repeated randomisation of the sample order and the calculations of mean species richness at each sample size (Gotelli & Colwell 2001) and a number of software programs e.g. *EstimateS* (Colwell 2013) have been designed to perform the randomisations and calculations from the raw data. The curve produced by randomised re-sampling of the dataset is called a sample-based rarefaction curve and is 'smoother' than the original species accumulation curve (Fig. 1.2). It is these sample-based rarefaction curves that facilitate the comparison of species richness between two sampling localities.

Repeated, randomised re-sampling of the data contained in repeated samples during a survey generates the statistically-expected species accumulation curve for the assemblage surveyed

(Colwell, Mao & Chang 2004). The re-sampling process can be conducted with or without replacement of the sample in the available pool of samples, depending on the assumptions one considers reasonable. These expected curves can be used to compare the species richness of two localities, even when the samples are of unequal sizes. If two 'unequal' curves are compared, the curve based on the larger sample is rarefied down to the total size of the smaller sample and the two curves are compared at this point (Hubálek 2000). Thus, while the standardisation of sampling effort is useful for comparing the relative rates of species discovery, it is not critical that equal numbers of individuals are sampled (Gotelli & Colwell 2001). Masterson *et al.* (2009) made use of this curve comparison method to assess differences in reptile assemblages between three habitat types in northern SNR. Finally, a sample-based rarefaction curve can be extrapolated in an attempt to identify the curve's asymptote, which is then used as an estimate of total species richness (Colwell, Mao & Chang 2004).

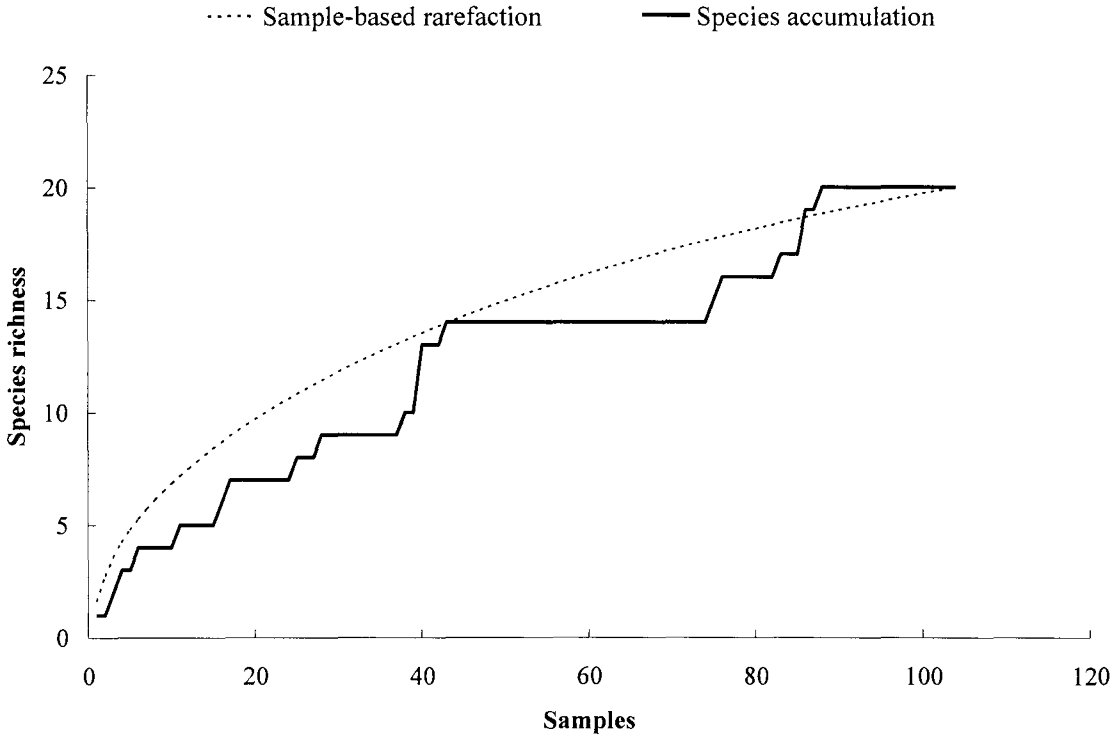

Fig. 1.2: The difference in the shape of species accumulation curves and sample-based rarefaction curves. Data for the curves are from the before-treatment phase of the reptile survey in Chapter 4. The species accumulation curve shows the accumulation of species as observed during the trapping. The

rarefaction curve was generated using 1000 randomisations of sample order and shows the statistical expectation of the curve for the data collected.

1.5.2. Non-parametric Richness Estimators

Non-parametric richness estimators have a long and respectable history of use in ecological studies e.g. Jacknife estimation (Burnham & Overton 1978). There are various types of non-parametric richness estimator but the common thread is that they estimate species richness directly from the data, or data summary e.g. Chao1 (Chao 1984). Non-parametric estimators are, usually, mathematically tractable in that they use the number of 'rare' species present in the observed sample to estimate the number of species that were not detected (Hortal, Borges & Gaspar 2006). From a sampling perspective, 'rare' species are usually defined as those species that are observed either once or twice in the entire sampling effort (Chao *et al.* 2005). The presence and number of rare species in a dataset provides information regarding the degree of undersampling of the true species richness (Coddington *et al.* 2009) and is a product of a variety of factors such as small population sizes (Gaston & Lawton 1990), species-specific detection probabilities (Gotelli & Colwell 2001) and seasonal variation in activity (Cavitt 2000). In terms of sample completeness, the greater the difference between the number of species observed and the estimated species richness, the less complete the sampling effort has been (Soberón *et al.* 2007). No matter what type of study is conducted, the data summary required by a given non-parametric estimator is the same in each case.

1.5.3. Site-occupancy modelling

Hierarchical, parametric models are incredibly flexible in their structure. Depending on the research aims, hierarchical models may be simple or complex, but increasing model complexity is usually just a function of extending a simpler model to include the additional research considerations (see Royle & Dorazio 2008; Kéry 2010). The greatest advantage of the hierarchical model approach is that there is a clear separation of the ecological parameters i.e. factors affecting ψ, and the 'nuisance' parameters i.e. factors affecting p (Royle & Kéry 2007; Kéry & Royle 2008; Bled, Royle & Cam 2011). Consequently, the hierarchical model is the researcher's representation of the data generation process, which fosters an understanding of the ecological processes from which outcomes, such as site occupancy, result (e.g. Royle, Nichols,

& Kéry 2005; Bled *et al.* 2011). The major difference between the non-parametric estimators and the hierarchical modelling approach is that the latter does not estimate species richness directly (Dorazio & Royle 2005a). The hierarchical model estimates the site occupancy of each species in light of its detection probability. Species richness is derived by summing the number of species that are estimated to occur at each site or in total (Kéry & Royle 2008). One drawback of the parametric approach is that model predictions of site occupancy (and therefore estimates of species richness) are sensitive to assumptions about the underlying distribution of detection probabilities within the assemblage (Dorazio & Royle 2003). When these estimates differ vastly, it becomes difficult to select the best distribution to use (Link 2003). Prior knowledge about sources of variation in detection probability offers the only means to resolve such an impasse (Dorazio & Royle 2003).

1.6. Summary

The aim of this thesis is to investigate the effects of habitat modification on reptiles in SNR. Southern Africa supports a rich variety of reptile species that are often overlooked during conservation planning because they typically have little economic value. Reptiles are also challenging to survey, which means that methods need to be chosen to address the objectives of each study.

During my review of the literature, I struggled to find studies that made use of similar methods to those that I employed. For example, while all of the reptile studies I reference in this thesis provide valuable information, few of these studies make use of hierarchical modelling techniques (but see Kéry & Schmidt 2008; Kéry *et al.* 2009a). Analyses of the 'suitability' of habitat types for various reptile species are often based on raw counts (e.g. Masterson, Maritz & Alexander 2008), or on estimates of species richness that use summaries of the count data (e.g. Masterson *et al.* 2009).

CHAPTER 2

Trap Design and Efficacy

The combined use of pitfall and funnel traps for sampling reptile assemblages originated from the understanding that pitfall and funnel traps are complementary in their sampling efficacy. Nevertheless, many herpetological studies make use of only a single type of trap in their sampling methodology, with little or no justification for the use of a single trap type. The use of a single trap type seems based on the assumption that various trap types detect reptile species at similar rates. I tested the hypothesis that pitfall and funnel traps are equally effective i.e. identical sampling units, for the purposes of reptile surveys. Using data from an eight-month reptile survey in Suikerbosrand Nature Reserve, I estimated the mean detection probability of all reptile species in funnel or pitfall traps, as well as the detection probability of each reptile species in pitfall and funnel traps. Estimates of the mean detection probability of the entire reptile assemblage indicated no significant differences in the overall efficacy of either trap type. While the mean detection probability of reptiles in funnel traps was slightly greater than in pitfall traps, there was a large degree of overlap in the posterior distributions of the two estimates. Nine of the 20 reptile species detected during the survey were significantly more likely to be detected in one or other of the trap types. Of these nine species, four species (two lizard and two fossorial snake species) were more likely to be detected in pitfall traps than funnel traps, while five species of terrestrial or semi-fossorial snakes were more likely to be detected in funnel traps than pitfall traps. The results of my comparison indicate that pitfall and funnel traps are complementary in sampling efficacy. The combined use of pitfall and funnel traps in my survey led to the detection of a greater number of species than would have been detected by the use of a single trap type. These findings provide strong justification for the use of both pitfall and funnel traps in studies of terrestrial reptile species richness patterns. The work in this chapter demonstrates that the quantitative analysis of variation in detection probability can be used to decide on the most effective method for the detection of a target species in studies of reptile assemblages or single, target species.

2.1. Introduction

Trap arrays used for sampling terrestrial reptiles usually consist of traps and drift fences. The combined use of drift fences with traps greatly increases the capture rates of target individuals because the drift fences intercept and guide animals towards the traps. The documented use of a system of traps (referred to here as a trap array) to census vertebrate populations and compile species inventories dates back to 1945 (Gibbons & Semlitsch 1981). Their usefulness as tools for ecological studies and the design of new trap types (e.g. funnel traps; Campbell & Christman 1982) has led to development of a 'pro-trap-array' paradigm in reptile ecological research. This is evident in the number and variety of recent studies that report the use of trap arrays in their methodology (Akani *et al.* 2002; Thompson & Withers 2003; Letnic *et al.* 2004; Andrews & Gibbons 2005; Wilgers & Horne 2006; Thompson *et al.* 2007).

There are several advantages to using trap arrays in faunal research. Trap arrays allow for the continuous, simultaneous, standardised sampling of multiple areas, which is more efficient than active searching and not subject to the same bias in sampling efficiency (Maritz *et al.* 2007). Trap arrays can provide valuable data on habitat preferences, species abundance distributions, seasonal activity etc. and are useful for detecting the presence of rare or cryptic species (Maritz *et al.* 2007; Masterson *et al.* 2009). Finally, the use of trap arrays for passive sampling does not preclude the use of other sampling techniques in a study and may also be used as one of the components in multi-taxon studies (e.g. Maisonneuve & Rioux 2001; Jobin *et al.* 2004; Letnic *et al.* 2004; Gardner, Barlow & Peres 2007).

In order to make the best use of trap arrays, it is important to understand their strengths and weaknesses. Studies that have compared the effectiveness of different trap array designs or trap types (e.g. Hobbs *et al.* 1994; Enge 2001; Thompson *et al.* 2003; Maritz *et al.* 2007; Thompson 2007) play a fundamental role in shaping future survey designs. Typically, the design or layout of trap arrays varies between studies (Maritz *et al.* 2007), regions (Enge 2001), habitat types (Thompson *et al.* 2003) and researcher. Array layout can influence the interception of animals and thus affect the capture rates of the target species (Hobbs *et al.* 1994; Enge 2001). Trap arrays can take many shapes: closed crosses (Masterson *et al.* 2009), exploded crosses with a gap between drift fences in the centre of the trap array (Maritz *et al.* 2007), L-shaped, Y-shaped

(Enge 2001) or parallel rows of drift fences (Thompson *et al.* 2003). The types of traps that are used in conjunction with drift fences vary in similar fashion. Some studies make exclusive use of pitfall traps in their trapping (e.g. Block, Morrison & Scott 1998; Attum, Covell & Eason 2004; Donnelly, Chen & Watkins 2005), some make use of a combination of pitfall and funnel traps (e.g. Fabricius, Burger & Hockey 2003; Andrews & Gibbons 2005; Masterson, Maritz & Alexander 2008), while others report the exclusive use of funnel traps in their trap arrays e.g. (e.g. Wilgers & Horne 2006). The shape or layout of drift fences can be expected to influence the probability that reptiles are intercepted during movement periods (Ellis & Bedward 2014), whereas the trap types determine the probability that an intercepted reptile is successfully trapped (Greenberg, Neary & Harris 1994a).

I tested the assumption that pitfall and funnel traps are differentially effective for the sampling of reptiles. Pitfall traps are simple traps requiring little more than the time taken to install then, while funnel traps must be designed, manufactured and maintained. Funnel traps are easily damaged by wild animals and are, dependent on the materials used to construct them, also subject to weathering over the course of a survey. The primary goal of the reptile survey from which these data come was to compare reptile diversity before and after habitat disturbance and thus I was interested in confirming whether the extra effort involved in constructing and maintaining funnel traps improved the success of my sampling or not. If funnel traps are *less* or *only equally* as effective as pitfall traps, then there is no compelling reason to use the two trap types in combination. If funnel traps are more effective than pitfall traps, then there is little reason to spend time and energy in the installation of pitfall traps. However if differences in the two trap types are complementary, then there is good reason to make use of both pitfall and funnel traps in a single trap array. This is particularly pertinent for studies which aim to survey the richness of a diverse reptile assemblage.

Understanding the effects of sampling methods on estimates of species richness is an important component of the interpretation of species richness patterns. Methods that have little or no chance of detecting particular species or groups of species will result in negatively biased estimates of species richness and obscure true patterns of occurrence (Mao & Colwell 2005). While one may assume that these factors are less likely to influence the relative nature of results if all trap arrays are uniformly constructed and installed, it is not generally difficult for a researcher to test their assumptions about sampling efficacy or lack of bias and to report the results of such tests e.g. (Enge 2001; Hutchens & DePerno 2009).

2.2. Materials and Methods

Twelve, four-armed, cross-shaped trap arrays were installed in the southern grasslands of Suikerbosrand Nature Reserve (SNR) to record the effects of habitat modification on reptile diversity (the results of which are reported in Chapter 4). Traps were opened and checked from 29 August 2005 until 26 April 2006. Each trap array consisted of four 9-m drift fences, five pitfall traps and eight funnel traps (Fig. 2.1), as per Maritz *et al.* (2007) and (Masterson *et al.* 2009). Throughout the survey, all traps were checked at least daily (or occasionally every second day due to logistical constraints) resulting in 156 trap checks during the period of sampling. Drift fences were constructed using 300 mm-wide, bicoloured (one side blue, one side black; Fig. 2.2), 300 µm thick roofing plastic, and stood approximately 250 mm high when installed. Funnel traps, 600 mm long with a diameter of 100 – 150 mm, were constructed with steel window mesh. Funnel-entrances ranged from 50-70 mm in diameter. I used two bucket sizes for the pitfall traps; five-litre buckets were used for all peripheral pitfall traps and a 10-litre bucket was used for the centre pitfall trap.

I shaded both the funnel and pitfall traps in order to reduce heat stress and heat-related mortality of reptiles (or other animals) caught in the traps. Funnel traps were covered with cut grass while pitfall traps were covered with 6 mm thick plywood boards (Central pitfall: 300 mm x 300 mm; Peripheral pitfall: 260 mm x 260 mm). I inserted 90 mm nails in the corners of the cover boards to raise the central cover board 50 – 100 mm above the lip of the pitfall trap, and to brace the peripheral cover boards against the drift fence above the peripheral pitfall traps.

2.2.1. Data Analysis

I tested the null hypothesis that pitfall traps and funnel traps are equally effective at sampling the reptile assemblage in southern SNR. I assumed that there was no overall bias in the probability with which a reptile species encountered each of the two trap types. In other words, I assumed that the movement patterns of each reptile species did not lead to a greater number of encounters with either pitfall or funnel traps over the course of the survey. Based on the layout of my trap

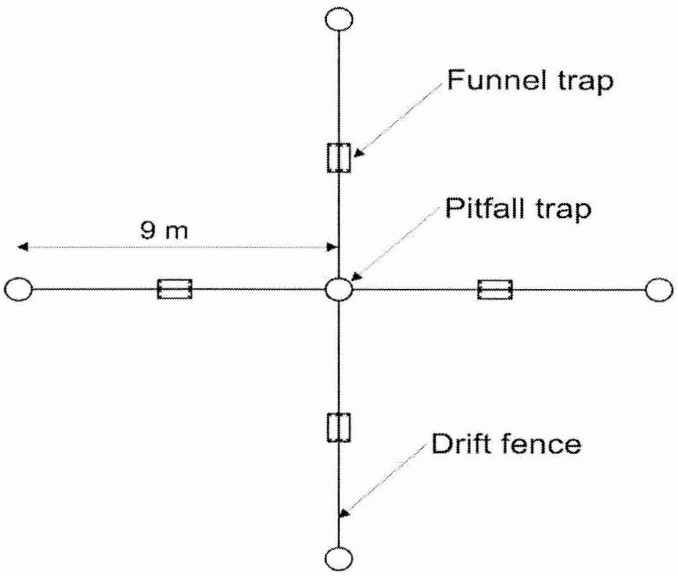

Fig. 2.1: Plan view of the layout of a trap array showing the position of the 8 funnel traps and the 5 pitfall traps (from Maritz *et al.* 2007).

Fig. 2.2: A trap array in the grasslands of Suikerbosrand Nature Reserve. The photograph shows the two-tone nature of the plastic.

arrays (Figs 2.1), this assumption seems reasonable as a reptile moving along a drift fence will encounter either a pitfall or a funnel trap.

For each day of trap checking ($N = 156$), I scored the detection and non-detection of each reptile species in the two trap types. A species detected once or multiple times on any given day scored a 1 (i.e. detection/s = 1, non-detection = 0). I used a Generalized Linear Mixed Model (GLMM) to estimate the detection probability of each reptile species in each trap type. The model is a mixed model because I assumed a common prior distribution for the random effect of species identity on detection probability, but a fixed effect of trap type on detection probability. In algebraic form, I assumed that:

$$Y_{ij} \sim \text{binomial}\ (N, p_{ij}) \qquad \text{eqn 2.1}$$

$$\text{logit}\ (p_{ij}) = \alpha_{ji} \qquad \text{eqn 2.2}$$

$$\alpha_{ji} \sim \text{normal}\ (\mu_j, var_j) \qquad \text{eqn 2.3}$$

where Y_{ij} is the observed vector of detections or non-detections for species i in trap type j during the survey period, N is the number of times that the traps were checked during the survey period, p_{ij} is the estimated daily probability of detecting species i in trap type j, α_{ji} is the logit-scale detection probability of each reptile species in each trap type. Lastly, I assumed that the mean detection probability of each reptile species in each trap type follows a normal distribution with a mean of μ_j and variance of var_j i.e. a hyper-distribution. For the purpose of this study, it is the parameter estimates of this hyper-distribution that are of primary significance as they indicate the overall effectiveness of the two trap types for sampling the entire reptile assemblage. The key assumption of this comparison is that all reptile species have a non-zero detection probability in both trap types.

Data were analysed in a Bayesian framework using WinBUGS 1.4 (Lunn *et al.* 2000). To summarise the posterior distributions of p_{ij}, α_{ji}, μ_j, var_j, I ran three Markov chains of 50000 iterations and discarded the first 25000 iterations as burn-in and thinned by 1, resulting in 25000 samples of the posterior distribution for each parameter. I assessed the convergence of the Markov chains for each parameter in two ways. The first assessment involved the visual inspection of the chains to look for trending in the values of the parameter estimates. Trends in

Markov chains indicate that some estimates are drawn from outside of the parameter's stationary distribution, thereby causing errors in estimation. The second assessment involved the inspection of the Gelman-Rubin statistic (Rhat; Gelman & Rubin 1992). To assess the fit of my model, I used a posterior predictive check recommended by Kéry (2010). The posterior predictive check is a comparison of the fit of the model to the actual, observed data with the fit of the model to an 'ideal' data set that is simulated using the parameter estimates (Kéry 2010). To graphically assess the model fit, the residuals of the model for the actual data are plotted against the residuals of the model for the 'ideal' data. The model fits the actual data well if the points are approximately evenly scattered around the 1:1 line (Kéry 2010). The summary statistic of the posterior predictive check for Markov chain models is called the Bayesian p-value and approaches 0.5 from either direction as the fit of the model improves. For the posterior predictive check of my binomial GLMM, I measured discrepancy using standardised chi-squared residuals.

In specifying the model, I used a non-informative, normal prior for the mean detection probability of a reptile species in each trap type i.e. $\mu_j \sim$ normal (0, 30). I also tested the hypothesis that the efficacy of each trap type did not differ for each reptile species i.e. H_0: $D_i = 0$, where D is the difference in mean detection probability between the two trap types for species i. Using each iteration of the estimated values of α_{ji} in eqn 2.2, I derived the posterior distribution for D according to:

$$D_i = \alpha^{funnel}{}_i - \alpha^{pitfall}{}_i \qquad \text{eqn 2.4}$$

Where $D_i > 0$, funnel traps are more effective than pitfall traps at detecting species i, but where $D_i < 0$, pitfall traps are more effective than funnel traps.

2.3. Results

Analysis of the Gelman-Rubin statistic (Rhat) for the binomial GLMM indicated satisfactory convergence of the Markov chains for each parameter (all Rhat values < 1.1; Gelman *et al.*, 2004). The Bayesian p-value for the sum of chi-squared residuals was calculated as 0.495, indicating that the fit of the model to the actual data was also satisfactory (Fig. 2.3). A poorly-fitting model would indicate the violation of the model assumptions or a structural flaw in the model specification (Kéry 2010).

The detection probability of reptiles varies between species and trap types. Species-specific detection probabilities in pitfall traps ranged from 0.43 ± 0.04 (mean ± 1 SE) for *Gerrhosaurus flavigularis* to 0.002 ± 0.003 e.g. *Psammophis crucifer* (Table 2.1). The estimated detection probability of funnel and pitfall traps differed for nine of the 20 reptile species detected during this survey i.e. 45% of the observed assemblage. Pitfall traps were more likely to detect the presence of *Agama aculeata distanti*, *G. flavigularis*, *Leptotyphlops* sp. and *Afrotyphlops bibronii*, while funnel traps were more likely to detect the presence of *P. crucifer*, *Psammophylax r. rhombeatus*, *Pseudaspis cana*, *Lycophidion c. capense* and *Causus rhombeatus* (Table 2.1). It is interesting to note the similarity in the trap-type detection probabilities for *Bitis a. arietans* and *Hemachatus haemachatus* (Table 2.1). Juvenile and adult individuals of the two species were detected in both funnel and pitfall traps. While juveniles were too small to escape from the pitfall traps, adult snakes of these two species appeared to use the pitfall traps as temporary retreats from which they could emerge at a time of their choosing (Fig. 2.4). It seems that the use of pitfall covers may have played an important role in the temporary use of the pitfall traps as retreat.

Estimates of the random effects i.e. μ_{funnel} and $\mu_{pitfall}$ (eqn 2.3) showed a high degree of overlap, The 95% credible interval for μ_{funnel} ranged from 0.006-0.043, with a mean of 0.017, while the 95% credible for $\mu_{pitfall}$ ranged from 0.001-0.031, with a mean of 0.007. This result indicates that there is no average difference in efficacy of the two trap types for sampling the reptile assemblage in SNR.

Table 2.1: Total detections observed and estimated daily detection probabilities (shown to two significant figures or a maximum of three decimal places) for each reptile species in funnel and pitfall traps between August 2005 and April 2006. In the case of non-overlap in the 95% credible intervals for detection probability of the two trap types, the trap type that is more effective at detecting the species is indicated using a double asterisk (**).

		Detections		**Detection Probability**	
Family		**Funnel**	**Pitfall**	**Funnel**	**Pitfall**
Lizards					
Agamidae	*Agama aculeata distanti*	1	19	0.008 ± 0.007	0.12 ± 0.026 **
	Agama a. atra	0	1	0.004 ± 0.004	0.007 ± 0.006
Gerrhosauridae					
	Gerrhosaurus flavigularis	39	67	0.24 ± 0.034	0.43 ± 0.040 **
Scincidae					
	Afroablepharus wahlbergii	13	16	0.080 ± 0.022	0.10 ± 0.024
	Trachylepis capensis	46	54	0.29 ± 0.036	0.34 ± 0.038
	Trachylepis varia	19	23	0.12 ± 0.026	0.15 ± 0.028
SERPENTES					
Leptotyphlopidae					
	Leptotyphlops sp.	0	6	0.004 ± 0.004	0.037 ± 0.015 **
Typhlopidae					
	Afrotyphlops bibronii	0	5	0.004 ± 0.004	0.031 ± 0.014 **
Lamprophiidae					
	Aparallactus capensis	1	1	0.008 ± 0.007	0.007 ± 0.006
	Boaedon capensis	0	1	0.004 ± 0.004	0.007 ± 0.006
	Duberria l. lutrix	1	0	0.008 ± 0.007	0.002 ± 0.003
	Lamprophis aurora	1	0	0.008 ± 0.007	0.002 ± 0.003
	Lycophidion c. capense	5	0	0.031 ± 0.013 **	0.002 ± 0.003
	Psammophis crucifer	18	0	0.11 ± 0.025 **	0.002 ± 0.003
	Psammophylax r. rhombeatus	4	0	0.025 ± 0.012 **	0.002 ± 0.003
	Pseudaspis cana	6	0	0.037 ± 0.015 **	0.002 ± 0.003
Colubridae					
	Dasypeltis scabra	1	0	0.008 ± 0.007	0.002 ± 0.003
Elapidae					
	Hemachatus haemachatus	5	3	0.031 ± 0.013	0.019 ± 0.011
Viperidae					
	Bitis a. arietans	5	5	0.031 ± 0.013	0.031 ± 0.014
	Causus rhombeatus	3	0	0.019 ± 0.011 **	0.002 ± 0.003

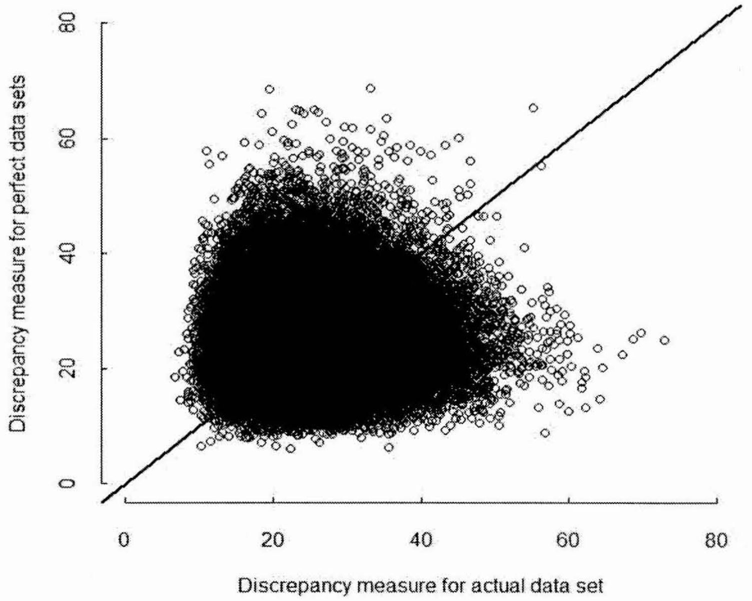

Fig. 2.3: A scatter plot of standardised chi-squared residuals for the actual and 'perfect' (simulated) data. A fitting model should produce residuals that lie around the 1:1 line (shown).

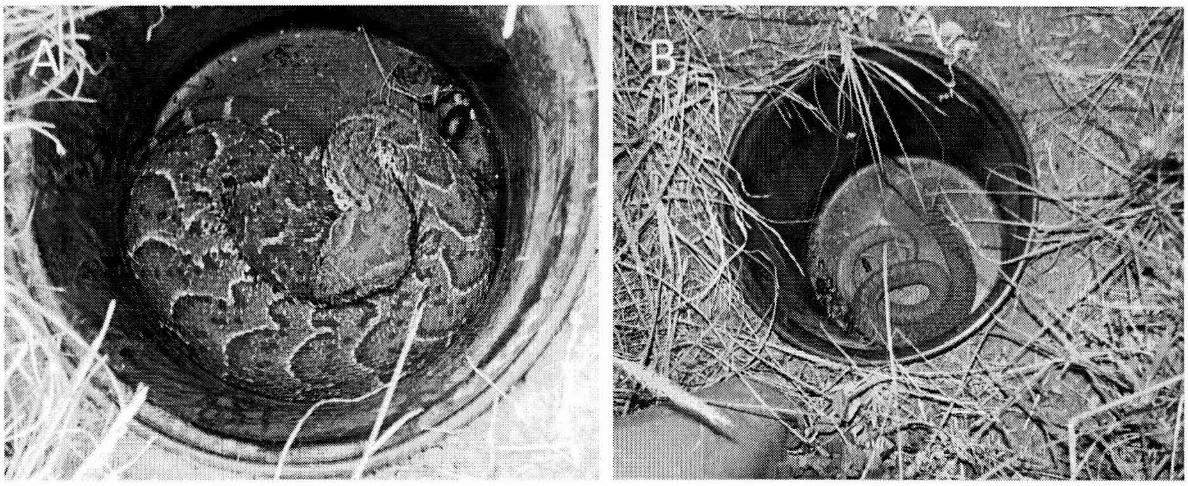

Fig. 2.4: (A) An adult Puff Adder (*Bitis arietans arietans*) in a pitfall trap at array 2B. This snake was observed entering the pitfall trap in a relaxed, unhurried manner. It did not fall into the trap and could easily have emerged from it. (B) A Rinkhals (*Hemachatus haemachatus*) discovered in a pitfall trap at array 3A. Shortly after this photo was taken the Rinkhals emerged from the trap and attempted to escape.

2.4. Discussion

My analysis of species- and trap-specific detection probabilities showed that pitfall and funnel traps were not equally effective at sampling the reptile assemblage at Suikerbosrand Nature Reserve. Funnel traps captured a greater number of reptile species (16 species) than pitfall traps (12 species) during the survey. Five terrestrial snake species were significantly more likely to be captured or detected by funnel traps than by pitfall traps, while four species (two terrestrial lizard and two fossorial snake species) were significantly more likely to be captured in pitfall traps than in funnel traps.

In spite of several clear examples of the sampling benefits of funnel traps (Gibbons & Semlitsch 1981; Campbell & Christman 1982; Greenberg, Neary & Harris 1994a), there are numerous studies that make exclusive use of pitfall traps in surveys of species richness (e.g. Read 1995; Moseby & Read 2001; Thompson *et al.* 2003; Watling & Donnelly 2008). Some of these studies appear to be based on the premise that pitfall traps are capable of detecting all species in the target assemblage, with none of the above studies explicitly testing this assumption or explaining the reasons for potentially sampling a subset of the herpetofauna in their study sites. Other authors recognise the limitation of pitfall traps and acknowledge that they are likely to sample only small, terrestrial reptiles, whilst missing the larger-bodied species (e.g. Shanas *et al.* 2006). Hobbs *et al.* (1994) did compare the efficacy of different drift fence and trap configurations, but used only pitfall traps (380 mm in depth) in their trap array configurations. Arguably any snake that exceeds 380 mm in snout-vent length (SVL) falls outside the expected sampling universe of these pitfall traps and that the conclusions of efficacy are thus limited to species less than 380 mm in length. During a study by Block *et al.* (1998), the only snake species detected by pitfall trapping was represented by a single individual of *Diadophis punctatus*, which has an adult length of 250 – 380 mm. Lizard species were far more frequently captured, as seen in the 174 individuals of *Sceloporus occidentalis*, 117 individuals of *Eumeces gilberti* and 5 individuals of *Elgaria multicarinatus* captured over the same period (Block *et al.*, 1998). The use of funnel traps in their study may have led to large changes in the relative capture frequencies of the observed species, as well as an increase in the number of snake species detected. Increasing the depth of a pitfall trap is one potential means of improving the sampling efficacy, but there are physical limits constraining the size of bucket that one can use when sampling habitat with various substrates. By contrast, a ‘small’ funnel trap e.g. 60 cm in length with a small funnel entrance can trap a large snake (Fig. 2.4). The capture of the animal is not therefore simply dependent on the individual’s behaviour e.g. refuge-seeking in a small pitfall trap (Fig. 2.4a), but is improved by the complexity of the trap type. There are also no limits regarding the size of funnel trap that may be used on any substrate or in any habitat, but larger snakes are likely to be able to break out of funnel traps made of lighter materials. From the results of this comparison, it appears that sampling recommendations such as those of Hobbs *et al.* (1994) or Thompson *et al.* (2007) could be improved by an explicit description of the strengths and limitations of the sampling methods used to gather the data in their analyses.

The modelling of detection probability is an important, even critical, yet oft-overlooked component of studies of species richness (Kéry & Royle 2008). Accounting for the probability of an observation allows a researcher to evaluate the certainty of any deductions or conclusions resulting from the observations. Methods that increase the probability of detecting a species are to be favoured as they will provide data from which more accurate inference can be drawn. Comparisons of competing methodologies lead to improvements in our understanding of our current methodological limitations e.g. Hutchens & DePerno (2009). The utility of trap arrays for surveys of cryptic taxa cannot be overstated, but their utilisation must be tempered by the consideration of the study context and relevant alternatives (Gibbons & Semlitsch 1981; Bowers *et al.* 2000; Hutchens & DePerno 2009; Driscoll *et al.* 2012). In habitat with a complex, three-dimensional structure, terrestrial trap arrays are not likely to be the most efficient or cost-effective sampling option available (Hutchens & DePerno 2009). To compensate for the cost of sampling by trap arrays i.e. fuel and manpower costs (Hutchens & DePerno 2009), it is important that researchers maximise the return for effort as far as is possible. Pitfall traps are relatively simple traps that require no manufacturing as they can be purchased as completed units e.g. buckets, yet become harder to bury in the ground depending on pitfall trap size and soil type/depth. Funnel traps usually require some form of manufacturing and deteriorate over time,

Fig. 2.4: An adult Puff Adder (*Bitis arietans arietans*) caught in a funnel trap at array 3C. Escape for this snake is neither as simple nor as likely when compared with snake of similar size caught in one of my pitfall traps (see Fig. 2.4). Also evident is the weathering i.e. rusting that funnel traps made of window mesh are prone to when used for several months during the rainy season.

but installation is quick and simple and they are better than pitfall traps at detecting snake species (Campbell & Christman 1982; this study). Without an understanding of the comparative efficacy of the two trap types i.e. their functional detection probabilities, no cost-benefit analysis is possible and each researcher is left to their own devices/opinions to determine the details of their sampling methodology.

In this study, I was primarily interested in the implications of my methodological choices for the completeness of the sampling I conducted. In testing the sampling efficacy of the two trap types used in this survey I have shown that pitfall and funnel traps are differentially effective at sampling the reptile assemblage at SNR. My data indicate that the combined use of funnel and pitfall traps in each trap array led to more frequent detections of a greater number of species than would have been detected by either trap type alone. At the very least, this finding provides a strong motivation for the combined use pitfall and funnel traps in future surveys in SNR. The broader implication of this result is that, unless the results of locally-conducted trapping indicate otherwise (e.g. Bowers *et al.* 2000), researchers should make use of both funnel traps and pitfall traps in any situation where the sampling of total species richness is the stated objective. This approach appears to compensate for the strengths and limitations of each single trap type. Relatively simple modifications to a study's sampling methodology, such as the combined use of pitfall and funnel traps, can lead to the detection of a greater number of species and, consequently, greater accuracy in subsequent analyses such as species richness estimation. This is not equivalent to saying that trap arrays are themselves the best method for surveying reptiles (see Hutchens & DePerno 2009; Driscoll *et al.* 2012), but rather that the performance of trap arrays relative to the study's objectives needs to be optimised.

My results also demonstrate that the perceived 'rarity' of a species may be significantly influenced by the chosen method of sampling. During this survey there were zero detections of *P. crucifer* in pitfall traps, despite the fact that *P. crucifer* was the most frequently detected snake species of the survey. Had I used pitfall traps only, I might have 'reasonably' – yet incorrectly – concluded that *P. crucifer* is a 'rare' species in SNR. This example highlights the importance of the assumption that all species have a non-zero detection probability during sampling. This assumption is very difficult to test using typical empirical data and has implications for inference e.g. species richness estimates (Link 2003; Mao & Colwell 2005). The presence of undetected species in the reptile assemblage I surveyed does not affect the comparison of trap-type efficacy as the data consist of pairwise comparisons for the species actually observed. Thus it is not the estimated values of detection probability for each species, but rather the relative detection probabilities of a species in the two trap types that are important. For example, it is, on average, 58 times more likely that you will detect *P. crucifer* in a funnel trap than in a pitfall trap on any single day (Table 2.1). Even if the probability of detecting *P. crucifer* in pitfall traps was 'acceptable' (where 'acceptable' would be determined by the constraints on sampling), the use of funnel traps to detect this species would be preferred, especially in shorter surveys, as they far more effective than pitfall traps for detecting this snake species. It seems reasonable to assume that many of the species that we consider as 'rare' are in fact species that our sampling methods fail to detect (Luiselli 2006), for any reason. Models that estimate site occupancy in conjunction with the species' detection probability (e.g. Kéry & Royle 2008) are appropriate means of quantifying our uncertainty in the classification of 'rare' species.

In summary, the observation process or sampling methodology employed to gather data for inference about an ecological phenomenon e.g. species richness plays a pivotal, yet often-overlooked role in the conclusions that result from the data. The explicit consideration of the consequences of methodological choices is to be recommended for all studies that wish to draw conclusions about an ecological phenomenon from their data. The knowledge that the efficacy of my trap arrays was improved through the combined use of funnel traps and pitfall traps indicates that the negative bias in the number of species observed versus the number of species actually present in the reptile assemblage I sampled was reduced. The extent of the negative bias is estimated in Chapter 3. The choice of study-appropriate methods for single or multispecies surveys is a significant challenge in ecological research that can be dealt with in a formal manner through the testing of methodological hypotheses.

CHAPTER 3

The Estimation of Species Richness

The presence or absence of species at a site cannot be determined with complete certainty during sampling. Species which are in fact absent from the site can obviously never be detected during sampling, but non-detection of a species during sampling does not necessarily mean the species is absent from the site. Some species which are present at a site will not be detected and this creates ambiguity in the interpretation of detection data. To compensate, it is customary to perform comparisons of sites using an estimate of species richness at each of them. There are many specific ways in which species richness can be estimated but the general theory is the same. Information about the undetected species is obtained from the data about the species observed. Such information may be contained in data summaries or even require that replicate samples at each site are conducted. This information is then used to adjust the number of species observed to the number estimated to occur. Using detection data collected at 12 sites during a trap survey of Suikerbosrand Nature Reserve (SNR), I compared site and total species richness estimates of one non-parametric species richness estimator (Chao2) and one parametric species richness estimator (a hierarchical, site-occupancy model). I also contrasted the utility of the two estimators for inference about reptile distribution in SNR. The number of reptile species detected, and the number of detections of each reptile species varied greatly between sites. As a result, Chao2 estimates of site species richness demonstrated large variation and produced counter-intuitive results i.e. situations where site richness exceeded the estimate of total species richness. By contrast the site-occupancy model estimate indicated that there was no difference in the species richness between sites, and indicated that total richness was greater than the richness of any single site. When inferring the distribution of reptile species within SNR, Chao2 is not as useful as the site-occupancy model. In the latter, estimates of site occupancy are specific to each species and provide testable hypotheses for further sampling. This comparison of the two estimators indicates that the hierarchical, site-occupancy model is more useful for decision making in that it better quantifies uncertainty, produces estimates that are intuitively coherent and retains species-specific information such that it can generate working hypotheses.

3.1. Introduction

The number of species present at a site or sample area is not usually known prior to sampling. After sampling, a proportion of the species present will have been detected (S_{obs}), but an unknown proportion of the assemblage will have remained undetected. If this fact is not acknowledged by the researcher, then comparisons of S_{obs} are (inappropriately) used to answer ecological questions about diversity, the suitability of habitat types, or rates of turnover, colonisation and others (Royle & Dorazio 2008). Such comparisons are problematic because they ignore the effect of detection probability (p) on the outcome of sampling (MacKenzie *et al.* 2002). When $p < 1$, analyses that ignore the effect of p produce parameter estimates that are biased low (towards zero) or, in some scenarios, may even estimate the opposite relationship between the parameter and response variable from what is true (Kéry & Schmid 2004). If the effects of imperfect detection probability are acknowledged, a researcher has to decide how to compensate for them. One option is to use the data or summaries of the data to directly estimate the number of species that were not detected. Species accumulation curves and non-parametric estimators (Colwell & Coddington 1994; Gotelli & Colwell 2001) make use of this approach and assume $p < 1$ but do not attempt to estimate it (Kéry & Schmid 2004). Another option is to explicitly estimate p and then to derive an estimate of the number of species that were not detected using a multispecies site occupancy model (e.g. Kéry & Royle 2008). The latter approach utilises parametric, hierarchical models that separate the sampling process from the parameter of ecological interest i.e. site occupancy (ψ; Royle & Kéry 2007). For many datasets, both of these methods can be applied, so how does one decide which method to use?

The use of either estimation approach is an improvement upon using the negatively-biased S_{obs} for analysis and inference (Walther & Moore 2005). The ideal estimator produces estimates that are unbiased, precise and insensitive to the amount of sampling conducted (Gotelli & Colwell 2011). In most cases true species richness is unknown, which makes it impossible to assess the bias of an estimator. Consequently, evaluations of estimator performance are based upon the simulation of datasets for which true species richness is known (Brose, Martinez & Williams 2003; Walther & Moore 2005; Hortal, Borges & Gaspar 2006). While the non-parametric estimators have fared well in such evaluations, they are sensitive to variables that affect the structure of the data e.g. non-random aggregation of species across samples (Walther & Moore 2005). The benefit of the non-parametric estimators is that they are typically simple to calculate and make clear assumptions about the assemblage in which sampling is undertaken e.g. constant p across all sample occasions and population closure. The difficulty for inference is that it is typically not possible to evaluate the validity of these assumptions on a case by case basis, and violation of these assumptions has severe implications for estimator performance (Walther & Moore 2005).

Hierarchical, parametric models are more flexible in their structure. Depending on the research aims, hierarchical models may be simple or complex, but increasing model complexity is usually just a function of extending a simpler model to include the additional research considerations (see Royle & Dorazio 2008; Kéry 2010). The greatest advantage of the hierarchical model approach is that there is a clear separation of the ecological parameters i.e. factors affecting ψ, and the 'nuisance' parameters i.e. factors affecting p (Royle & Kéry 2007; Kéry & Royle 2008; Bled, Royle & Cam 2011). Consequently, the hierarchical model is the researcher's representation of the data generation process, which fosters an understanding of the ecological processes from which outcomes, such as site occupancy, result (e.g. Royle, Nichols, & Kéry 2005; Bled *et al.* 2011). The major difference between the non-parametric estimators and the hierarchical modelling approach is that the latter does not estimate species richness directly (Dorazio & Royle 2005a). The hierarchical model estimates the site occupancy of each species in light of its detection probability. Species richness is derived by summing the number of species that are estimated to occur at each site or in total (Kéry & Royle 2008). One drawback of the parametric approach is that model predictions of site occupancy (and therefore estimates of species richness) are sensitive to assumptions about the underlying distribution of detection probabilities within the assemblage (Dorazio & Royle 2003). When these estimates differ vastly, it becomes difficult to select the best distribution to use (Link 2003). Prior knowledge about sources of variation in detection probability offers the only means to resolve such an impasse (Dorazio & Royle 2003).

Previous studies using trapping in SNR have demonstrated that reptiles are a difficult group to study *en masse* (Maritz *et al.* 2007; Masterson, Maritz & Alexander 2008; Masterson *et al.* 2009). Reptiles are cryptic, utilise life history strategies that limit their exposure to sampling e.g.

fossorial species, or may occur at low densities such that the detection probability of a species at a site is equivalent to the detection probability of an individual e.g. snake species. Previous analyses by myself and my colleagues made use of the observed counts of species to compare the reptile assemblages between various sample sites (Masterson, Maritz & Alexander 2008; Masterson *et al.* 2009). Additionally, we did not explicitly account for detection probability when modelling relationships between species richness and environmental factors e.g. grass cover (Masterson, Maritz & Alexander 2008). The correlations between grass cover and S_{obs} observed by Masterson *et al.* (2008) may alternatively be explained by the effect of grass cover on reptile activity at each site, which resulted in higher detection probabilities and higher *apparent* species richness at these sites. Masterson *et al.* (2009) used the non-parametric estimators Chao1 (Chao 1984) and Chao2 (Chao 1987) to estimate sample completeness and to compare species richness of three habitat types thereby avoiding some of the pitfalls of using S_{obs} for inference, but again we did not explicitly model the detection probability of each species.

In this chapter, I compare the non-parametric estimation procedure Chao2 (Chao 1987) and the hierarchical modelling approach of Kéry & Royle (2008). The aim of this comparison is to consider the merits of each estimation method within the context of passive trapping of reptiles when such a study aims to understand the richness and distribution of reptile species across a landscape. The merits of inference using the two estimation methods is relevant in a conservation management framework. To manage reptile species within a reserve one must first learn where they occur and why. The specific challenge when mapping species occurrence for management or conservation purposes is to find ways to quantify uncertainty in the results upon which inference is based. Conservation or management decisions taken in a transparent, well-reasoned manner with full awareness of the uncertainty involved are easier to defend if disputed, can be adjusted as uncertainty increases or decreases (Regan *et al.* 2005) and should therefore be preferred.

3.2. Methods

3.2.1. Reptile Data

Data used in this chapter were collected during trapping conducted between 29 August 2005 and 19 January 2006. Trap arrays were placed at 12 locations in low // short // tall, closed grassland (*sensu* Edwards 1983) in the southern portion of SNR. Nine of the 12 trap arrays were checked 104 times during the survey period. Three of the trap arrays i.e. sites 4A – 4C were installed and opened on 1 October 2005, to replace three sites that were burnt by a grass fire on 26 September 2005. Trap arrays 4A – 4C were checked 77 times during the survey. For additional information on the structure and layout of the trap arrays, refer to section 2.2 above. A total of 256 detections of 20 reptile species were recorded across the 12 trap arrays during the survey period. The estimator-specific preparation and analysis of these data are described for each of the two methods below.

3.2.2. The Models

3.2.2.1. Non-parametric estimation of species richness: Chao2

The first method of estimation has been widely used since it was proposed by Chao (1987). The estimator, now commonly referred to as Chao2 (Colwell & Coddington 1994), was developed as a non-parametric estimator of species richness for replicated incidence data (Chao 1987; Gotelli & Colwell 2011). Chao2 has generally fared well in comparisons of non-parametric estimators over the past few decades (Colwell & Coddington 1994; Walther & Morand 1998; Walther & Moore 2005; Hortal, Borges & Gaspar 2006; Gotelli & Colwell 2011), although some reviews differ in their conclusions (Chiarucci *et al.* 2003). The Chao2 estimator offers a simple method of estimating species richness from typical survey data. Species detections recorded during the sampling process are collated as summed frequencies. For Chao2 (Chao 1987), the estimate of species richness involves only the number of species observed during sampling (S_{obs}), which is then increased by the ratio of uniques (q_1, species that are detected just once during sampling) to duplicates (q_2, species that are detected just twice during sampling). The classic Chao2 estimate of species richness ($\hat{S}_{Chao2}$) is calculated as:

$$\hat{S}_{Chao2} = S_{obs} + (q_1^2 / 2q_2) \qquad \text{eqn 3.1}$$

Equation 3.1 is undefined when $q_2 = 0$, and so a bias-corrected, always attainable version of eqn 3.1 has been developed (Gotelli & Colwell 2011):

$$\hat{S}_{Chao2} = S_{obs} + (m - 1 / m)\, (q_1^2 / 2q_2) \qquad \text{for } q_2 > 0 \qquad \text{eqn 3.2}$$

or

$$\hat{S}_{Chao2} = S_{obs} + (m - 1 / m)\, (q_1 (q_1 - 1) / 2(q_2 + 1)) \qquad \text{for } q_2 = 0 \qquad \text{eqn 3.3}$$

where m is the total number of sampling occasions during the survey period. Equation 3.2 is simply eqn 3.1 but scaled with a measure of effort i.e. m sample, when the number duplicates is non-zero i.e. $q_2 > 0$. When $q_2 = 0$, then eqn 3.3 is used. The only difference between eqn 3.3 and eqn 3.2 is that because $q_2 = 0$, we use one of the unique species (q_1) to make the denominator non-zero.

As a non-parametric method of estimation, the user is not forced to specify a probability distribution for the species detections during sampling but is forced to assume that the *information about undetected species is concentrated in the two lowest detection frequencies* i.e. the unique and duplicate classes (Chao 1987; Chao, Shen & Hwang 2006). Chao *et al.* (2006) have demonstrated the validity of Chao2 as an estimator of total species richness under certain conditions. However, when the above assumption is violated, the Chao2 estimator will asymptotically underestimate the true species richness (see Mao *et al.* 2005) and is thus typically referred to as a minimum species richness estimator (Chao *et al.* 2009). Chao2 assumes that detection probabilities are constant across sampling occasions i.e. population closure (Chao 1987) and sampling with replacement (Gotelli & Colwell 2011), but does allow for heterogeneous detection probabilities between species (Chao 1987). Lastly, the Chao2 estimator provides a logical stopping rule for the sampling process (Chao *et al.* 2009). From eqn 3.1 we can see that when $q_1 = 0$, the Chao2 estimator predicts that all species were detected during sampling i.e. $\hat{S}_{Chao2} = S_{obs} + 0$. Ideally then sampling can be concluded when all species have been detected at least twice (Chao *et al.* 2009). This outcome is unlikely in practice because the additional time taken to detect all species a second time leads to the detection of additional species or reduces the likelihood of population closure.

3.2.2.2. Applying the Chao2 estimator

All calculations for the Chao2 estimator were performed using R version 2.15.1 (R Core Team 2012). Using descriptions of the Chao2 estimator (Chao 1984, 1987; Colwell & Coddington 1994; Chao, Shen & Hwang 2006; Gotelli & Colwell 2011; Colwell *et al.* 2012), I wrote a script to perform the calculation of $\hat{S}_{Chao2}$, its variance and 95% asymmetric confidence intervals for my dataset (Appendix 1). All calculations were performed using the sample size correction factor i.e. $(m - 1) / m$. Bias-reduction calculations for $\hat{S}_{Chao2}$, the variance and 95% confidence intervals were used as specified by Chao, Shen, & Hwang (2006). A detailed description of the equation selection process for calculating the Chao2 estimator is available on the EstimateS website (http://viceroy.eeb.uconn.edu/estimates/). All Chao2 estimates of species richness as well as the confidence intervals are rounded off to the nearest species. Means and variances for $\hat{\mathrm{S}}_{\mathrm{Chao2}}$ are shown to two decimal places while sample completeness is shown to one decimal place.

I calculated $\hat{S}_{Chao2}$, its variance as well as 95% confidence intervals for each of the 12 sites sampled between 29 August 2005 and 19 January 2006. Additionally I calculated $\hat{S}_{Chao2}$ for the reptile assemblage in the greater study area i.e. the southern grasslands of SNR. Data from all sites were pooled to calculate the summed incidence frequencies of all species across all sites. Note that the summed incidence frequencies in the pooled dataset are different from those generated using site level data. Lastly, I used S_{obs} and the mean of $\hat{S}_{Chao2}$ to calculate the sample completeness at each site and in total. Sample completeness is the percentage of the estimated total number of species that were actually observed during sampling and provides a measure of the success of the sampling effort (see Masterson *et al.* 2009).

3.2.2.3. Parametric estimation of species richness: Hierarchical Model

The second method of estimation was recently proposed by Dorazio & Royle (2005), and subsequently demonstrated by Kéry & Royle (2008). There are several important differences between the model of Chao (1985) and that of Kéry & Royle (2008). The first is that the model of Kéry & Royle (2008) is parametric in its form. In order to estimate the species richness of a site, we specify the probability distribution of the parameters of interest e.g. site occupancy *a priori*. Various specifications of the parameter probability distributions are typically possible, and it is often difficult to select the true model from the set of alternative forms of the same model (Dorazio & Royle 2003). The second difference is that the model is hierarchical in structure. A hierarchical model contains multiple linear/non-linear models that collectively describe the system for which inference is desired. In typical ecological applications, one model describes the ecological process of interest (the 'process model') and another describes our observation of the ecological process (the 'observation model' e.g. Mackenzie *et al.* 2002; Dorazio & Royle 2003; Kéry & Schmid 2004; Royle, Nichols, & Kéry 2005; Dorazio *et al.* 2006; Kéry & Royle 2008; Kéry, Royle, & Schmid 2010; Yamaura *et al.* 2011). A parameter that influences both the occurrence of the species as well as our ability to observe it during sampling, e.g. vegetation type, can be incorporated into both the process and observation model. A parameter that influences only our ability to observe the species if it is present e.g. weather conditions, can be included in the observation model but excluded from the process model. The separation of the 'nuisance' parameters from those relevant to the ecological question of interest is incredibly useful in the modelling of ecological systems (Royle & Dorazio 2008). An additional strength of hierarchical models lies in the stepwise, 'organic' nature in which they are constructed (Royle & Dorazio 2008), which facilitates the testing of hypotheses and the development of predictive models for ecological applications (see Bled *et al.* 2011; Gormley *et al.* 2011).

The core of the hierarchical model used to estimate species richness in this chapter is the species-by-site incidence matrix (Dorazio *et al.* 2006; Kéry & Royle 2008). This matrix is only partially observed during sampling due to the presence of false negatives that result during sampling, i.e. failures to detect a species when it is actually present at a site or in the study area. The primary objective of the hierarchical model is to estimate the true species-by-site incidence matrix. Following Kéry & Royle (2008), assume that the presence of species i at site j (z_{ij}) follows a Bernoulli distribution with success probability ψ_i i.e. $z_{ij} \sim$ Bernoulli (ψ_i). The number of times that species i is detected at site j (Y_{ij}) during m samples follows a binomial distribution with success probability p i.e. $Y_{ij} \sim$ binomial (N_j, p_i). Conversely, it follows that species i is absent from site j with a probability of $1 - \psi_i$ and that if it is absent, then $Y_{ij} = 0$ (Dorazio & Royle 2005a). The probability that a species is present at a site but not detected during N samples is (as per Royle & Dorazio 2008):

$$\Pr(z_{ij} = 1 | Y_{ij} = 0) = \psi_i (1 - p_i)^m / \psi_i (1 - p_i)^m + (1 - \psi_i) \qquad \text{eqn 3.4}$$

The challenge is that both ψ and p are latent variables that must be estimated from the observed detection data. To estimate them, a sampling design must include replicate surveys at every sample site (Dorazio & Royle 2005); a design which is referred to as the robust design (Williams *et al.* 2000). While this requirement of the model represents a 'cost' in terms of time and effort, such replication is typical of most surveys or monitoring programs (see Kéry & Schmid 2004). Estimates of ψ_i and p_i can be obtained for species that are detected during sampling however there are an unknown number of species that are not detected during any of the sampling occasions. The challenge of estimating the number of additional species that are present at each site or in the study area can be addressed using a random effects model to describe both the occurrence and detection probabilities, and a technique referred to as data augmentation (Royle *et al.*2007).

To estimate species richness, hyperparameters (random effects) for the mean and standard deviation of the occurrence and detection probabilities for all species detected are included as an additional hierarchical component in the site occupancy model. The function of these hyperparameters is to facilitate extrapolation from our data to a larger set of species, which is of unknown size and of which the S_{obs} are but a part (Kéry & Royle 2008). To make this extrapolation possible, the data are augmented by including a large, but finite, number of species with all-zero detection histories (S_0), such that $M = S_{obs} + S_0$. In ecological terms, these additional species, hereafter referred to as 'hypospecies', are species which may have been present at the sites sampled but which were not detected during sampling (Royle, Dorazio & Link 2007). The inclusion of each hypospecies in the assemblage is determined using a latent, zero-inflation parameter (Kéry & Royle 2008). The inclusion parameter (Ω) has a uniform prior (Kéry & Royle 2008) and is used to generate the indicator variable ω_i for each of the M species, where $\omega_i \sim$ Bernoulli (Ω). During the model run, the occurrence probability of each hypospecies (ψ'_i) is drawn from the posterior distribution of the random effect for occurrence probability of the entire reptile assemblage. The binary estimate of whether the hypospecies is present or absent at a site is the result of a Bernoulli trial with a success probability of ψ'_i conditional on ω_i i.e. $z_{ij} =$ Bernoulli ($\omega_i * \psi'_i$). Hypospecies for which $\omega_i = 0$ cannot occur at any of the sites sampled, while those for which $\omega_i = 1$ will occur at sites in proportion to the model estimate of ψ'_i. The model-based estimates of species richness are then calculated by summing ω_i for the M species ($S_{HMtotal}$), and summing z_{ij} at each site (S_{HMsite}). This method of reducing the problem of estimating the total number of species present to that of estimating the distribution of the latent indicator variable ω has been justified by Dorazio *et al.* (2006) and Royle *et al.* (2007), and results in a model that is readily implemented using Gibbs samplers such as WinBUGS (Lunn *et al.* 2000).

3.2.2.4. Fitting the Model

I used the multispecies, multisite occupancy model of Kéry & Royle (2008) to estimate the detection probability and occurrence probability for each species and the reptile assemblage as a whole. In the first model, I assumed that species identity was the only determinant of detection or occurrence probability i.e. the null model. In the second model, I tested for an effect of site on occurrence probability. As no effect of site on occurrence probability was evident for this dataset, I present only the results for the null model below. Model predictions of site occupancy for each species and hypospecies were used to derive estimates of species richness for each of the 12 sites and in total. Lastly, as for the Chao2 estimator above, I used these richness estimates to calculate the estimated sample completeness according to the hierarchical model.

The hierarchical models used in this analysis were fitted using Markov chain Monte Carlo (MCMC) methods in WinBUGS (Lunn *et al.* 2000). Models were coded for WinBUGS using R version 2.1.5.1 (R Core Team 2012) and executed from within R using R2WinBUGS (Sturtz *et al.* 2005). Posterior distributions for each parameter were calculated using three parallel Markov chains of 50*k* iterations each. Each chain was initialised with different starting values, from which I discarded 10*k* iterations and thinned by 10, leaving 12*k* iterations for inference. Chains of this length showed sufficient convergence with Gelman-Rubin statistic values of < 1.003 (Gelman & Rubin 1992).

Bayesian credible intervals can be constructed in several ways. A 95% credible interval can be constructed to include any interval that contains 95% of the mass of the posterior distribution, with the narrowest of these intervals referred to as the highest posterior density interval (HPDI; Kéry 2010). Neither WinBUGS nor R2WinBUGS calculates the HPDI for each model parameter (Kéry 2010), so I used the coda package (Plummer *et al.* 2006) to calculate the HPDI's for several parameters and compared them with the central 95% credible intervals calculated by WINBUGS. Differences between the HPDI's and WinBUGS 95% credible intervals were typically slight with no effect on inference about the parameters and so the latter are presented in the tables below. The only HPDI that I report here is for the estimate of total species richness. Due to the right-tailed distribution of the posterior distribution the HPDI offers a slightly improved interval for inference as compared to the central interval.

Implementing an analysis in the Bayesian framework requires the specification of prior information regarding the parameters to be estimated. The choice of prior distribution for a parameter is sometimes viewed as problematic for being subjective, and because the same data can be generated by very different underlying distributions (Link 2003). In addition to this, a recent study demonstrates some of the problems with estimating occupancy when the data are sparse, and the fact that estimating equations can have multiple solutions (Welsh, Lindenmayer & Donnelly 2013; but note that this study was conducted using maximum likelihood methods and not the Bayesian framework). The work of Welsh, Lindenmayer & Donnelly (2013) indicates that under certain conditions the use of detection-explicit approaches to estimation of occupancy can be as biased as those approaches which ignore detection entirely. The development of this discussion will be important for the future of hierarchical models of occupancy. Some prior information about the detection probability of reptile species during trapping surveys in SNR is available from the work by Masterson *et al.* (2008) and Masterson *et al.* (2009), however I specified flat, conventional priors for all model parameters (Appendix 2). Using this approach, the difference between the two methods is only related to their use and interpretation of the data. The inclusion of prior information for use in the hierarchical model would risk complicating comparisons between them. It must still be noted that the use of prior information in the Bayesian framework is one of the rarely utilised strengths thereof (Kéry 2010).

3.3. Results

3.3.1. Non-parametric species richness estimation

The species richness estimates given by Chao2 for each of the 12 sites and for the total dataset are shown in Table 3.1. Total reptile richness for the 12 sites surveyed was estimated at 26.066 species, with a 95% confidence interval of 21.735 – 41.210 species (Table 3.1). There is no

Table 3.1: A comparison of the number of species observed (S_{obs}) with the mean Chao2 ($\hat{S}_{Chao2}$) estimates of species richness and their 95% confidence intervals (CI) at each site and for the full survey dataset. Chao2 estimates are calculated by adjusting S_{obs} using the ratio of uniques (q_1) to duplicates (q_2) in combination with the number of sampling occasions (m). See Methods section for the specific calculations.

Site	m	S_{obs}	q_1	q_2	$\hat{S}_{Chao2}$	**Variance** $\hat{S}_{Chao2}$	**95% Conf. Int.**	**Sample Completeness (%)**
1A	104	7	4	1	15	17.194	10 – 28	46.9
1B	104	5	3	0	8	14.677	5 – 26	62.7
1C	104	10	8	0	38	432.899	17 – 113	26.5
4A	77	4	1	1	4	0.061	4 – 5	89.0
4B	77	7	4	1	15	17.087	10 – 28	47.0
4C	77	5	3	0	8	14.565	5 – 26	62.8
2A	104	5	2	0	6	1.443	5 – 11	83.5
2B	104	5	2	0	6	1.443	5 – 11	83.5
2C	104	5	2	1	7	1.660	6 – 11	71.6
3A	104	3	0	1	3	0.000	–	100
3B	104	7	5	0	17	93.741	9 – 56	41.4
3C	104	8	5	1	20	35.910	13 – 38	39.3
All Sites	104	20	7	4	26	18.532	22 – 41	76.7

expected hierarchy in the estimates for species richness at each site and in total due to the fact that the summed incidence frequencies, upon which the estimates are based, change at each scale of consideration (Table 3.1). Site-specific estimates of mean richness vary considerably from 3 species at site 3A to 37.731 species at site 1C (Table 3.1). The variance of the site-specific estimates ranged from 0 at site 3A to 432.899 at site 1C (Table 3.1). By comparing site 3A and site 1C, we can see that the site surveys produced datasets with starkly contrasting characteristics. At site 3A, each of the three species were detected on two or more occasions, while at site 1C, eight of the 10 species were detected on just one occasion (Table 3.1). Consequently, Chao2 predicts that 100% of species present at 3A but just 26.5% of the species occurring at 1C were detected during sampling.

Richness estimates for sites 2A, 2B and 2C were remarkably similar. At each site, a total of five species were detected during sampling with two of these species detected just once (Table 3.1). At site 2C a single species was detected twice during sampling, whereas at site 2A and 2B, the remaining species were detected on more than two occasions. The net result of these similarities is that the Chao2 means, variances and confidence intervals are virtually identical for these three sites (Table 3.1). However if we compare site 2A with site 1B, the effect of uniques on the Chao2 estimate becomes clear. The additional unique recorded at site 1B led to a tenfold increase in the variance of the estimate with a consequent increase in the confidence interval and a 20% reduction in estimated sample completeness (Table 3.1). The sensitivity of the site-level estimates to minor differences in the outcome of sampling indicates that the Chao2 estimates are functioning as minimum richness estimates.

3.3.2. Parametric species richness estimation

Species-level estimates of detection probability (p) were very low for the majority of the species detected during sampling. Four species, all lizards, had an estimated mean $p > 0.01$ i.e. *Gerrhosaurus flavigularis*, *Trachylepis capensis*, *Agama aculeata distanti* and *Trachylepis varia* (Table 3.2). The remaining 16 species, two lizard species and 14 snake species, were detected infrequently resulting in model estimates of mean $p < 0.01$ (Table 3.2). There are two important consequences of low detection probability. The first consequence is that the sampling effort required to detect a species increases as its detection probability decreases. Increased sample effort comes with increased costs in terms of both time and resources. The second important consequence of low detection probability is that it leads to a posterior distribution for occurrence probability that is similar to the prior distribution. For example, *Boaedon capensis* has an estimated mean detection probability of 0.001 and a 95% credible interval for occurrence probability of 0.044 – 1 (mean = 0.877; Table 3.2). The uncertainty evident in the 95% credible interval indicates that the data gathered during sampling has barely modified our prior expectation for *B. capensis*.

Estimates of the mean occurrence probability for 19 of the 20 species detected during sampling were very high i.e. >0.80 (Table 3.2). The exception to this trend was *A. a. distanti*, which had an estimated mean occurrence probability of 0.248 (Table 3.2). Species with low detection probability had highly imprecise estimates of occurrence probability e.g. *B. capensis*. Species with higher detection probabilities had more precise estimates of occurrence probability e.g. *A. a. distanti*, *G. flavigularis*, *T. capensis*, *T. varia*, *Afrotyphlops bibronii*, *Psammophis crucifer*, and *Bitis arietans arietans* (Table 3.2). Six of these seven species i.e. *G. flavigularis*, *T. capensis*, *T.*

varia, *A. bibronii*, *P. crucifer* and *B. a. arietans* are widespread – occurring at most sites – with 95% credible intervals that range from a minimum 0.416 (*B. a. arietans*) to 1. By contrast, *A. a. distanti* is patchy in occurrence, with a 95% credible interval that ranges from 0.068 to 0.542 (Table 3.2). Given that the posterior distributions of *A. a distanti* and *T. capensis* do not overlap (Fig. 3.2), the prediction of the hierarchical model is that *A. a. distanti* occupies significantly fewer sites than *T. capensis* in the southern grasslands of Suikerbosrand Nature Reserve.

Posterior distributions of the hyperparameters of occurrence and detection probability for the reptile assemblage – detected and undetected – are shown in Fig. 3.2.The posterior estimate for the mean of occurrence probability is 0.599 (95% credible interval: 0.097 – 0.951). When plotted as a density function, the posterior distribution for occurrence probability is bimodal, with peaks at high and low probabilities (Fig. 3.2A). The posterior estimate for the mean of detection probability is 0.001 (95% credible interval: 0.0001 – 0.005). As a density function, the posterior distribution of detection probability is heavily weighted towards 0 (Fig. 3.2B). In combination, these two results suggest that detection failures at sample sites are caused by both low occurrence probability and low detection probability of the species concerned. Consequently, the number of species detected at each site is predicted to be significantly lower than the number estimated to occur there (Table 3.3).

Table 3.2: Estimated mean detection and occurrence probabilities, with 95% credible intervals (as per the WinBUGS output) for the 20 species detected between 29 August 2005 and 19 January 2006. Estimates are shown up to three decimal places.

Family	**Species**	**Detection Probability**			**Occurrence Probability**		
		2.5% CI	**Mean**	**97.5% CI**	**2.5% CI**	**Mean**	**97.5% CI**
Lizards							
Agamidae							
	Agama atra	0.000	0.001	0.010	0.045	0.882	1.000
	Agama aculeata distanti	0.039	0.063	0.094	0.068	0.248	0.542
Gerrhosauridae							
	Gerrhosaurus flavigularis	0.065	0.080	0.098	0.698	0.934	0.995
Scincidae							
	Afroablepharus wahlbergii	0.000	0.002	0.009	0.162	0.941	1.000
	Trachylepis capensis	0.064	0.079	0.095	0.843	0.994	1.000
	Trachylepis varia	0.007	0.014	0.024	0.543	0.965	1.000
Snakes							
Leptotyphlopidae							
	Leptotyphlops sp.	0.003	0.008	0.025	0.196	0.842	1.000
Typhlopidae							
	Afrotyphlops bibronii	0.001	0.004	0.010	0.501	0.978	1.000
Lamprophiidae							
	Aparallactus capensis	0.000	0.001	0.013	0.037	0.868	1.000
	Boaedon capensis	0.000	0.001	0.010	0.044	0.877	1.000
	Duberria l. lutrix	0.000	0.001	0.010	0.044	0.878	1.000
	Lamprophis aurora	0.000	0.001	0.013	0.041	0.873	1.000
	Lycophidion c. capense	0.000	0.002	0.008	0.163	0.942	1.000
	Psammophis crucifer	0.001	0.004	0.010	0.500	0.978	1.000
	Psammophylax r. rhombeatus	0.000	0.001	0.011	0.047	0.882	1.000
	Pseudaspis cana	0.001	0.003	0.009	0.269	0.959	1.000
Colubridae							
	Dasypeltis scabra	0.000	0.002	0.009	0.168	0.940	1.000
Elapidae							
	Hemachatus haemachatus	0.000	0.002	0.009	0.165	0.940	1.000
Viperidae							
	Bitis a. arietans	0.001	0.003	0.009	0.416	0.972	1.000
	Causus rhombeatus	0.000	0.002	0.009	0.159	0.939	1.000

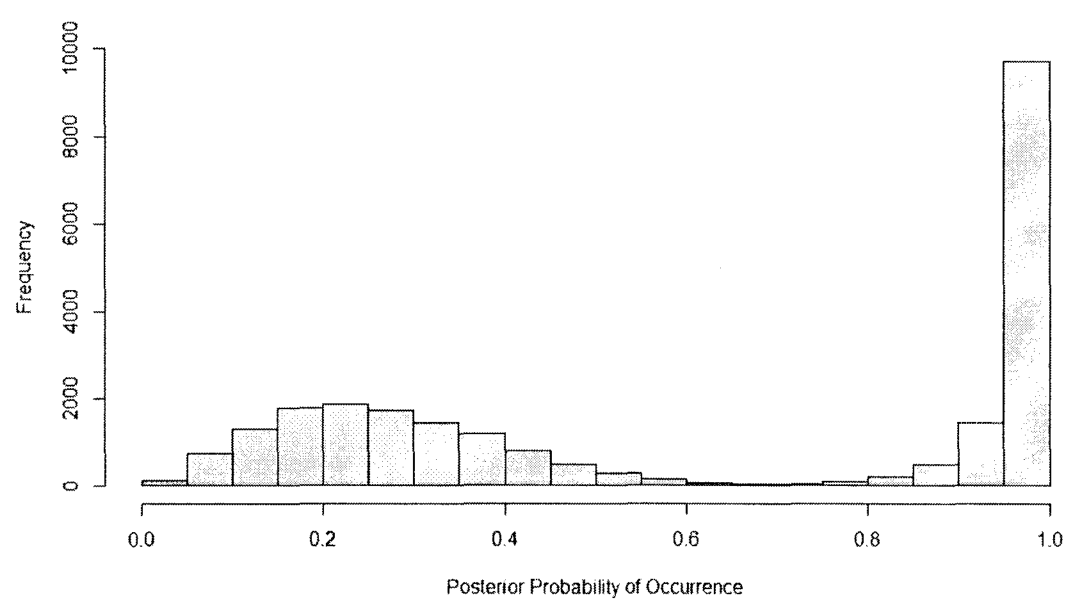

Fig. 3.1: Posterior distributions of occurrence probability for *Agama aculeata distanti* (blue) and *Trachylepis capensis* (red) in the southern grasslands of Suikerbosrand Nature Reserve. The 95% credible intervals for occurrence probability of the two species are shown in Table 5.2.

The estimated species richness at each of the 12 sites is much higher than the number of species detected during sampling. Mean species richness estimates for each site ranged from 28 – 30 species, while the number of species detected during sampling ranged from 3 – 10 species (Table 5.3). Estimates of sample completeness at the site level ranged from 12.8 – 39.8% (Table 3.3; mean = 24.3%) suggesting that the majority of species were not detected at each site. Species richness estimates of the hierarchical model show less variation between sites than those of the Chao2 estimator (Table 3.2), which is expected because the hierarchical model does not deal with each site's information in isolation. Posterior-predictive distributions of species richness for two sites – site 1B and site 3C – are shown in Fig. 3.3. Five species were detected at site 1B during sampling, while eight species were detected at site 3C (Table 3.3), yet the posterior predictions of richness are very similar to each other (Fig. 3.3). The low detection probability of reptile species during sampling meant that site effects on occurrence probability could not be confirmed. Consequently, estimates of species richness at each site depend on the posterior of the hyperparameter of occurrence probability and are therefore similar across the sample sites.

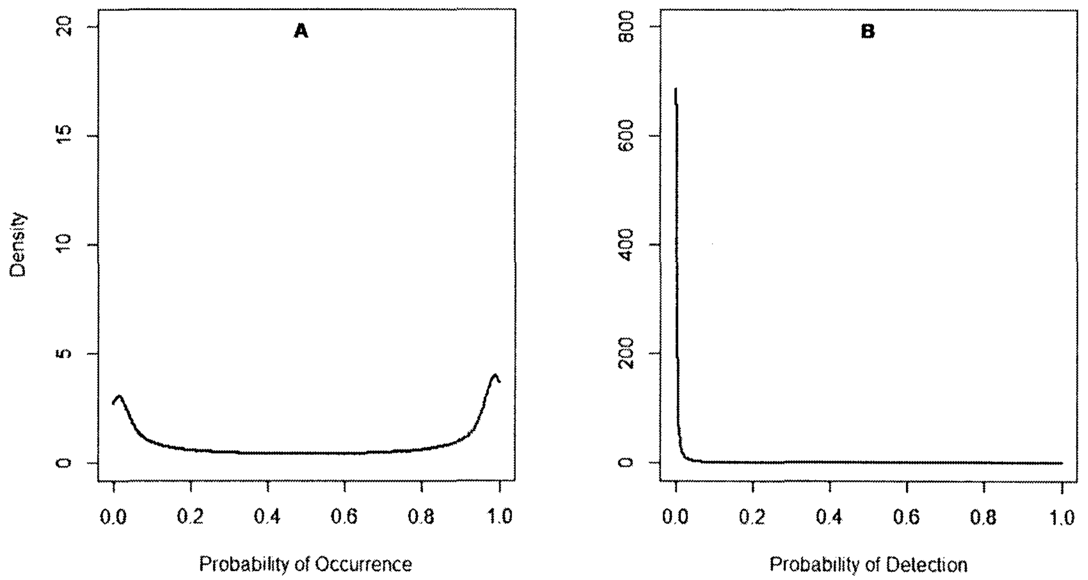

Fig. 3.2: Posterior distributions for the hyperparameters of (A) occurrence and (B) detection probability for the reptile assemblage in the southern grasslands of Suikerbosrand Nature Reserve.

The posterior-predictive distribution of total species richness is shown in Fig. 3.4. A total of 20 species were detected during sampling (Fig. 3.4), yet the hierarchical model predicts a mean richness of 48 species for the reptile assemblage (Table 3.3). The frequency of richness estimates peaks between 37 and 43 species (Fig. 3.4), but the credible interval of the posterior-predictive distribution is wide due to the uncertainty in the hyperparameter of occurrence probability. Using the estimated mean of 48 species to calculate sample completeness, the hierarchical model predicts that the sampling exercise detected 41.7% of the assemblage (Table 3.3). Given the skewed nature of the posterior distribution of total species richness (Fig. 3.4), the mean is right-shifted from the mode and median, making the estimate of sample completeness slightly more conservative. The central 95% credible interval of 28 to 82 species, as produced by WinBUGS and shown in Table 3.3, differed from the HPDI of 25 to 75 species (see Fig. 3.4). While the HPDI is narrower than the central credible interval by just four species, it represents a large reduction in the upper limit of the interval, a shift of the lower limit towards S_{obs}, and an increase in the precision of the estimate.

Table 3.3: Comparison of the number of species observed (S_{obs}) and estimated species richness according to the hierarchical model (S_{HM}) for each sample site and for all sites sampled between 29 August 2005 and 19 January 2006. Mean sample completeness is calculated as (S_{obs} / S_{HM})*100. The WinBUGS output for the 95% credible intervals is shown.

Site	**S_{obs}**	**S_{HM}**	**Variance S_{HM}**	**95% Cred. Int.**	**Mean Sample Completeness (%)**
1A	7	24.9	25.32	17 - 36	28.1
1B	5	23.6	25.95	15 - 35	21.2
1C	10	25.1	23.76	17 - 36	39.8
4A	4	23.7	26.17	15 - 35	16.9
4B	7	24.7	24.88	17 - 36	28.3
4C	5	24.4	25.38	16 - 36	20.5
2A	5	23.8	25.88	15 - 35	21.0
2B	5	23.9	25.67	16 - 35	21.0
2C	5	24.8	25.67	16 - 36	20.2
3A	3	23.4	26.24	15 - 35	12.8
3B	7	24.2	25.09	16 - 36	28.9
3C	8	24.5	24.80	16 - 36	32.7
All Sites	20	48.0	190.38	28 - 82	41.7

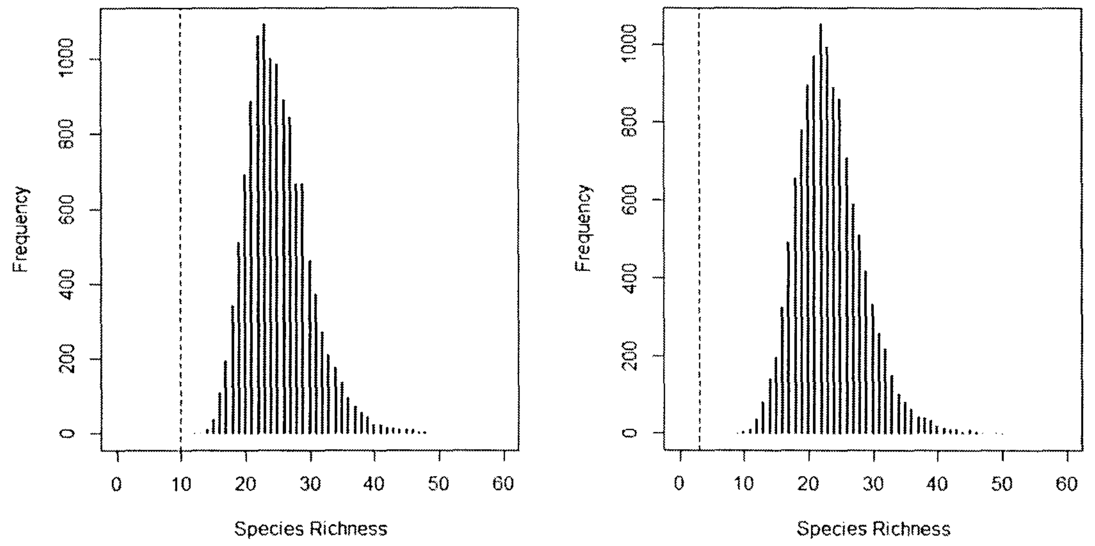

Fig. 3.3: Frequency plots of the posterior-predictive distributions of species richness for (A) site 1C and (B) site 3A. Mean and median estimates of species richness for these two sample sites are similar despite differences in the number of species detected during sampling (dashed line).

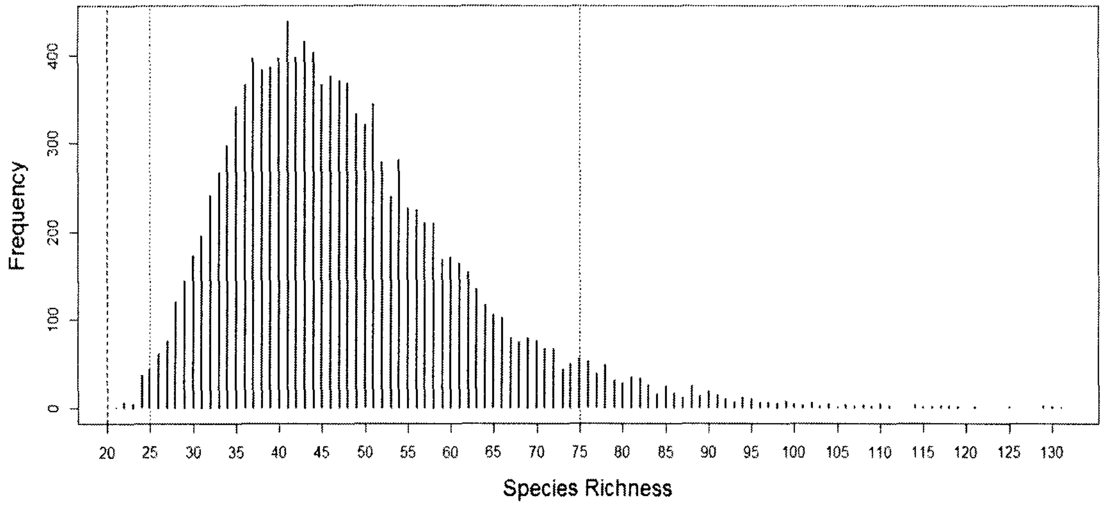

Fig. 3.4: Posterior-predictive distribution of total species richness for the southern grasslands of Suikerbosrand Nature Reserve. The number of species detected during sampling is indicated (dashed line) as are the lower and upper values of the highest posterior density interval (HPDI; see Methods) for the estimate of species richness (dotted lines).

3.4. Discussion

Species richness estimates reflect the consequences of our assumptions about the system we are studying. Estimates of richness depend on the success of sampling activities and the estimation method employed. As is evident in the Chao2 and hierarchical model estimates, different assumptions about the system lead to different estimates of richness (Link 2003). When using the Chao2 estimator, we assume that the information regarding unseen species is concentrated in the two lowest frequency classes of the species actually seen (Chao 1984, 1987, 2005). Species identity is not retained in the incidence frequency summary of the data. As a result, the Chao2 estimator produces a simple, direct estimate of species richness but provides no information regarding the distribution of individual species. When using the hierarchical model, we make an assumption about the form of heterogeneity in detection probability within the reptile assemblage (Dorazio & Royle 2003), and estimate site occupancy of each species to estimate species richness. Information about individual species is retained throughout the steps of the analysis.

For this reason, the hierarchical model provides a detailed picture of the characteristics of the reptile assemblage, of which the richness estimates form a single part.

3.4.1. Inference under the Chao2 estimator

Chao2 estimates are remarkably simple to calculate from a data summary, but the estimator provides minimal assistance to a person interpreting them. At site level, the Chao2 estimator produces highly variable and relatively conservative estimates of species richness. The behaviour of Chao2 as a 'minimum species richness' estimator (Chao *et al.* 2009) can be clearly seen for site 3A (Table 3.1). Comparing S_{obs} across all 12 sites, it seems unlikely that all species have been detected at site 3A, yet this is what Chao2 predicts (Table 3.1). Such an estimate is extremely conservative. A strict application of the stopping rule for Chao2 (Chao *et al.* 2009) would lead to the discontinuation of sampling as all three species present at site 3A are assumed to have been detected. The opposite criticism can be levelled at the Chao2 estimate for site 1C. The Chao2 estimate for site 1C is substantially greater than estimates for the other 11 sites (Table 3.1). Such a result is certainly plausible unless one considers that the mean estimate for site 1C is also greater than the mean estimate for the entire study area (Table 3.1), which is counterintuitive. Even though one could argue that the estimate for 1C and the estimate for the entire study area may both be correct because the Chao2 estimates represent minima not maxima, and are therefore not mutually exclusive, this still runs counter to the expectation that a larger dataset, from a larger sampling effort, will typically contain more information about unseen species (Cherry *et al.* 2007).

If we accept their conservative nature and take the estimates of Chao2 at face value, further challenging questions present themselves. Firstly, how does one use a 'minimum richness estimate' to make decisions when mean estimates range from 3 – 38 species, and standard errors vary dramatically? In the context of species richness, a conservative estimate runs the risk of under-valuing a site for conservation purposes, where the primary objective is to protect a greater number of species per unit area (e.g. Rey Benayas & de la Montaña 2003; Rey Benayas *et al.* 2006). This contrasts with other scenarios e.g. population management of threatened species, where a conservative estimate of population size and the sustainable mortality rate is preferable (Perrings & Walker 2004; Cherry *et al.* 2007). Secondly, what does it mean that the minimum species richness estimate of site 1C is much higher than those of sites 2A, 2B and 2C (Table 3.1)? To conclude that there are true differences in species richness of these sites, a decision maker would need to be certain that the estimates represent true variation in species distribution and not variations in detection probability across different sites. Competing hypotheses to explain site-specific estimates cannot be tested using the Chao2 estimator because parameters such as detection probability are not estimated, and each site's data is considered in isolation. Questions such as these highlight the phenomenological nature of the Chao2 estimates and demonstrate why inference using the Chao2 estimates is vulnerable to criticism of the data generation process.

Recently the Chao2 estimator has come in for criticism during the ongoing debate about grizzly bear (*Ursus arctos horribilis*) conservation in the Greater Yellowstone Ecosystem e.g. Doak & Cutler 2013. The yearly population estimate of the grizzly bear is based on the numbers of females with cubs-of-the-year (F_{COY}; IGBST 2012). The Chao2 estimator was recommended by Cherry *et al.* (2007) and has been used by the Interagency Grizzly Bear Study Team (IGBST) to estimate the number of the total number of F_{COY} from the incidence frequencies of seen F_{COY}. Chao2 estimates of F_{COY} have increased from ± 20 F_{COY} in1983 to ± 50 in 2010 (Doak & Cutler), which has led to increasing estimates of grizzly bear population size and recent calls for them to be removed from the U.S. Endangered Species Act. Doak & Cutler (2013) have criticised these calls as misguided citing problems with the Chao2 estimator, which they show to be sensitive to search effort and to be producing less uniques despite increases in search effort and coverage. Doak & Cutler (2013) argue that the number of uniques should be increasing if the grizzly bear population is in fact increasing as the trend since 1983 suggests. While Doak & Cutler (2013) do not argue that the Chao2 estimates are inaccurate, they caution that the correlations between search effort and estimated F_{COY} are grounds to re-evaluate the apparent trend in numbers of F_{COY} since 1983. The IGBST are reportedly considering alternative methods for estimating population size (Doak & Cutler; IGBST 2012), yet it is not apparent that hierarchical modelling is being considered. One of the great strengths of hierarchical modelling is the accurate estimation of trends in scenarios of varying sample effort or efficacy (Kéry *et al.* 2009a).

3.4.2. Inference under the hierarchical model

The hierarchical model provides a far more coherent picture than Chao2 of reptile richness across the 12 sites and in total. This coherence results from the fact that the model components are logically linked to each other and that the estimates derived at any level of analysis depend on the estimates of the level preceding it (Dorazio & Royle 2005a). Richness estimates derived using the hierarchical model showed little variation across the 12 sample sites despite differences in the detection frequencies of species across sites. In the absence of discernible site effects on detection or occurrence probability, the estimates for each species are treated as uniform across all sites. As the detection probabilities of the species observed decrease, the likelihood that they were present at sites where they were not detected increases. This leads to higher estimates of occurrence probability and similar estimates of species richness for each site. This does not mean that these richness estimates are necessarily more accurate (see Link 2003 and Dorazio & Royle 2003), but the hierarchical model offers a clear explanation for them. Referring back to the difficulties of interpreting the Chao2 estimates for each site, the hierarchical model shows us that, in the absence of increased sampling efficacy, it is premature to treat the reptile assemblages found at each of the 12 sites as distinct. Due to the inclusion of information from all 12 sites, the hierarchical model is able to 'see past' the site-specific variations in species detections.

The benefit of implementing the hierarchical model in the Bayesian framework is that estimates of detection probability, occurrence probability and species richness are exact for the dataset used. In this case, the model illustrates that a lack of repeated detections of species at each site lead to problems of inference regarding occurrence probability. Low numbers of detections may have been caused by a violation of the closure assumption, small populations of the species at each site, trap avoidance behaviours and/or trap damage. Whatever the reason/s, the limited number of detections for many species should lead to cautious inference about their presence/absence. The uncertainty evident in the model estimates for these species' occurrence probability illustrates this point definitively. The other benefit of the Bayesian approach is that there is a full accounting for uncertainty as the model proceeds through the hierarchy of estimates. It follows then that site richness estimates should have narrower credible intervals than the estimate of total richness, and indeed this is what we observe (Table 3.3).

3.4.2.1. Patterns of Reptile Distribution

According to the hierarchical model, failure to detect reptile species in the southern grasslands of SNR is typically the result of low detection probability and not due to the species' absence. *Agama a. distanti* was the only exception to this trend, and is predicted to have a patchy occurrence in grassland sites such as those sampled. The prediction was based on a low mean detection probability of 0.04 (Table 3.2). This result is encouraging in light of the fact that the detection probability for many of the species appears at first glance to be inadequate for ecological inference. The fact that a detection probability of 0.04 was sufficient to reduce the estimated occurrence probability of *A. a distanti* to levels significantly lower than those of the more common species e.g. *T. capensis* (Fig. 3.1) suggests that even slight improvements in the average detection probability of the reptile assemblage will lead to more precise estimates of species richness. The increased detection probability would also reduce survey duration and costs.

Estimates of the richness of the assemblage become more accurate as the proportion of species that have a non-zero probability of detection increases (Mao & Colwell 2005). In the grasslands of SNR, terrestrial and fossorial reptiles are expected to dominate the assemblage. It is therefore encouraging that the trap arrays employed in this survey were able to detect the presence of fossorial species such as *Leptotyhplops* sp. and *Afrotyphlops bibronii*. The detection of species with a fossorial life history means that the estimates of richness can be considered to encompass both the terrestrial and fossorial components of the reptile assemblage. Surprisingly, while the detection probabilities of the two fossorial species are low i.e. < 0.01, they are slightly higher than the detection probability of some of the terrestrial snakes e.g. *Duberria lutrix* (Table 3.2). Many fossorial species are extremely difficult to detect during surveys e.g. *Homoroselaps* spp., yet the capture of the more common fossorial species offers hope that they might be detected in such surveys in the future.

Considering the limited sampling success in this survey, the hierarchical model's HPDI estimate of between 25 and 75 reptile species occurring at SNR is a reasonable outcome of a survey that struggled to repeatedly detect many of the reptile species it recorded. The fact that the posterior distribution of the estimate is right-tailed further indicates that increased average detection probability would have led to more precise estimates of species richness. As with all survey methods, the goal of improving the efficacy of trap arrays is shown to be an important consideration for researchers who wish to survey reptile assemblages or monitor them across longer time frames (Jones 2011). Simulation studies which aim to improve sampling efficacy, such as the one by Ellis & Bedward (2014), are very important for rapid advances in our ability to use hierarchical models on data that is collected more efficiently. For this survey however, the benefit of using the hierarchical model as the basis for inference about the reptile assemblage of SNR's grasslands is that we have generated a few ecological predictions, while simultaneously confirming realising that the survey's sampling efficacy was far from ideal. Consequently the hierarchical model appears preferable to the Chao2 estimator for inference.

3.4.3. Conclusion

Given the vast differences in the approach to estimation of Chao2 and the hierarchical model, a comparison of the two methods using their estimates is neither suitable nor the goal of this chapter. My aim in this chapter was to ascertain which of the two methods improves our understanding of the reptile assemblage at SNR and facilitates defensible inference. Under these criteria, the hierarchical model is more useful than Chao2. This is not to say that the Chao2 estimator is performing poorly or giving demonstrably inaccurate estimates of species richness, it is simply not offering a defensible framework for inference using the estimates. This is exactly where the hierarchical model performs well. The model's construction means that the estimate of species richness depends on the estimated site occupancy matrix for each species – including those not detected during sampling (Kéry & Royle 2008). As demonstrated in this chapter, the estimated site occupancy matrix can be used for inference about each species, each site, and total species richness. It can also be used for other purposes such as calculations of similarity or dissimilarity between sites, co-occurrence patterns of species, and many other questions of biogeographical interest (Dorazio & Royle 2005a). While the hierarchical model's results are sensitive to an analyst's choices about the distribution of detection probabilities within the assemblage, this simply puts a greater emphasis on the model selection process or the reasoning for particular choices, and rightly so.

CHAPTER 4

The Effects of Fire and Grass Cutting on Reptile Distribution

Reptile responses to habitat change are poorly understood, particularly in southern Africa. In protected areas, reptiles are still vulnerable as reserve management is usually aimed at large mammal management. Such practices lead to increased grazing pressures and result in the use of fire to improve the quality of the vegetation for herbivore consumption. I investigated the effects of small-scale burns and grass cutting (to simulate vegetation removal by means other than fire) on reptiles in the grasslands of Suikerbosrand Nature Reserve (SNR). I surveyed reptiles at 12 sites in southern SNR between August 2005 and April 2006 using trap arrays consisting of drift fences, pitfall traps and funnel traps. In January 2006, I burnt four sites, cut four sites and left four sites as controls. All sites were re-surveyed following the treatments. Only species that were detected on more than one occasion in each phase of trapping were selected for analysis. Nine species were selected using this criterion. An additional species i.e. *Agama aculeata distanti*, was also selected as it is of conservation concern due to its apparent restricted distribution. Using a hierarchical, dynamic, site-occupancy model, I tested for changes in the site occupancy status of sites in the different treatment groups for each of the 10 species. There was no evidence that burning or cutting resulted in changes in site occupancy for reptile species. There was evidence of an increase the detection probabilities of all reptile species between the first and second phase of trapping, but for eight species, the change was general and not linked to any treatment group. For two species i.e. *Gerrhosaurus flavigularis* and *T. capensis*, there was evidence of treatment-specific changes in detection probability. Analysis of this result using vegetation covariate data indicated that *T. capensis* responds positively as the height and ground cover of a site's vegetation increases. For *G. flavigularis*, there is some uncertainty regarding the effect of vegetation covariates, which may be resolved with further investigation. The finding of no effect of site treatment relates only to those species which were detected sufficiently for analysis. Of greater concern is the unknown response of the infrequently detected or 'rare' species. The cryptic nature of reptiles is a barrier to informed and effective habitat management for their conservation.

4.1. Introduction

The modification of natural habitats by humans is the greatest single threat to global biodiversity (Brook, Sodhi & Bradshaw 2008). While all vertebrate taxa are adversely impacted by habitat modification, reptiles are thought to be more susceptible than either birds or mammals, with similar, if not greater sensitivity than amphibians (Gibbons *et al.* 2000; Gardner, Barlow & Peres 2007). As a group, reptiles are typically less mobile than birds and mammals (Masterson *et al.* 2009), are often habitat or substrate specialists (Urbina-Cardona, Olivares-Perez & Reynoso 2006), and are consequently at greater risk in the face of changing conditions (Gibbons *et al.* 2000; Kearney, Shine & Porter 2009; Bates *et al.* 2014). A recent assessment by Böhm *et al.* (2013) reports that an estimated 80% of the world's Threatened reptile species are threatened by multiple processes, of which the most serious threat involves land-use changes due to agriculture, logging, harvesting of natural resources or modification of natural systems. In southern Africa approximately 10% of the 384 recognised reptile species are presently threatened with extinction, where habitat loss/degradation is cited as the commonest threat (Bates *et al.* 2014). Here again, agriculture, infrastructural development and fire are reported to have the greatest impact on species of conservation concern (Bates *et al.* 2014). In light of these facts, it follows that the study of habitat modification and disturbance on reptile species and populations is fundamental to their conservation.

Given the widespread reports about the species-threatening effects of habitat modification, it is worrying that the effects of habitat change on reptile species are still poorly understood. In a recent review of the literature, Gardner *et al.* (2007) revealed that, despite six decades of research, there is no clear consensus regarding the consequences of various forms of habitat change for reptiles. The literature is characterised by geographic and process biases, with the majority of studies based in North America and focussing on fragmentation, and also indicates that reptiles have, for all forms of habitat modification, received less research attention than either birds or mammals (Gardner, Barlow & Peres 2007). While there has been an upswing in the numbers of studies in recent years, Gardner *et al.* (2007) highlight several factors common to most studies that limit the rate at which our understanding has improved. The three most important of these are (1) the cryptic habits of reptiles, which has direct consequences for (2) the logistical challenges of effective, replicated sampling across various scales, and (3) the lack of standardised reporting, which precluded any attempt at a meta-analysis (Gardner, Barlow & Peres 2007). In their recommendations for future research, Gardner *et al.* (2007) argue for the need to shift away from traditional hypothesis-testing approaches in favour of analyses that better deal with uncertainty e.g. Bayesian methods. Bayesian methods are particularly suited for the sequential analysis of datasets, thereby facilitating incremental improvements in understanding over time. This is particularly relevant to studies conducted in geographic regions with a dearth of historical information e.g. southern Africa.

In southern Africa, conservation management has historically been geared towards the protection of mammal species, particularly large, charismatic species e.g. the Big Five. This is not altogether surprising as reptiles provide minimal direct economic benefit e.g. ecotourism. The main economic uses of reptiles relate to the leather industry (Abensperg-Traun 2009) and pet trade (Van Wilgen *et al.* 2010), and the latter is difficult to quantify and regulate (Schlaepfer, Hoover & Dodd Jr 2005). The management of species for conservation purposes necessarily involves the manipulation of habitat conditions and the control of unwanted types of disturbance. Fire is one of the few tools available to conservation managers that can be used to influence habitat characteristics across large areas (Hudak, Fairbanks & Brockett 2004; Govender, Trollope & Van Wilgen 2006). It is therefore concerning that there are so few studies investigating the effects of fire on southern African reptiles (Parr & Chown 2003). Studies conducted in fire-prone habitats outside of southern Africa offer valuable context and demonstrate the challenges involved in the research (Greenberg, Neary & Harris 1994b; Ford *et al.* 1999; Cavitt 2000; Hailey 2000; Cunningham *et al.* 2002; Letnic *et al.* 2004; Driscoll & Henderson 2008; Smith, Bull & Driscoll 2013), but have limited applicability for conservation managers tasked with protecting the species in southern Africa (Masterson, Maritz & Alexander 2008).

Our inadequate understanding of southern African reptile species' responses to habitat modification – broadly and individually – compromises the conservation of these species in protected areas and may also result in the implementation of management plans that are inadvertently detrimental to their persistence. Recent studies on the topic have provided several insights but represent only the beginning of what must become a sustained research agenda.

Masterson, Maritz & Alexander (2008) concluded that vegetation structure is an important factor structuring herpetofaunal assemblages in South Africa's grasslands. A related study by Masterson *et al.* (2009) found that habitat modification associated with agricultural practices led to reduced species richness when compared with undisturbed grassland. Unfortunately, neither study explicitly accounted for detection probability to compensate for the presence of false negatives in the detection data. The recent advancements in our understanding of the effects of less-than-perfect detection probability on sampling efficacy and ecological inference (see Kéry 2002; MacKenzie & Kendall 2002; Kéry & Schmid 2004; Dorazio & Royle 2005; Royle & Dorazio 2006; Royle & Kéry 2007; Kéry & Royle 2008, 2010; Yamaura *et al.* 2011; Bled, Royle & Cam 2011) indicate that this oversight may be material to the conclusions of both Masterson *et al.* (2008) and Masterson *et al.* (2009). As the detection probability of a species decreases, it introduces a bias into naive estimates of model coefficients (Kéry 2010). In extreme cases, this can result in conclusions that are the opposite of the ecological reality. Such conclusions would be of even less use for conservation managers as they might provide a false sense of confidence in the actions undertaken.

In this chapter I have attempted to address the two primary deficiencies in the current literature regarding habitat modification and reptiles in southern Africa. Firstly, I investigated the impacts of habitat changes resulting from fire or grass cutting on a site's reptile assemblage. The study took an experimental approach in that the habitat at the sample sites was actively modified during the sampling period. Secondly, I used a hierarchical model, which incorporates an explicit model of detection probability, to discriminate between the two possible causes of non-detection i.e. true absence or detection failure. The use of hierarchical models in studies investigating the effects of habitat modification on reptiles are uncommon, thus this study represents, globally, one of the first to make use of this relatively new method of analysis. Thus the goal of this study was to apply recommended analytical techniques to a critical conservation issue, thereby contributing to the discussion of both topics simultaneously.

4.2. Methods

4.2.1. Reptile Survey

I sampled reptiles at 12 sites in the southern portion of Suikerbosrand Nature Reserve (SNR) between 29 August 2005 and 26 April 2006 using trap arrays consisting of drift fences, funnel traps and pitfall traps. I aimed to select management blocks in SNR that: (1) were in the lower-lying i.e. non-plateau portion of the reserve; (2) had a well-developed grass layer (in terms of vegetation height and cover); and that (3) were large enough and sufficiently homogeneous to accommodate the placement of three trap arrays in similar microhabitat. Management blocks surveyed during 2005 and 2006 are shown in Fig. 4.1(a). Trap array placement on each of the four blocks aimed to maximise the distance between them, reduce site differences and optimise the accessibility of the site (Fig. 4.1(b)). Ultimately, trap arrays were placed between 80 to 100 m from either the tourist road or the closest management road and between 308 to 1137 m from the nearest neighbouring array.

Due to the heterogeneity of SNR and constraints that resulted from accidental fires in June 2005, an 'ideal' set of homogeneous trap sites could not be selected. Blocks 1 and 3, were irregularly shaped with many small to large, rock-covered hills scattered across them (Figs 4.2 and 4.4).

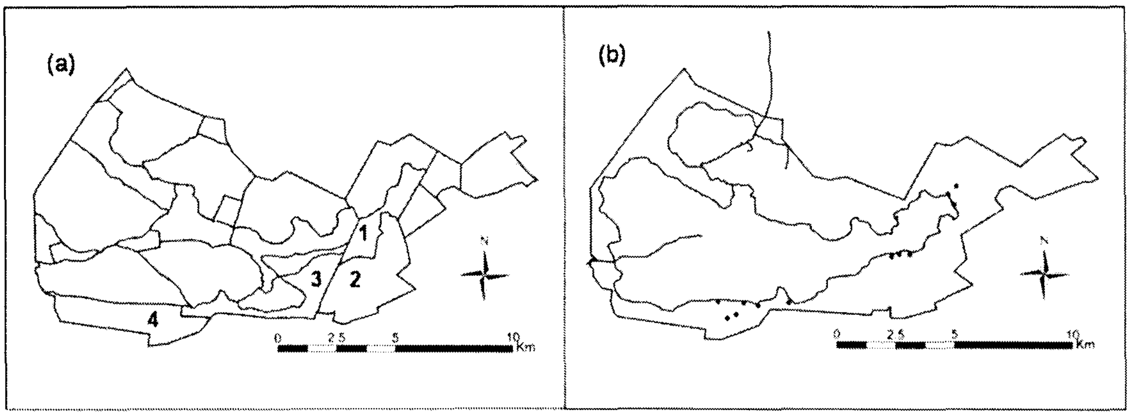

Fig. 4.1: Two images of Suikerbosrand Nature Reserve (as per the proclamation in 1973) showing (a) the delineation of the reserve's management blocks and the blocks surveyed (numbered 1-4) between August 2005 and April 2006; and (b) the tourist route through the reserve and the relative positions of the individual trap arrays.

Fig. 4.2: Satellite imagery from 10 September 2006 (downloaded from Google Earth ver. 4.2.0205.5730 on 05/05/2008). The image shows a bird's eye view of the sites surveyed on Block 1 between 29 August 2005 and 26 April 2006. The colour of the cross denotes the treatment applied to the site i.e. black = control, green = cut, and red = burnt. The image also shows how the habitat is different in composition around sites 1A (Cut) and 1C (Burnt) and the untreated grassland surrounding them, which is still evident even 7 months after the treatments in January 2006. (Note: The number displayed above the scale bar in the bottom left corner indicates the total distance represented by the scale bar and not of each subdivision within it.)

Despite this, trap sites on these blocks had gentler slopes than the trap sites on blocks 2 and 4. Block 2 (Fig. 4.3) was relatively homogeneous in grass cover and slope, yet due to limited access the southern parts of the management block trap arrays were placed on a south-facing slope closer to the management road. Scattered rocks were more common at trap sites on blocks 1 and 4 (Fig. 4.5) than on blocks 1 and 3, but none of the trap sites had a noteworthy proportion of 'rocky' habitat. Additional details about the trap array layout and position of funnel and pitfall traps are given in Chapter 2.

Fig. 4.3: Satellite imagery from 2 May 2007 (downloaded from Google Earth ver. 4.2.0205.5730 on 05/05/2008). The image shows a bird's eye view of the sites surveyed on Block 2 between 29 August 2005 and 26 April 2006. The colour of the cross denotes the treatment applied to the site i.e. black = control, green = cut, and red = burnt. The image also shows the visible difference in habitat between sites 2A (Burnt) and 2B (Cut) and the untreated grassland surrounding them, which is still evident even 15 months after the treatments in January 2006. (Note: The number displayed above the scale bar in the bottom left corner indicates the total distance represented by the scale bar and not of each subdivision within it.)

Reptiles caught in the traps were identified to species and released near the site of capture. In addition to the basic processing of the other species, individuals of four lizard species i.e. *Trachylepis capensis*, *Trachylepis varia*, *Gerrhosaurus flavigularis* and *Agama aculeata distanti* were toe-clipped with an array-specific code (two toes were clipped on each lizard, where one toe indicated the block of first capture and the second indicated the trap array on that block). The species selected for marking are the most commonly captured species in Suikerbosrand Nature Reserve, thus I expected that many individuals of these species would be recaptured throughout the course of the survey. Recaptures were recorded along with the initial site of the lizard's capture in order to determine whether the trap arrays were too close together and were sampling

Fig. 4.4: Satellite imagery from 2 May 2007 (downloaded from Google Earth ver. 4.2.0205.5730 on 05/05/2008). The image shows a bird's eye view of the sites surveyed on Block 3 between 29 August 2005 and 26 April 2006. The colour of the cross denotes the treatment applied to the site i.e. black = control, green = cut, and red = burnt. (Note: The number displayed above the scale bar in the bottom left corner indicates the total distance represented by the scale bar and not of each subdivision within it.)

the same individuals. If the recapture site and the initial site of capture differed, the lizard was neither remarked nor translocated back to the site of its initial capture.

The collection of reptile data was divided into two sampling periods: Phase 1: 29 August 2005 – 19 January 2006, and Phase 2: 16 February 2006 – 26 April 2006. During Phase 1, traps were visited and checked a total of 104 times, with the exception of sites 4A – 4C, which were only installed on 30 September 2005 following the loss of three sample sites to an unplanned grass fire. Sites 4A, 4B and 4C were subsequently checked a total of 77 times during Phase 1. All trap arrays were checked 52 times during Phase 2. Between Phase 1 and Phase 2, I modified the habitat characteristics at eight of the 12 sites i.e. two of the three sites per management block. Four sites were burnt, the grass at four sites was cut and four sites were left unmodified as

Fig. 4.5: Satellite imagery from 2 May 2007 (downloaded from Google Earth ver. 4.2.0205.5730 on 05/05/2008). The image shows a bird's eye view of the sites surveyed on Block 4 between 29 August 2005 and 26 April 2006. The colour of the cross denotes the treatment applied to the site i.e. black = control, green = cut, and red = burnt. (Note: The number displayed above the scale bar in the bottom left corner indicates the total distance represented by the scale bar and not of each subdivision within it.)

controls. Details of the sites which were treated or left unmodified are shown in Table 4.1 (as well as Figs 4.2, 4.3, 4.4 and 4.5). At each treated site, a square of 120 m by 120 m centred on the trap array was burnt or cut resulting in a treated area of approximately 1.5 ha.

I tested the effects of grass cutting and burning on site occupancy of reptile species in phase 2. Detection data from Phase 1 were used for baseline comparative purposes and to estimate the occupancy state of each site. A total of 20 and 12 reptile species were detected in Phase 1 and Phase 2 respectively. Due to large variation in the numbers of detections for each species in each phase, I restricted my analysis to species which were detected more than once in both phases of sampling. Nine of the 20 species recorded during sampling met these criteria; four lizard and five snake species. They were (in descending order of total number of detections): *Gerrhosaurus flavigularis*, *Trachylepis capensis*, *Trachylepis varia*, *Afroablepharus wahlbergii*, *Psammophis* *crucifer*, *Bitis arietans arietans*, *Pseudaspis cana*, *Hemachatus haemachatus* and *Lycophidion capense capense* (see Table 4.2). Additionally, I included and analysed the data for *Agama aculeata distanti*, because the species was detected frequently in Phase 1 and because of the species' low occurrence probability (see Chapter 3).

4.2.2. Vegetation Monitoring

To quantify the effects of burning or grass cutting on the vegetation at each treated site, I measured the grass height and grass cover at each site both before and after the treatments in February 2006. Four sets of vegetation measurements were taken in September 2005 (the start of the survey), January 2006 (prior to habitat modification), February 2006 (immediately after habitat modification) and April 2006 (the end of the survey). These four sampling periods correspond to (1) early spring prior to the rainy season and growth, (2) midsummer, (3) late summer and (4) mid-autumn when the dry season starts. During each vegetation survey I measured grass height and grass cover in an area of approximately 1.5 ha centred on the trap array i.e. 120m x 120m. In each of 30 1m x 1m quadrats, I estimated the percentage of soil covered by vegetation and measured the height of the grass/vegetation at each of the four corners of the quadrat. In this context, grass cover is defined as the percentage of soil obscured by the vegetation when looking down on the soil from a height of 1.9 m (observer height). The terms 'grass cover' and 'grass height' are used because grass species dominated at each of the 12 sites, however shrubby components of the vegetation e.g. *Stoebe vulgaris* were not excluded from measurements of the two variables.

Using these data, I calculated the average grass cover and grass height for each site during each phase of the reptile survey and assessed their effect on the site-specific detection probability of *T. capensis* and *G. flavigularis*.

4.2.3. Dynamic Occupancy Models

Static occupancy models are appropriate when population/community closure is a valid assumption for the period of sampling. When the occupancy state of sites is expected to change during the study period, models of occupancy dynamics must be included to account for the fact

Table 4.1: Details of the 12 sites sampled between 29 August 2005 and 26 April 2006. The Phase 1 structural classification of each site's habitat (*sensu* Edwards 1983), the treatment applied at each site, and the mean grass height and grass cover at each site in each phase are shown.

Site	Phase 1 Structural Classification	Treatment	Grass Height (cm; Mean ± 1 SE)		Grass Cover (%; Mean ± 1 SE)	
			Phase 1	Phase 2	Phase 1	Phase 2
1A	low, closed	Cut	44.83 ± 30.22	23.50 ± 18.66	77.67 ± 15.50	66.33 ± 22.09
1B	low, closed	Control	47.86 ± 29.54	51.53 ± 26.60	72.33 ± 13.94	83.67 ± 12.78
1C	short, closed	Burnt	50.41 ± 32.51	25.52 ± 21.44	73.75 ± 15.28	49.17 ± 19.70
2A	short, closed	Burnt	51.79 ± 27.56	20.29 ± 17.49	63.42 ± 16.61	36.08 ± 20.83
2B	short, closed	Cut	54.27 ± 29.64	24.55 ± 13.80	79.17 ± 13.78	70.91 ± 18.33
2C	low, closed	Control	42.08 ± 28.45	64.35 ± 32.08	71.33 ± 18.47	87.58 ± 11.77
3A	short, closed	Cut	59.45 ± 34.88	34.26 ± 25.02	69.83 ± 19.33	75.58 ± 17.22
3B	tall, closed	Control	104.43 ± 50.44	96.80 ± 46.40	74 ± 17.78	86.17 ± 12.53
3C	short, closed	Burnt	72.23 ± 41.12	32.78 ± 27.78	83.83 ± 11.29	49.08 ± 23.59
4A	low, closed	Burnt	40.47 ± 29.55	13.91 ± 7.40	84.50 ± 10.28	34.08 ± 15.77
4B	short, closed	Cut	52.47 ± 37.77	25.98 ± 15.54	82.42 ± 11.22	85.75 ± 9.47
4C	low, closed	Control	30.85 ± 33.36	61.96 ± 37.54	66.83 ± 26.15	87.75 ± 9.47

that non-detections of species at sites where they were previously detected may result from a change in the species' occupancy of the site. The assumption of population closure is clearly unreasonable for a combined analysis of the detection data from Phase 1 and Phase 2 because changes in site occupancy following the treatment of sites must be allowed for. In terms of structure, a hierarchical formulation of a dynamic occupancy model is only slightly different to a static occupancy model. For both types of occupancy model, one model describes the occupancy process and the second represents the sampling process i.e. the detection of species conditioned upon the occupancy state of each site. In dynamic occupancy models the difference is that the occupancy state is allowed to vary between primary sampling periods. In the formulation of Royle & Kéry (2007), the occupancy state in each primary sampling period, other than the first, depends on two parameters: (1) the species' survival probability between primary sampling periods and (2) the probability that the species colonises the site between primary sampling periods. Application of the survival or colonisation probabilities for each site depends upon the occupancy of the site in the preceding primary period. Following the notation of Royle & Dorazio (2008), let z_{it} denote the occupancy of site i in primary sampling period t; then

$$z_{i,t} \mid z_{i,t-1} \sim \text{Bernoulli}\ (\pi_{i,t}) \qquad \text{eqn 4.1}$$

and

$$\pi_{i,t} = z_{i,t-1}\, \phi_{i,t-1} + (1 - z_{i,t-1})\, \gamma_{i,t-1} \qquad \text{eqn 4.2}$$

where ϕ represents the species' survival probability at site i in the preceding primary sampling period, and γ represents the colonisation probability of site i for the preceding primary sampling period. From Eqn 4.2 we see that an occupied site in period $t-1$ remains occupied in period t with a probability of ϕ_{t-1}, while a site that is unoccupied in period $t-1$ becomes occupied in period t with a probability of γ_{t-1}. However when $t = 1$, no information about the occupancy states of our sites is available to estimate ϕ or γ. For $t = 1$,

$$z_{i,1} \sim \text{Bernoulli}\ (\psi_1) \qquad \text{eqn 4.3}$$

where ψ is the occurrence probability of the species at each site for the first primary sampling period.

Multiple forms of the dynamic occupancy model have been demonstrated in the literature (e.g. MacKenzie *et al.* 2003; Royle & Kéry 2007; Kéry *et al.* 2009). Covariates thought to influence site-specific or period-specific survival or colonisation probabilities can be included using the generalised linear modelling (GLM) framework and an appropriate link function e.g. logit (Kéry & Schaub 2011). Alternatively the model for occurrence probability can be specified in an auto-logistic formulation (Royle & Dorazio 2008). The benefits of the auto-logistic formulation are: (1) that the effects of a covariate on *net* occupancy can be tested without having to specify covariate effects on survival and colonisation probability individually, (2) improved orthogonality of the parameters in the posterior and (3) reduced auto-correlation in the Markov chain simulations of the parameter's posterior distributions (Royle & Dorazio 2008). To specify a site covariate occupancy model in auto-logistic format, we modify equation 4.2 such that

$$\text{logit}\ (\pi_{i,t}) = a_t + b_t\, z_{i,t-1} + \beta_1\, x_i \qquad \text{eqn 4.4}$$

where a_t and b_t represent auto-regression parameters on the logit-normal scale and β_1 is the effect of site covariate x_i on the occupancy of site i. Model estimates of the auto-regression parameters from eqn 4.4 are used to calculate ϕ and γ, such that

$$\phi_{t-1} = \text{logit}^{-1} (a_t + b_t) = 1 / (1 + \exp(-(a_t + b_t)) \qquad \text{eqn 4.5}$$

and

$$\gamma_{t-1} = \text{logit}^{-1} (a_t) = 1 / (1 + \exp(-a_t)) \qquad \text{eqn 4.6}$$

The effect of the site covariate x_i has no direct effect on survival and colonisation probability (equations 4.5 and 4.6), but does affect the occupancy of site i (equations 4.1 and 4.4; Royle & Dorazio 2008)

The model for detections of the species being conditional upon a site's occupancy is similar to that of the static occupancy models (see Chapter 3), and also allows for one to test for site- or period-specific variation in detection probability (p) using relevant covariates.

4.2.3.1. Fitting the Model

For the 10 selected species, I used the auto-logistic formulation of the dynamic occupancy model (Royle & Dorazio 2008) to estimate the detection probability, occurrence probability, the number of occupied sites in the two phases of sampling and the phase-specific finite-sample occupancy rate (ψ^{fs}) i.e. the proportion of the 12 sites occupied in each phase. I tested the effect of site treatment on site occupancy in Phase 2 using eqn 4.4 and specifying β_1 as a factor with three levels i.e. ANOVA format with β_k where k = control, cut, or burnt sites.

For eight of the 10 species (not including *G. flavigularis* and *T. capensis*), I assumed that phase was the only factor affecting detection probability and that the detection probability in the two phases were independent. Let $y_{i,t}$ denote the number of detections at site i in Phase t, then

$$y_{i,t} \sim \text{binomial} (N_t, z_{i,t} p_t) \qquad \text{eqn 4.7}$$

where N represents the number of samples or trap visits, $z_{i,t}$ represents the occupancy status of site i in Phase t and where $p_t \sim$ uniform (0, 1). For *G. flavigularis* and *T. capensis* i.e. the two most frequently detected species, I used the logit-link function of the GLM framework to model two forms of structure in each species' p. For the first model of p, I used an ANOVA format where I allowed p to vary between each treatment type. In means parameterisation (see Kéry 2010), the linear model for the detections of *G. flavigularis* and *T. capensis* extends from eqn 4.7 to

$$y_{i,t} \sim \text{binomial}\ (N_t, z_{i,t} p_{i,t})$$

for

$$\text{logit}\ (p_{i,t}) = \alpha_{k,t} \qquad \text{eqn 4.8}$$

where $\alpha_{k,t} \sim$ normal (0,10) and represents the logit-normal detection probability at sites in treatment group *k* in Phase *t*. In the second model of *p*, I used a linear regression structure and included the two vegetation covariates i.e. grass height and grass cover in the linear model as follows:

$$\text{logit}\ (p_{i,t}) = \mu_t + \nu_t * \text{cover}_{i,t} + \delta_t * \text{height}_{i,t} \qquad \text{eqn 4.9}$$

where μ_t is the intercept of the detection probability in phase *t*, ν_t is the coefficient for the effect of average grass cover at site *i* during phase *t*, and δ_t is the coefficient for the effect of average grass height at site *i* during phase *t* (see Table 4.1). I used standardised normal distributions of the measures of grass height and grass cover to prevent issues with parameter estimation when using MCMC (see Kéry 2010).

The extension of the detection model for *T. capensis* and *G. flavigularis* was motivated by two factors: (1) the high number of detections in total and per phase (see Table 4.2) and (2) the high occupancy rates of the both species i.e. >10 sites in each phase. In combination these observations confirm that *G. flavigularis* and *T. capensis* are abundant, widespread species in the open grasslands of SNR. As a consequence of these species' abundance, the site treatments are more likely to affect detection probability resulting from changes in abundance or behaviour of the species at affected sites with no change in site occupancy. In using the two models I aimed to assess whether any differences in *p* between sites was a general outcome of the treatments or a result of changes in the two vegetation covariates measured during the vegetation surveys.

All models were implemented according to the Bayesian framework for inference. The advantage of the Bayesian implementation of the dynamic occupancy model is that the latent variable for occupancy in each period is retained (Royle & Kéry 2007), whereas it is integrated out of the model when using likelihood estimation (MacKenzie *et al.* 2003). Markov Chain Monte Carlo simulations of the dynamic occupancy model for each species were executed using JAGS v. 3.4.0 (Plummer 2013a) called from within R v. 2.15.1 (R Core Team 2012) using the rjags package (Plummer 2013b). I used vague normal priors for parameters a, b, β_1, and α (for *G. flavigularis* and *T. capensis*), and specified a vague uniform prior on p (for the other eight species). Posterior distributions for all parameters were calculated using three parallel chains of 20*k* iterations from which I discarded the first 4*k* iterations as burn-in. Chains were initialised using different starting values and thinned by 8, leaving a total of 6*k* iterations for inference. Chains of this length appeared to have converged sufficiently with Gelman-Rubin statistic values of < 1.003 for all the structural model parameters (Gelman & Rubin 1992).

4.3. Results

The total numbers of detections for each species across all 12 sites in each phase are shown in Table 4.2. *Gerrhosaurus flavigularis* and *T. capensis* were the most frequently trapped species with 152 and 151 detections respectively, followed by *T. varia* (52) and *A. wahlbergii* (35; Table 4.2). Thirteen of the 20 species were detected less than 10 times in total across both phases of sampling (Table 4.2). The most commonly detected snake species were *P. crucifer* (23) and *B. a. arietans* (11; Table 4.2). Seven of the 10 species selected for analysis (indicated using ** in Table 4.2) were detected more times in Phase 2, despite its shorter duration and number of trap visits i.e. 52 (Table 4.2). The exceptions were *G. flavigularis*, *T. capensis* and *A. a. distanti*, but while the number of detections for *G. flavigularis* and *T. capensis* exceeded 50 in Phase 2, the number of detections of *A. a. distanti* decreased from 21 in Phase 1 to zero in Phase 2 (Table 4.2).

The model-based estimates for the relevant ecological parameters are shown in Table 4.3. The posterior mean detection probability of all species increased from Phase 1 to Phase 2 (Table 4.3), which is to be expected given that most species were detected a greater number of times in half the number of trap visits i.e. 104 in Phase 1 vs 52 in Phase 2 (Table 4.2). The increase in detection probability in Phase 2 was significant for *T. varia*, *A. wahlbergii* and *P. crucifer* (Table 4.3). A re-analysis of the data for these three species, using the model which included an effect of treatment type on detection probability in Phase 2, indicated that the increases in Phase 2 detection probability were general in nature and not restricted to any particular treatment type. For *A. a. distanti* the increase in mean detection probability is a function of the lack of detections

Table 4.2: Total number of detections across all sites per phase for each of the 20 reptile species recorded between 29 August 2005 and 26 April 2006. Species selected for analysis using the dynamic occupancy model are indicated (**).

Family	**Species**	**Phase 1**	**Phase 2**
Lizards			
Agamidae			
	Agama a. atra	1	0
	Agama aculeata distanti	21	0
Gerrhosauridae			
	Gerrhosaurus flavigularis	87	65
Scincidae			
	Afroablepharus wahlbergii	2	33
	Trachylepis capensis	93	58
	Trachylepis varia	15	37
Snakes			
Typhlopidae			
	Afrotyphlops bibronii	5	0
Leptotyphlopidae			
	Leptotyphlops sp.	7	0
Lamprophiidae			
	Aparallactus capensis	1	1
	Boaedon capensis	1	0
	Duberria l. lutrix	1	0
	Lamprophis aurora	1	0
	Lycophidion c. capense	2	3
	Psammophis crucifer	5	18
	Psammophylax r. rhombeatus	1	3
	Pseudaspis cana	3	4
Colubridae			
	Dasypeltis scabra	2	0
Elapidae			
	Hemachatus haemachatus	2	5
Viperidae			
	Bitis arietans arietans	4	7
	Causus rhombeatus	2	1

in Phase 2 and the mean of the prior distribution, as is evident in the precision of the posterior distribution (Table 4.3). For *G. flavigularis* and *T. capensis*, there was minor variation in the species' detection probability at sites in each treatment group in Phase 1, but in Phase 2 the detection probability of *G. flavigularis* was greater at cut sites than at control or burnt sites, and the detection probability of *T. capensis* was lower at burnt sites than at cut or control sites (Table 4.3). On the probability scale, the mean detection probability of *G. flavigularis* at cut sites in Phase 2 was 0.18 compared with 0.09 and 0.08 at control and burnt sites respectively. The mean detection probability of *T. capensis* at burnt sites in Phase 2 was 0.04, as compared with 0.12 and 0.11 for the control and cut sites respectively. These results suggest that a change in the behaviour or abundance of these two common lizards occurred at one or all of the sites in the relevant treatment group.

The effects of treatment type on net occupancy rates varied between positive and negative means with large posterior standard deviations, which resulted in overlapping posterior distributions for $\beta_{control}$, β_{cut}, and β_{burnt} that included 0 i.e. had no net positive or negative effect on occurrence probability in eqn 4.4 (Table 4.3). The estimates of the number of occupied sites (N_{occ}) for each species in each phase are also shown in Table 4.3. The model estimates of the finite-sample occupancy rates (ψ^{fs}), which depend on the estimates of N_{occ}, were typically more precise in Phase 2 than in Phase 1. For *A. wahlbergii* the Phase 2 estimates were much more precise; for *P. crucifer* and *H. haemachatus* the precision of the Phase 2 estimates increased and the upper limit of the 95% credibility interval decreased to < 1; for *P. cana* and *L. c. capense* the precision and the mean occupancy rate increased (Table 4.3). Again, the exception to this trend was *A. a distanti* for which the estimated occupancy rate was significantly lower than in Phase 1, but the estimated occupancy rate was less precise in Phase 2 (Table 4.3). In the absence of discernible effects of treatment type on the occurrence probability of each species, the most likely cause of the differences in N_{occ} and the estimates of ψ^{fs} between phases is the difference in the detection probability of the species in Phase 2. However, for *A. a. distanti* it is difficult to be certain that the treatments had no effect on the species' site occupancy in Phase 2. Model estimates of N_{occ} in Phase 1 predict that the species occurs only at the sites at which it was detected i.e. site 1A, 2A and 2C (Table 4.3). With no detections of *A. a. distanti* at these three sites in Phase 2, the 95% credible interval for N_{occ} shifts downwards to the range of 0 to 2 sites for Phase 2 (Table 4.3). Site 2C was not treated between Phase 1 and Phase 2, but site 1A was cut and site 2A, which

Table 4.3: Model-based parameter estimates for each of the 10 species selected for analysis. Parameters estimated by the dynamic occupancy model are: the logit-scale survival (ϕ) and colonisation (γ) probability of each species from Phase 1 to Phase 2; the logit-scale effect of treatment type ($\beta_{control}$, β_{cut}, β_{burn}) on site occupancy in Phase 2; the initial occupancy probability of occurrence in Phase 1 (ψ_1); the occupancy rate i.e. finite-sample estimates of occurrence probability (ψ^{fs}) in Phase 1 and 2, which are derived from the number of occupied sites in each phase (N_{occ}). Apart from *G. flavigularis* and *T. capensis*, the model assumed a constant detection probability (p) for each species in the two phases of sampling. For *G. flavigularis* and *T. capensis*, detection probability was allowed to vary by treatment type in each phase ($\alpha_{control}$, α_{cut}, α_{burn}; as per eqn 4.8) and estimates are shown on the logit scale. The posterior mean, standard error (posterior standard deviation) and 95% credible interval are shown for all parameters. The phase of sampling relevant to each parameter is shown in square brackets.

Species	**Parameter**	**Mean**	**SE**	**Credible Interval**		
				2.5%	**50%**	**97.5%**
Gerrhosaurus flavigularis						
	$\alpha_{control}[1]$	-2.455	0.189	-2.835	-2.450	-2.097
	$\alpha_{cut}[1]$	-2.561	0.197	-2.961	-2.557	-2.186
	$\alpha_{burnt}[1]$	-2.224	0.199	-2.629	-2.219	-1.851
	$\alpha_{control}[2]$	-2.314	0.238	-2.799	-2.304	-1.874
	$\alpha_{cut}[2]$	-1.483	0.208	-1.902	-1.480	-1.089
	$\alpha_{burnt}[2]$	-2.428	0.254	-2.952	-2.421	-1.954
	ψ_1	0.859	0.090	0.639	0.876	0.982
	ϕ	3.367	2.202	-0.796	3.341	7.866
	γ	2.123	2.328	-2.299	2.096	6.756
	$\beta_{control}[2]$	1.738	2.547	-3.076	1.637	7.065
	$\beta_{cut}[2]$	-1.587	2.247	-5.942	-1.623	2.793
	$\beta_{burnt}[2]$	2.089	2.485	-2.544	1.997	7.278
	$N_{occ}[1]$	11.002	0.039	11	11	11
	$N_{occ}[2]$	11.003	0.056	11	11	11
	$\psi^{fs}[1]$	0.917	0.003	0.917	0.917	0.917
	$\psi^{fs}[2]$	0.917	0.005	0.917	0.917	0.917
Trachylepis capensis						
	$\alpha_{control}[1]$	-2.231	0.169	-2.571	-2.228	-1.913
	$\alpha_{cut}[1]$	-2.419	0.185	-2.790	-2.416	-2.070
	$\alpha_{burnt}[1]$	-2.773	0.216	-3.208	-2.768	-2.363
	$\alpha_{control}[2]$	-1.954	0.212	-2.384	-1.947	-1.561
	$\alpha_{cut}[2]$	-2.047	0.219	-2.492	-2.041	-1.642
	$\alpha_{burnt}[2]$	-3.162	0.392	-3.961	-3.147	-2.434
	ψ_1	0.929	0.067	0.752	0.949	0.998
	ϕ	5.126	2.795	0.226	4.907	11.231
	γ	2.600	2.587	-2.443	2.577	7.722
	$\beta_{control}[2]$	1.107	2.724	-4.154	1.079	6.637

	$\beta_{cut}[2]$	1.165	2.710	-4.142	1.200	6.560
	$\beta_{burnt}[2]$	0.308	2.912	-5.103	0.196	6.180
	$N_{occ}[1]$	12	0	12	12	12
	$N_{occ}[2]$	11.747	0.435	11	12	12
	$\psi^{fs}[1]$	1	0	1	1	1
	$\psi^{fs}[2]$	0.979	0.036	0.917	1	1
Trachylepis varia						
	$p[1]$	0.017	0.005	0.009	0.017	0.029
	$p[2]$	0.078	0.013	0.054	0.078	0.105
	ψ_1	0.773	0.139	0.465	0.790	0.983
	ϕ	2.086	2.189	-1.881	2.001	6.568
	γ	1.335	2.236	-3.003	1.319	5.699
	$\beta_{control}[2]$	-1.432	2.099	-5.496	-1.444	2.667
	$\beta_{cut}[2]$	2.522	2.370	-1.865	2.396	7.437
	$\beta_{burnt}[2]$	0.189	2.388	-4.332	0.074	5.185
	$N_{occ}[1]$	9.777	1.262	8	10	12
	$N_{occ}[2]$	9.356	0.612	9	9	11
	$\psi^{fs}[1]$	0.815	0.105	0.667	0.833	1
	$\psi^{fs}[2]$	0.780	0.051	0.750	0.750	0.917
Afroablepharus wahlbergii						
	$p[1]$	0.007	0.006	0.001	0.005	0.024
	$p[2]$	0.066	0.012	0.044	0.065	0.093
	ψ_1	0.485	0.245	0.103	0.454	0.961
	ϕ	1.655	3.113	-3.871	1.396	8.566
	γ	2.061	2.228	-2.302	2.026	6.451
	$\beta_{control}[2]$	0.851	2.518	-3.849	0.770	6.148
	$\beta_{cut}[2]$	0.676	2.423	-3.787	0.574	5.912
	$\beta_{burnt}[2]$	0.518	2.414	-3.962	0.408	5.695
	$N_{occ}[1]$	5.798	3.021	2	5	12
	$N_{occ}[2]$	9.934	0.908	9	10	12
	$\psi^{fs}[1]$	0.483	0.252	0.167	0.417	1
	$\psi^{fs}[2]$	0.828	0.076	0.750	0.833	1
Agama aculeata distanti						
	$p[1]$	0.070	0.015	0.044	0.069	0.101
	$p[2]$	0.478	0.300	0.004	0.476	0.975
	ψ_1	0.283	0.116	0.089	0.272	0.54
	ϕ	-5.128	3.346	-11.941	-4.972	0.88
	γ	-4.043	2.314	-8.66	-4.021	0.311
	$\beta_{control}[2]$	-1.316	2.692	-6.987	-1.214	3.696
	$\beta_{cut}[2]$	-1.386	2.615	-6.761	-1.265	3.532
	$\beta_{burnt}[2]$	-1.317	2.626	-6.595	-1.262	3.675
	$N_{occ}[1]$	3.014	0.119	3	3	3
	$N_{occ}[2]$	0.171	1.071	0	0	2

	$\psi^{fs}[1]$	0.251	0.010	0.250	0.250	0.250
	$\psi^{fs}[2]$	0.014	0.089	0	0	0.167
Psammophis crucifer						
	$p[1]$	0.007	0.003	0.002	0.006	0.015
	$p[2]$	0.047	0.012	0.026	0.046	0.074
	ψ_1	0.741	0.171	0.369	0.763	0.986
	ϕ	1.503	2.381	-2.798	1.413	6.607
	γ	0.814	2.369	-3.731	0.771	5.596
	$\beta_{control}[2]$	2.762	2.366	-1.850	2.718	7.494
	$\beta_{cut}[2]$	-0.068	2.299	-4.381	-0.163	4.913
	$\beta_{burnt}[2]$	-1.975	2.253	-6.247	-2.031	2.541
	$N_{occ}[1]$	9.364	1.875	6	10	12
	$N_{occ}[2]$	7.875	1.177	7	7	11
	$\psi^{fs}[1]$	0.780	0.156	0.500	0.833	1
	$\psi^{fs}[2]$	0.656	0.098	0.583	0.583	0.917
Bitis arietans arietans						
	$p[1]$	0.007	0.004	0.002	0.006	0.016
	$p[2]$	0.017	0.007	0.007	0.016	0.035
	ψ_1	0.658	0.202	0.266	0.667	0.979
	ϕ	3.803	2.929	-1.398	3.605	10.124
	γ	1.338	2.714	-3.722	1.253	6.876
	$\beta_{control}[2]$	0.866	2.746	-4.29	0.737	6.463
	$\beta_{cut}[2]$	1.008	2.722	-4.109	0.947	6.469
	$\beta_{burnt}[2]$	-0.463	2.857	-5.778	-0.63	5.499
	$N_{occ}[1]$	8.217	2.33	4	8	12
	$N_{occ}[2]$	9.548	1.978	6	10	12
	$\psi^{fs}[1]$	0.685	0.194	0.333	0.667	1
	$\psi^{fs}[2]$	0.796	0.165	0.500	0.833	1
Hemachatus haemachatus						
	$p[1]$	0.007	0.006	0.001	0.005	0.022
	$p[2]$	0.048	0.024	0.011	0.044	0.101
	ψ_1	0.509	0.241	0.108	0.494	0.956
	ϕ	-2.791	3.052	-8.906	-2.776	3.268
	γ	-1.065	2.161	-5.276	-1.123	3.286
	$\beta_{control}[2]$	0.630	2.201	-3.588	0.626	4.954
	$\beta_{cut}[2]$	0.566	2.166	-3.589	0.549	4.980
	$\beta_{burnt}[2]$	-2.273	2.521	-7.301	-2.24	2.567
	$N_{occ}[1]$	6.094	2.912	2	6	12
	$N_{occ}[2]$	2.791	1.526	2	2	7
	$\psi^{fs}[1]$	0.508	0.243	0.167	0.500	1
	$\psi^{fs}[2]$	0.233	0.127	0.167	0.167	0.583

Pseudaspis cana						
	$p[1]$	0.007	0.005	0.001	0.006	0.020
	$p[2]$	0.010	0.006	0.003	0.009	0.025
	ψ_1	0.582	0.226	0.175	0.577	0.972
	ϕ	3.761	3.017	-1.673	3.578	10.105
	γ	1.724	2.66	-3.334	1.697	7.025
	$\beta_{control}[2]$	0.454	2.859	-4.965	0.369	6.155
	$\beta_{cut}[2]$	1.189	2.705	-3.987	1.129	6.67
	$\beta_{burnt}[2]$	0.109	2.897	-5.280	-0.025	6.036
	$N_{occ}[1]$	7.123	2.708	3	7	12
	$N_{occ}[2]$	9.703	2.076	5	10	12
	$\psi^{fs}[1]$	0.594	0.226	0.250	0.583	1
	$\psi^{fs}[2]$	0.809	0.173	0.417	0.833	1
Lycophidion capense capense						
	$p[1]$	0.007	0.006	0.001	0.005	0.024
	$p[2]$	0.012	0.008	0.002	0.010	0.034
	ψ_1	0.479	0.245	0.095	0.446	0.958
	ϕ	0.556	3.941	-6.667	0.300	8.797
	γ	1.014	2.510	-3.671	0.916	6.287
	$\beta_{control}[2]$	2.003	2.546	-2.893	1.966	7.027
	$\beta_{cut}[2]$	-1.741	3.088	-7.665	-1.897	4.795
	$\beta_{burnt}[2]$	0.847	2.620	-4.237	0.809	6.27
	$N_{occ}[1]$	5.706	3.005	2	5	12
	$N_{occ}[2]$	7.405	2.702	3	7	12
	$\psi^{fs}[1]$	0.476	0.250	0.167	0.417	1
	$\psi^{fs}[2]$	0.617	0.225	0.250	0.583	1

produced the greatest number of detections in Phase 1, was burnt prior to the sampling in Phase 2. The fact that *A. a. distanti* was not detected in any treatment group means that alternate explanations for the change in detection probability cannot be ruled out, thereby leaving the issue of the effects of burning and cutting on *A. a. distanti* at an ambiguous outcome.

The results of the regression of vegetation covariates on the detection probability of *G. flavigularis* and *T. capensis* are shown in Table 4.4. The parameter estimates for the effects of grass cover and grass height on the detection probability of *G. flavigularis* in Phase 2 indicate that grass cover and detection probability were positively related while grass height and detection probability were negatively related. The 95% credible intervals for the two parameters do include zero (Table 4.4) and thus are not unambiguous, yet they explain the possible mechanism for the changes in detection probability of *G. flavigularis* in Table 4.3 (above). Burning caused a decrease in both grass cover and grass height relative to a site's pre-treatment condition, whereas grass cutting reduced a site's grass height with minimal impact on the grass cover (Table 4.1). To explain the observation that the species' detection probability at control sites was the same as at burnt sites in Phase 2, the effects of a change in both grass cover and grass height must cancel each other out. The fact that the species' detection probability was highest at cut sites in Phase 2 means that the model predicts a negative relationship between grass height and detection probability. For *T. capensis*, model estimates of the coefficients for the effects of grass cover and grass height in Phase 2 are unambiguous. The estimated effects of grass cover and grass height are both positive, such that detection probability of *T. capensis* increases as the percentage grass cover and the average grass height of a site increases (Table 4.4). Again, this matches the result shown in Table 4.3, where the lowest detection probability of *T. capensis* in Phase 2 was at burnt sites i.e. low grass cover and low grass height.

Table 4.4: The effects of grass cover (v) and grass height (δ) on the detection probability of *G. flavigularis* and *T. capensis* in Phase 1 and Phase 2 of the reptile survey. Detection probability was modelled according to eqn 4.9 using standardised normal distribution of the two covariates for each phase (see Table 4.1 for actual measures). All non-detection parameters shown in Table 4.3 were equivalent between the two models (down to MCMC error), and are not shown again. Parameter estimates are shown on the logit-normal scale, and the number in square brackets indicates the phase of sampling to which the estimate pertains.

Species	**Parameter**	**Mean**	**SE**	**Credible Interval**		
				2.50%	**50%**	**97.50%**
Gerrhosaurus flavigularis						
	$\mu[1]$	-2.425	0.118	-2.658	-2.423	-2.195
	$\mu[2]$	-2.106	0.142	-2.400	-2.102	-1.837
	$v[1]$	-0.076	0.168	-0.403	-0.076	0.256
	$v[2]$	0.223	0.139	-0.042	0.220	0.504
	$\delta[1]$	-0.071	0.119	-0.317	0.066	0.156
	$\delta[2]$	-0.283	0.158	-0.602	-0.276	0.015
Trachylepis capensis						
	$\mu[1]$	-2.484	0.113	-2.714	-2.481	-2.269
	$\mu[2]$	-2.458	0.170	-2.810	-2.453	-2.141
	$v[1]$	-0.057	0.113	-0.274	-0.059	0.165
	$v[2]$	0.572	0.191	0.211	0.563	0.953
	$\delta[1]$	0.195	0.098	-0.003	0.198	0.382
	$\delta[2]$	0.334	0.134	0.072	0.335	0.600

4.4. Discussion

In the context of species management, the model parameters of greatest importance are (1) detection probability, (2) occurrence probability and (3) the occupancy rate i.e. the number of the 12 sampled sites that were occupied by each species in each phase of sampling. While the ecological parameters i.e. occurrence probability and occupancy rate are the focus of this investigation, the detection probability determines the data available to estimate them. As the detection probability of a species increases, so does the accuracy of model-based estimates of ecological parameters. The benefit of using a model that explicitly accounts for detection probability in each phase is that the estimates of occurrence probability in Phase 1 are not biased low simply because the detection probability is low (Kéry 2002; MacKenzie & Kendall 2002; MacKenzie *et al.* 2003). This compensation for detection probability is clearly demonstrated for species such as *H. haemachatus*, where the upper bound of the 95% credible interval for ψ^{fs} in Phase 1 is greater than in Phase 2 (Table 4.3). Discriminating between false negatives and the actual absence of a species was one of the primary motivations for the development of these hierarchical models (Kéry 2002; MacKenzie *et al.* 2003; Dorazio & Royle 2005b). For example, *G. flavigularis* was detected at 11 sites in Phase 1 and Phase 2, but was considered absent at the 12th site due to the high detection probability of the species. The ability to distinguish between sites at which a species is not detected and those from which a species is absent is crucial in studies where a change in the occupancy state variable is the focus of investigation.

From the data collected for this study, there appears to be a negligible effect of habitat modification on the site occupancy status of the reptile species in the southern grasslands of SNR. The general increase in the species' mean detection probability between Phase 1 and Phase 2 of the sampling led to improved precision in the estimates of site occupancy and the occupancy rate in the latter, yet reductions in site occupancy were not attributed to the treatment of the sites. For example, the estimated mean occupancy rate of *H. haemachatus* decreased from 0.508 in Phase 1 to 0.238 in Phase 2, but this was primarily explained by the seven-fold increase in detection probability and not by the treatment of the sites (Table 4.3). *Gerrhosaurus flavigularis* and *T. capensis*, the two widespread and abundant lizard species, showed variations in detection probability per treatment type, yet their occupancy rate was not affected by the habitat modifications. While these variations are of interest from an ecological perspective, on the whole the two species are resilient to changes in their habitat. Unfortunately, firm conclusions regarding the sensitivity of the infrequently detected species to habitat modification are not possible as it would be unwise to base management decisions on an analysis of data with low information content.

One species that does merit further consideration is *A. a. distanti*. Analysis of the distribution of the species both here and in Chapter 4, as well as the additional detection data presented in Chapter 5, supports the inference that the species is patchily distributed across SNR. Three competing hypotheses can explain the observed detection data for this species. Firstly, the detection probability of *A. a. distanti* may vary in response to factors not considered here or elsewhere in the thesis e.g. seasonal peaks in activity, yet the species may have high occupancy rates in general. Secondly, the species' abundance may vary dramatically between sites such that sites with lower rates of detection represent marginal habitat in the framework of a source-sink population model (Pulliam 1988). Thirdly, the species may occur at low abundance levels (even in suitable habitat) and the detection probability increases the closer a trap array is to the centre of the few individuals' activity areas. Testing of these hypotheses falls outside of the scope of my analysis, but is certainly relevant to the management and conservation of the species within SNR.

The results of my analysis highlight several important issues for studies of reptile site occupancy. The first is that difficulty in detecting a species has direct consequences for our understanding of the impacts of site-level factors on its occurrence and, thus, its ecology. The number of trap visits required to infer the absence of a species increases as the detection probability decreases (Kéry 2002), which adds both time and cost to a survey. As the duration of sampling increases, the likelihood that model assumptions may be violated increases e.g. population closure (Kéry & Schaub 2011). In certain cases, the interpretation of model parameters can be adjusted to accommodate these violations (see Royle & Dorazio 2008 and Kéry & Schaub 2011), yet these adjustments may also invalidate the purpose of an investigation. For example in this study, Phase 1 of sampling spanned approximately five months. The interpretation of site occupancy could be modified from 'permanent site occupancy during the sampling period' (residency) to the 'use of the site at some point during the sampling period' (use). For some of the larger bodied snake species e.g. *P. cana*, the latter interpretation may be more accurate as individuals may display low site fidelity if the site represents a sub-unit within the individual's broader area of occupancy. The same issue must be considered for Phase 2, which despite being shorter in duration, still presents the opportunity for species to make use of the site and then emigrate (temporarily or otherwise) from it. The short-term use of a site that was modified during treatment might result in detection and the assumption of site occupancy, when in fact the site's habitat characteristics may be detrimental to permanent site occupancy. The dynamics of temporary emigration can be compensated for using model extensions such as demonstrated by Kéry *et al.* (2009), yet with the low number of detections in this survey there is limited information available to model trends in availability for detection through time.

In this study, the 'use' interpretation of site occupancy would result in challenges for management of fire within SNR. The areas of habitat affected by the treatments in this survey were smaller than the areas typically burnt by fires (natural or controlled) in SNR. Impacts of fire on species might reasonably be expected to increase with the size of the area burnt, as emigration from affected sites may not be possible when fires burn large swathes of grassland. Building on the work of this survey and the baseline data of reptile site occupancy that has developed over the course of repeated surveys (i.e. Masterson, Maritz & Alexander 2008; Masterson *et al.* 2009; Koen & du Toit 2007; Chapter 3 & Chapter 6), future surveys should sample sites under more natural disturbance conditions e.g. wildfires, heavy grazing and controlled management burns. Trap placement might also be modified to tackle specific questions about species movement or to improve trapping efficacy i.e. placing multiple trap arrays across a burnt area. Importantly, the marking of individuals of all species could be considered to establish local population sizes, thereby addressing issues of the equivalence of individual and species detection probability for rare or wide-ranging species e.g. *H. haemachatus.* Some of these suggestions may be mutually exclusive so the trade-offs between resources and study objectives will need to be carefully considered (see Mackenzie & Royle 2005).

The second issue is that impacts of site-level factors are unlikely to affect the site occupancy of abundant species except in very extreme cases. Locally abundant species tend to be more widespread (Gaston & Lawton 1990), which buffers the species from impacts of habitat in two ways. Firstly, a greater number of individuals must be negatively affected by habitat modification in each instance i.e. either through direct mortality or through increased attrition in the new habitat. Logically, if the probability of death associated with a disturbance is equal for all individuals, then extinction probability decreases as the number of individuals present at a site increases (Mackenzie *et al.* 2006). Secondly, recolonisation of the site following a disturbance is more likely if there are large populations in the surrounding habitat i.e. the rescue effect (Brown & Kodric-Brown 1977). With reference to the management of SNR's abundant and widespread reptile species, small-scale disturbances that affect localised areas for short periods of time are highly unlikely to compromise the species persistence within the total protected area. Species that are not widespread e.g. *A. a. distanti* merit greater consideration in management scenarios, as they may be highly impacted by localised disturbance, with a reduced likelihood of site recolonisation in the event of local extirpation (Mackenzie *et al.* 2006).

The third issue is one of model selection. In this chapter I have used a Markovian process of occupancy dynamics when modelling changes in site occupancy between the two primary sampling periods. For abundant species displaying high site fidelity, a site's occupancy status will be determined by occupancy in the previous sampling period and the species' dynamics i.e. survival and colonisation, thus the Markovian process of occupancy is reasonable. However, for species with low abundance or low site fidelity, the occupancy of a site may be more adequately described by a random process, with no relation to occupancy in previous sampling periods. While this observation relates to the scale at which sampling is conducted, there are implications for the analysis of the data. The model construction and parameters relevant to the occupancy of a site would vary between the Markovian or random processes (Mackenzie *et al.* 2006). The model used for analysis represents our attempt to make sense of the data we observe, so a naive model represents a naive attempt to explain the data (see Kéry 2010). Estimates of population size e.g. via mark-recapture would provide the ancillary information for changes in model construction and analysis across different species. An alternative is to exploit the link between abundance and detection (Royle & Nichols 2003; McCarthy *et al.* 2013) in order to explore patterns of abundance under various assumptions regarding the detection probability of individuals. The need to develop successful models of the detection process is applicable to all sampling methodologies given the logistical challenge that the sampling of reptiles in field studies presents (Gardner, Barlow & Peres 2007).

As an example, the estimated effects of grass cover and grass height on the detection probability of *T. capensis* (Table 4.4) predict that the species is less trappable in areas with low grass height and little grass cover. While there may be many reasons for this the consequence is that more effort must be invested to trap *T. capensis* individuals at these types of sites. Thus, while the site occupancy of the species was not affected by the site treatments, our ability to confirm the species' presence was reduced at the burnt sites in Phase 2. The caveat to this result is that it is based on a sample size of four treated sites. Consequently, one anomalous site has a disproportionate influence on model-based conclusions. Unfortunately, I could not have sampled additional sites as I was constrained by the availability of similar sites within SNR, and time (to check and maintain traps on a near daily basis). Nevertheless, this result is encouraging in that it suggests that an experimental approach to studying habitat modification, even though small, can detect species responses to the changes.

In summary, the results of this analysis indicate that, for the reptile species analysed, the treatment of grassland sites in SNR had no detectable impact on a site's occupancy status. For the readily detected species such as *G. flavigularis* and *T. capensis*, the conclusion of no adverse impact on occupancy has high confidence. For species less readily detected, the finding of no impact must be interpreted with the caveat that it is based on less information than we would ideally like. Importantly, the observed increases in detection probability from Phase 1 to Phase 2 complicate the detection of *changes* in site occupancy between phases. The survey was designed with the aim of detecting the majority of species that occupied each site prior to treatment, and then confirming these species' presence or absence in the subsequent sampling period. The data presented here (and in Chapter 3) show this to be a very ambitious objective when using passive trapping alone. The consequence for this analysis was that 10 of the 20 species detected in Phase 1 were not analysed here because there is essentially no information available to modify any prior expectations we might have. These rare species may well be rare because of negative impacts of current management activities, but unfortunately this can neither be confirmed nor denied using this survey's data. Nevertheless, this survey's data can be incorporated into future attempts to tackle species-specific questions about distribution e.g. *A. a. distanti*.

CHAPTER 5

The Effects of Vegetation Restoration on Reptile Assemblages

Reptile responses to habitat modification are both poorly understood and difficult to evaluate given the fact that habitat changes may make species that are already cryptic even more difficult to detect. Previous research in Suikerbosrand Nature Reserve (SNR) has indicated that previously cultivated areas of grassland support fewer reptile species than unmodified habitats. Hypotheses for the observed differences include 1) the consequence of changes to the vegetation and 2) the loss of microhabitats associated with the removal of rocks from areas that are ploughed. Between 2005 and 2009, the management of SNR invested in a vegetation restoration programme in previously cultivated areas of the reserve's grassland. In 2009, I surveyed reptiles at nine sites across three habitats i.e. pristine or unmodified grassland; previously cultivated areas that were treated during the restoration programme (treated sites); and previously cultivated areas that were not treated during the restoration programme (untreated sites). Sites were surveyed for 110 days between 18 November 2009 and 26 March 2010. As with previous work in the northern grasslands of SNR, I detected a greater number of species at each of the three sites in pristine grassland during the survey than in the corresponding treated and untreated sites. I analysed these detection/non-detection data using a hierarchical site-occupancy model that separates the ecological process of site occupancy from the observation process, which depends upon the strengths and weaknesses of the chosen sampling method. I also extended the model to allow me to estimate the species richness of the reptile assemblage at each site and in total. The model results suggested that the greater number of species detected in pristine grassland was not a function of differences in the site occupancy of the three habitats, but was a function of the generally low detection probabilities of most reptile species. Model estimates of site species richness indicated that the nine sites supported a similar number of reptile species and that additional sampling is required to increase sampling efficacy at the site level. Estimates of the total species richness of the assemblage indicated that the sampling was able to detect the majority of species present in the study area during the survey. Thus while the survey appears to have been effective for providing a broad description of the reptile assemblage in the grasslands of SNR, there remain several challenges at the site level of analysis. The low detection probability of the reptile species at SNR, which is a combination of their stealthy movements, periods of inactivity and site-level variation in abundance, is currently the greatest obstacle to the rapid assessment of reptile richness at multiple sites. The consequent challenge is to develop an observation model that allows for the effects of reptile-specific factors to be evaluated. Recommendations for such improvements are discussed.

5.1. Introduction

The effects of habitat change on reptile assemblages are generally poorly understood and in need of greater attention due to the increasing global rate of anthropogenic habitat transformation (Gardner, Barlow & Peres 2007; Ellis *et al.* 2010; Klein Goldewijk *et al.* 2011). Reptiles are a highly diverse taxon and the response to habitat change differs between species (Meik *et al.* 2002; Castellano & Valone 2006; Masterson *et al.* 2009). At a landscape scale (> 10 km^2), the occurrence of reptile species has been linked to the presence and abundance of different habitat patches (Atauri & de Lucio 2001; Michael, Cunningham & Lindenmayer 2008), the distances between patches of suitable habitat or fragmentation (Atauri & de Lucio 2001; Fischer *et al.* 2005; Kanowski *et al.* 2006; Michael, Cunningham & Lindenmayer 2008), and types of management (Fabricius, Burger & Hockey 2003). At the patch or site scale (< 2 km^2), occupancy is influenced by factors such as habitat structure and complexity (East, East & Daugherty 1995; Galán 1997; Webb & Whiting 2005; Webb, Shine & Pringle 2005; Castellano & Valone 2006; Attum & Eason 2009), vegetation type, grazing regimes (Fabricius, Burger & Hockey 2003), aspect, the presence of refugia (Márquez-Ferrando *et al.* 2009) and invertebrate abundance (Fischer, Lindenmayer & Cowling 2004). The interaction of landscape and site characteristics with individual species responses can play an important role in the composition of reptile assemblages across different sites (Fischer *et al.* 2005). The response of a few species may be so large that they 'overwhelm' the responses of the other species in the assemblage (Castellano & Valone 2006), while some species in the assemblage may display no response at all (Fabricius, Burger & Hockey 2003; Masterson *et al.* 2009). Variation in the response of individual species to land-use change or management introduces subtle changes across landscapes that may be hard to detect or may complicate the description of general patterns. From a conservation manager's perspective, the general pattern will be of greater importance than the specifics of individual responses, unless there are species of special concern in the assemblage such as threatened or endemic species.

The modification of grassland for cultivation has had a negative impact on the diversity of reptiles in the grasslands of SNR (Masterson *et al.* 2009). In a 2005/2006 survey, Masterson *et al.* (2009) found that reptile assemblages in historically cultivated areas were depauperate when compared with untransformed grassland, and that the relative abundance of widespread, common reptile species also differed between habitat types. Species such as *Trachylepis capensis* exhibited no obvious response to the modification of habitat associated with cultivation, while other species such as *Gerrhosaurus flavigularis* and *Nucras lalandii* appeared to be quite sensitive, with notably fewer individuals captured in the modified areas (Masterson *et al.* 2009). Masterson *et al.* (2009) argued that the loss of primary vegetation and/or the transformation of habitat structure via rock removal might be the causes of the reduced species richness in historically cultivated areas.

In 2005, the management of Suikerbosrand Nature Reserve initiated a restoration programme aimed at improving the composition and cover of the vegetation communities in historically cultivated areas (old lands) and reducing the predominance of weedy species. The primary objectives of the programme were (1) to hasten the re-establishment of naturally-occurring grass species in the old lands, (2) to increase basal and ground cover to reduce soil erosion, (3) to limit the production and competitiveness of invasive weeds on the old lands and (4) to stimulate a natural increase in the biodiversity of the old lands (du Toit & Koen 2006). During 2005 and 2006, selected old lands were either slashed and seeded, or disked i.e. ploughed with a disk harrow, and seeded with a standardised seed mix (see Methods section for details). Follow-up monitoring of the vegetation at seeded and unseeded old lands in 2006, 2007 and 2008 indicates that there has been an increase in the overall species diversity and soil cover of the seeded old lands i.e. objectives (1) and (2) were met (du Toit & Koen 2006; du Toit & Koen 2007; du Toit & Koen 2008). The monitoring also found that positive changes in the composition and cover of the vegetation proceed more rapidly in the disked and seeded plots as compared with the slashed and seeded plots (du Toit & Koen 2008).

The restoration programme offered the opportunity to evaluate the effects of vegetation restoration on the richness and composition of the reptile assemblages in the northern grasslands of Suikerbosrand Nature Reserve. During the summer of 2009-2010, I surveyed reptiles in the treated and untreated old lands of Suikerbosrand Nature Reserve. My survey aimed to assess whether or not reptile assemblages benefit from management attempts to restore natural vegetation in previously disturbed areas. The survey also aimed to provide information pertaining to objective (4) above. Firstly, there is limited, published research regarding the structure of reptile assemblages in natural and disturbed habitats. Secondly, the Grassland Biome is already highly transformed, which means that natural and semi-natural habitats, as found at Suikerbosrand Nature Reserve, are valuable sites for baseline research. Thirdly, the funding for the restoration programme was withdrawn in 2009, which means that the 'restored' grasslands may revert to their pre-treatment condition and that the opportunity to study the effects of these efforts on the reptile assemblages may be lost. Lastly, nearly a decade has passed since the cessation of commercial agricultural practices at the site, which offers an opportunity to evaluate the effects of both time and vegetation restoration on reptile assemblage recovery.

5.2. Methods

Between 18 November 2009 and 26 March 2010, I trapped reptiles at nine sites in three habitat types, which I qualitatively defined according to their site history (Table 1; Fig. 1). The three habitat types surveyed were (1) *pristine grassland*: sites which have not, according to available information, ever been ploughed for cultivation (equivalent to the 'pristine' sites sampled in Masterson *et al.* 2009), (2) *treated old lands*: old lands which were disked and seeded using a seed mix recommended by Fritz van Oudtshoorn (University of South Africa) and (3) *untreated old lands*: old lands which were not disked and seeded during vegetation restoration efforts but were left to recover unaided. All traps arrays in old lands were located more than 100 m from the edge of the boundary of the old land. According to data in the Ecological Filing System of Suikerbosrand Nature Reserve, sites 2U and 3U were last ploughed in the spring of 2001, while the data available for site 1U indicates that it was last ploughed prior to 2000 (exact year unknown). In the years since these lands were last ploughed, there has been no direct manipulation of the vegetation characteristics at these three sites but the sites have been burnt

Table 5.1: Locality details for the nine trap arrays used to survey reptiles between 18 November 2009 and 26 March 2010. Old Land ID identifies the old land in which the trap array was placed and is based on the names as they relate to the electronic filing system of Suikerbosrand Nature Reserve. Latitude and longitude are in decimal degrees.

Site ID	Old Land ID	Habitat Type	Latitude	Longitude
1P		Pristine Grassland	-26.461950	28.232505
1T	Land 15E	Treated Old Land	-26.457628	28.236904
1U	Land 14	Untreated Old Land	-26.450844	28.23514
2P		Pristine Grassland	-26.465747	28.243173
2T	Land 21	Treated Old Land	-26.468084	28.237131
2U	Land 20	Untreated Old Land	-26.472766	28.24201
3P		Pristine Grassland	-26.463468	28.270874
3T	Land C19	Treated Old Land	-26.464701	28.27459
3U	Land C33	Untreated Old Land	-26.469874	28.270564

during management and accidental fires. Site 3T was treated in the spring of 2005, while sites 1T and 2T were treated in the spring of 2006. All treated old lands were seeded with a 13 kg.ha^{-1} seed mix that consisted of, in decreasing kg.ha^{-1}, *Themeda triandra*, *Heteropogon contortus*, *Chloris virgata*, *Cymbopogon excavatus*, *Melinis repens*, and eight other grass species with less than 1 kg of seed per ha.

Trap arrays were grouped into three spatial clusters with one array in each habitat type per cluster (Fig. 5.1). Trap clusters were 2935 ± 1128 m apart (mean ± 1 SD; min = 1721 m, max = 3951 m) apart, while trap arrays within clusters were 739 ± 225 m apart (mean ± 1 SD; min = 398 m, max = 1257 m). Trap arrays consisted of four drift fences, five pitfall traps and eight funnel traps arranged in a closed-cross formation (as per Masterson *et al.*, 2009). Drift fences were constructed using three 3.5 m segments of Nutec ceiling board (Everite Pty (Ltd)) buried 5 to10 cm into the soil and held upright using fence poles hammered into the ground. Traps were opened on 18 November 2009 and checked once daily until 26 March 2010, excluding a two week period from 27 December 2009 to 11 January 2010, during which the traps were closed.

All reptiles captured during the survey were identified to species level, except in the case of the Leptotyphlopidae (Thread Snakes) where the confidence of species level identifications is limited by the poor taxonomic resolution in the genus *Leptotyphlops* (Adalsteinsson *et al.* 2009). There are potentially three species (and four taxa) of *Leptotyphlops* occurring in Suikerbosrand Nature Reserve i.e. *L. scutifrons scutifrons*, *L. s. conjuctus*, *L. incognitus*, and *L. distanti* (Bates *et al.* 2014). Due to issues with unresolved taxonomy and difficulties identifying species within the genus (Adalsteinsson *et al.* 2009), I treated all captured *Leptotyphlops* individuals as members of a single unspecified species. Consequently, the distribution of *Leptotyphlops* species in SNR will need to be re-investigated when the delineation of species is complete and the taxonomic issues have been resolved. I clipped one toe of every *Agama aculeata distanti*, *Gerrhosaurus flavigularis*, *Nucras lalandii*, *Trachylepis capensis* and *T. varia* individual I captured to identify recaptures in these frequently captured or important lizard species. All species were marked with the same toe-clip code as no individuals of these species have been observed to disperse between trap arrays further than 200 m apart in a single season (Masterson *et al.* 2009).

To estimate and compare the site occupancy of reptile species in SNR, I used a hierarchical linear model known as a multispecies, multisite occupancy model. The model was described by Dorazio & Royle (2005) and subsequently demonstrated by various authors (e.g. Dorazio *et al.* 2006; Royle, Dorazio & Link 2007; Kéry & Royle 2008). The model is structured as a coupled, two-process model with a Bernoulli process describing the probability that a site is occupied by a species (typically referred to as the "ecological process model") and a logistic process describing the probability that a species is detected during sampling (typically called the "observation process model"). Structuring the model in this way facilitates an explicit ecological interpretation of the model parameters. Detection probability relates to the power of the sampling method and allows discrimination between detection/non-detection (what the data represent) and the presence/absence of a species at a site (what I am attempting to observe for my evaluation of habitat suitability). The occurrence probability of a species is then estimated by combining the number of sites at which the species is detected and the detection probability of the species. Species with a very low detection probability at sites at which they are detected are still likely to occur at sites where they are not detected i.e. we have limited certainty regarding their presence or absence. Species with a very high detection probability are most likely to be absent from sites

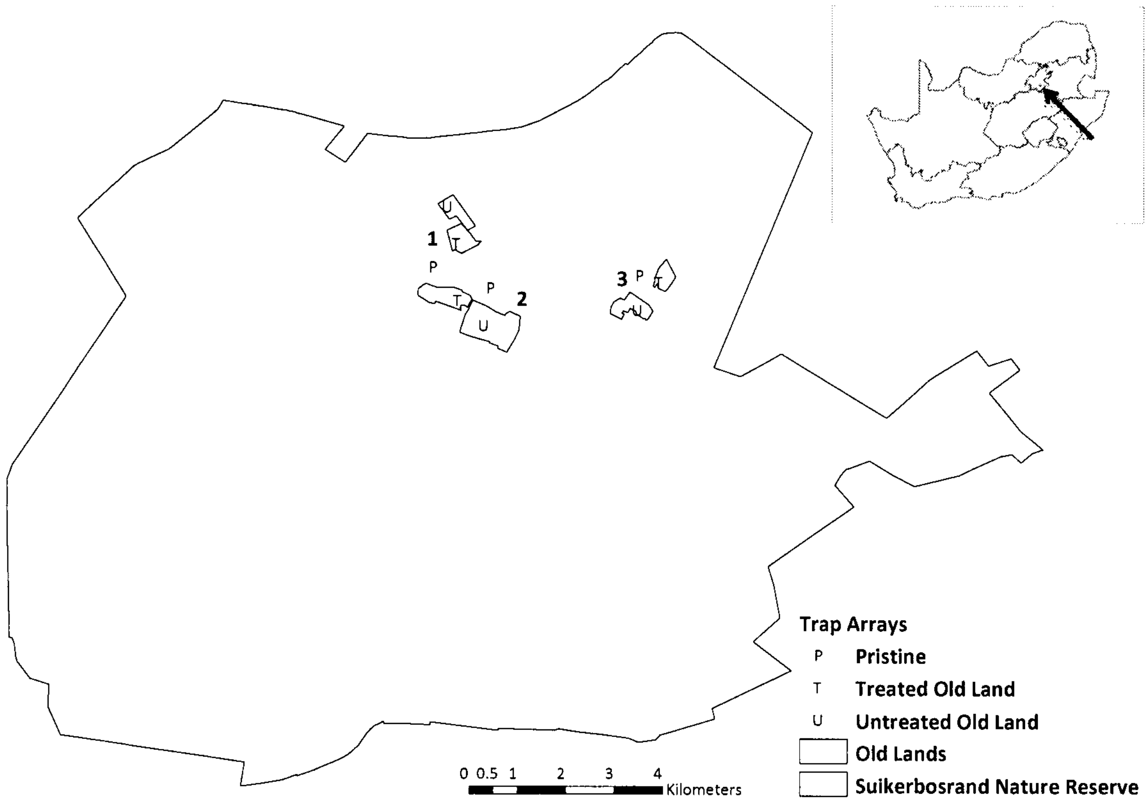

Fig. 5.1: Map showing the location and habitat type of the nine trap arrays used to survey reptiles between 18 November 2009 and 26 March 2010. Numbers indicate the cluster ID and the resulting site names in Table 5.1 e.g. 1P, 2T, 3U etc. The location of Suikerbosrand Nature Reserve in Gauteng, South Africa is shown (inset).

at which they are not detected. There are several useful features and extensions of the multispecies multisite occupancy model. These include (1) estimating the presence or absence of species at a site, (2) estimating site occupancy probabilities in relation to site characteristics, (3) implementing any of the classic model forms of Otis *et al.* (1978), (4) estimating site-specific or total species richness and/or (5) estimating species turnover and accumulation with increasing area of sampling (Kéry 2002; Dorazio *et al.* 2006; Kéry & Royle 2008).

To estimate species richness, hyperparameters (random effects) for the mean and standard deviation of the occurrence and detection probabilities for all species detected are included as a hierarchical component in the model. The hyperparameters allow us to extrapolate from our data to a larger set of species, which is of unknown size and of which the species actually detected are but a part (Kéry & Royle 2008). To make this extrapolation possible, the data are augmented by including a large, but finite, number of species with all-zero detection histories or 'hypospecies' (Royle, Dorazio & Link 2007). Hypospecies are those species which were theoretically present at the sites sampled, but which were never detected during sampling (Royle, Dorazio & Link 2007). To account for the uncertainty as to the number of hypospecies that were exposed to sampling but not detected, a latent indicator variable w is included in the model. In practice, the probability that a particular hypospecies occurs at a site is drawn from the estimated mean and standard deviation of the random effect of the occurrence probability of the greater reptile assemblage. The binary estimate of whether the hypospecies is present or absent at a site is then the result of a Bernoulli trial with this random draw as its success probability. The number of detections of a species can then be conditioned on the indicator variable w such that a species that is not present at the site cannot be detected (Royle, Dorazio & Link 2007). This method of reducing the problem of estimating the total number of species present or N, to that of estimating the distribution of the latent indicator variable w has been justified by Dorazio *et al.* (2006) and Royle, Dorazio & Link (2007), and results in a model that is readily implemented using Gibbs samplers such as WinBUGS (Lunn *et al.* 2000).

Using the multispecies, multisite occupancy model, I tested the effect of habitat condition on the occupancy and detection probability of reptile species in the open grasslands of Suikerbosrand Nature Reserve. I used WinBUGS 1.4 (Lunn *et al.* 2000) to implement a Bayesian form of the model using Gibbs sampling and Markov-chain Monte Carlo methods. Posterior distributions for the model parameters were calculated from three Markov chains of 15 000 draws, discarding the first 5 000 draws as burn-in and thinning by one. The 'burn-in' period of the Markov chain is caused by the fact that an initial value must be specified for each chain in the model run. The initial value may not lie within the posterior distribution of the parameter and thus we say the chain 'converges' on the posterior distribution, and we must therefore discard the values that are generated prior to convergence. Where multiple Markov chains are used, chain convergence can be visually assessed in a time-series of estimated parameter values. At convergence, the chains oscillate around a mean and overlap with one another. I thinned by one as model tests indicated chain convergence to have occurred by 5 000 draws. Thinning of the Markov chains is typically used to reduce the autocorrelation of the values generated at each iteration of the chain i.e. to acquire more concentrated information per saved estimate (Kéry 2010), however discarding draws from the posterior distribution after the chains have converged only has the effect of increasing model run times while discarding useful estimates of parameter values from their posterior distributions. Consequently, all parameter estimates were calculated from 30 000 samples of their posterior distribution.

The use of prior distributions in a Bayesian analysis allows one to include prior information in an analysis of a dataset. Vague priors are used when we wish to conduct an objective Bayesian analysis i.e. we pretend to have no prior information or wish to make no assumption about the distribution of a model's parameters (Link & Barker 2010). As model complexity increases, such as in the inclusion of hierarchies, it becomes relatively simple to accidentally introduce information into the analysis through the improper specification of prior distributions (Kéry 2010). The consequence of introducing information via the prior distributions is that model estimates are no longer based on the information in the data alone, and the inference of the model is compromised (Kéry 2010). This phenomenon is called prior sensitivity and should be tested for using various appropriate prior specifications (Link & Barker 2010). Models that return similar estimates as the priors vary indicate insensitivity to the priors used and are desirable in an objective Bayesian analysis. I performed a test of prior sensitivity in the structural parameters of the model, i.e. the effect of habitat condition on both detection and occurrence probabilities. Model estimates generated using logistic-normal or uniform priors for the effects were indistinguishable so here I show only those estimates generated under the logistic-normal priors for the effect of habitat condition.

From the model-based estimates of the parameters, I derived a posterior distribution of the estimated total number of reptile species that occur at each of the nine sites (Kéry & Royle 2008). The strength of the Bayesian framework for this analysis is that the full uncertainty associated with each parameter estimate is propagated through to the estimates of species richness (Dorazio *et al.* 2006; Royle & Dorazio 2008). As a measure of 'sample completeness', I divided the number of species detected by the number of species estimated to occur at each site. Sample completeness facilitates a rapid assessment of the estimated success of the sampling at each site. For example, a sample completeness of 50% indicates that half of the species estimated to occur at a site were detected during sampling. Next, I estimated the total species richness of the reptile community in the grasslands of the survey area. Lastly, I used the posterior distribution of the hyperparameter for occurrence probability to estimate the accumulation of reptile species with increasing numbers of sites surveyed (as per Dorazio *et al.* 2006). Species-accumulation curves derived from hierarchical models of detection and occurrence differ from the curves generated empirically by randomised resampling of the dataset or interpolation (Gotelli & Colwell 2001) in that they do not depend on *which* sites are considered and can better account for the uncertainty regarding species richness and species occurrence at each site (Dorazio *et al.* 2006). I was interested in estimating the number of additional species that would have been exposed to sampling by increasing the number of locations sampled to 30.

There are a number of key assumptions implicit in the multispecies, multisite occupancy model. The first is that the 'population' of species present (N) at each site is closed during the survey period. The second assumption is that the heterogeneity in species detection and occurrence probability is suitably described by a normal distribution on the logit scale. In addition to these two assumptions, the model demonstrated by Kéry & Royle (2008) assumed that species identity is the sole determinant of detection probability i.e. they included no covariates. In this model, I explicitly considered the treatment or condition of the habitat and its effect on the detection probability and occurrence of each species. Consequently, my model assumes that the only two factors influencing occurrence or detection of a species are species identity and site treatment. Finally, the model assumes that there are no false positive identifications i.e. that a species can only be identified as present if it is indeed present (Royle & Dorazio 2008).

To evaluate the vegetation characteristics of the nine sites surveyed, I identified the dominant grass species at each site using the Braun-Blanquet cover classification. At each of the nine sites, I identified each grass species present and estimated its ground cover within a 10 x 10 m quadrat (100 m^2 relevé). For ease of presentation, I report only the 'dominant' grass species for each site i.e. species that covered more than 5% of the quadrat's surface area. Using Van Wyk & Malan (1998), I categorised the dominant species according to the condition of habitat in which they dominate i.e. climax/sub-climax grassland or disturbed areas, or according to their status as pioneer or alien species.

5.3. Results

In 110 days of trapping between 18 November 2009 and 26 March 2010, I detected a total of 620 reptiles, comprising 22 species, at the nine sites (Table 5.2). This amounts to an average of 5.64 detections per day, or 0.63 detections per trap array day. A combined total of 373 detections (60.16%) were the two common lizard species i.e. *T. capensis* (239) and *G. flavigularis* (134; Table 5.2). The mean number of detections for each of the other 20 reptile species was 12.35 ± 12.85 (mean ± 1 SD) detections during the study period (Table 5.2). A total of 15, 16, and 20 reptile species were detected at sites in the untreated old lands, the treated old lands and the pristine grassland respectively. Fig. 5.2 is a summary of the total number of sites at which each of the 22 species was detected during the survey period. Six species were detected at just one site during the survey; five species were detected at all nine sites; and four species were detected at six sites (Fig. 5.2). Eleven of the 22 species were detected at six or more sites (Fig. 5.2). Four of the six species detected at just one site were also detected only once at these sites (Table 5.2) i.e. *Aparallactus capensis* (site 3P), *Boaedon capensis* (site 2P), *Lycodonomorphus inornatus* (site 1T), and *Duberria lutrix* (site 2U). *Afroablepharus wahlbergii* was detected twice at site 1P, and *Crotaphopeltis hotamboeia* was detected on four occasions at site 1P (Table 5.2). The five species detected at all nine sites were (by descending number of detections) *T. capensis* and *G. flavigularis*, *Psammophylax rhombeatus*, *Dasypeltis scabra*, and *Causus rhombeatus*. *Nucras lalandii, A. wahlbergii* and *C. hotamboeia* were detected multiple times but only at sites in pristine grassland (Table 5.2). Thread Snakes (*Leptotyphlops* sp.) were detected on a single occasion at a single site in each of the three habitat types i.e. sites 2P, 3T, and 3U (Table 5.2).

A density plot of the posterior distribution for the distribution of occurrence probabilities in the reptile assemblage indicates a bimodal distribution, where the majority of species have a high probability of occurrence and the rest have a very low probability of occurrence (Fig. 5.3A). There was no evidence of an effect of habitat type on the probability of occurrence for any of the 22 species detected during the survey. Model estimates of detection probability for the reptile assemblage indicated that the vast majority of reptile species have a very low detection probability (Fig. 5.3B). The model therefore predicts that the majority of detection failures at any given site are the result of the low detection probability and not low rates of occurrence. This is a natural consequence of the model assumptions about population closure, which may be violated e.g. by temporary emigration. Species-specific estimates of detection probability in the three habitats were broadly similar, and typically quite low i.e. less than 0.01 per day of trapping (Table 5.3). Model estimates of the effect of habitat type on detection probability were significantly different for three species i.e. *G. flavigularis*, *T. capensis* and *L. aurora* (Table 5.3). *Gerrhosaurus flavigularis* is significantly more likely to be detected in pristine grassland than in either the treated or untreated old lands. By contrast, *T. capensis* is significantly less likely to be detected in pristine grassland than in either the treated or untreated old lands. *Lamprophis aurora* is significantly less likely to be detected in treated old lands than in pristine grassland. Estimates of species-specific occurrence probability were typically high i.e. > 0.70, and varied non-significantly between the three habitat types for all species (Table 5.3).

Estimates of site species richness for each of the sites I surveyed are shown in Table 5.4. There was no significant difference in the estimated species richness of the nine sites, although the mean estimated species richness of the sites in pristine grasslands was one or two species higher than the mean estimated richness of the 'disturbed' sites in their respective clusters (Table 5.4). The sample completeness of the sites surveyed ranged from 50 – 70% (Table 5.4), indicating that significantly more effort is required in order to detect all reptile species estimated to occur at a single site. The posterior-predictive distribution of species richness at each site provided little or no support for any assertion that the number of species detected at each site during sampling is a good estimate of the site's species richness (e.g. Fig. 5.4). The mean total species richness for the reptile assemblage in the northern grasslands of SNR was estimated at 27.5 species with a 95% credible interval of 22 – 35 species. The posterior distribution of total species richness is left-skewed such that the posterior probability for a total species richness of 22 species is 0.051, the posterior probability for a richness of 27 species is 0.108, and the posterior probability for a richness of 35 species is 0.015 (Fig. 5.5). According to the posterior probabilities, a total species richness of 27 species is 2.11 times more likely than a richness of 22 species, while it is 3.4 times more likely that the species richness is 22 species rather than 35 species. The predicted accumulation of species in samples of 1-30 sites did not reach the asymptotic richness of 27.5 species despite the fact that 30 sites is more than triple the number of sites I actually surveyed (Fig. 5.6). This result simultaneously indicates the model's prediction that the majority of species in the reptile assemblage occur at nearly every site in the grasslands, but also that the species

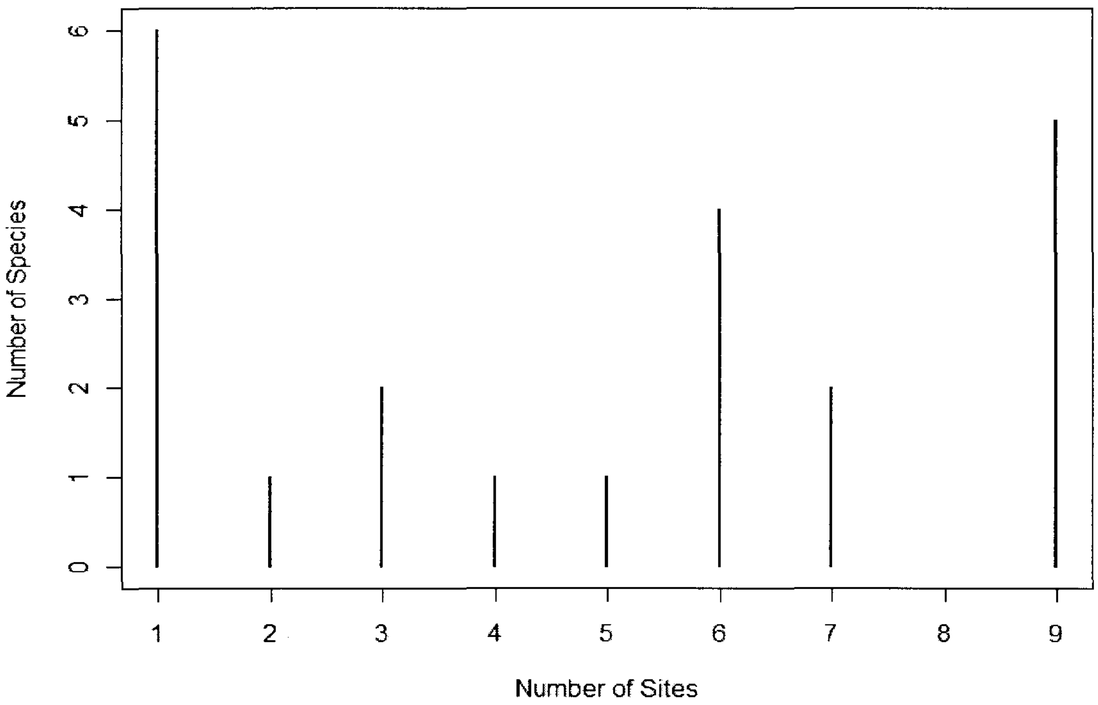

Fig. 5.2: Summary of the number of sites at which various reptile species were captured during trapping between 18 November 2009 and 26 March 2010. Six species were recorded at only one site, whilst five species were recorded at all nine sites.

with low rates of occurrence (Fig. 5.3A) may not be exposed to sampling even with a significant increase in the number of sites sampled.

Vegetation characteristics of the three habitat types ranged from 'poor' in the untreated old lands to 'good' in the pristine grassland (Table 5.5). Pristine grassland sites were dominated by *Themeda triandra*, *Setaria nigrirostris*, *Eragrostis chloromelas* and *Brachiaria serata*, which are all climax or sub-climax species that are indicative of grassland that is in good condition (Van Wyk & Malan 1998). Untreated old lands were predominantly covered by *Hyparrhenia hirta*, *Eragrostis curvula* and *Aristida congesta*, which tend to dominate in highly disturbed grassland (Van Wyk & Malan 1998). Treated old lands were covered by a mix of climax species e.g. *T. triandra*, pioneer species e.g. *Pogonarthria squarrosa*, disturbance-favouring species e.g. *H. hirta* and alien invasive species e.g. *Paspalum dilatatum* (Van Wyk & Malan 1998). In summary,

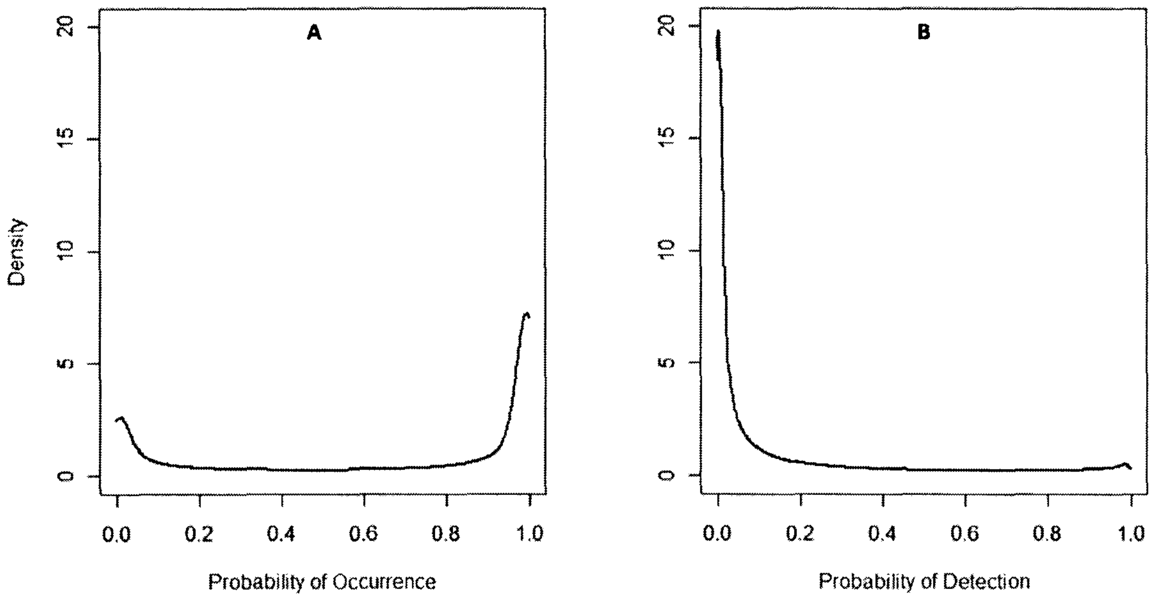

Fig. 5.3: Distributions of probabilities of (A) occurrence and (B) detection of the reptile assemblage in the northern grasslands of Suikerbosrand Nature Reserve as per estimates of model parameters.

the treated old lands show signs of improving vegetation condition but the presence of pioneer and disturbance-favouring species indicate that the legacy of disturbance (including the disturbance associated with the disking and seeding of the sites during restoration treatments) persists. From a habitat condition point of view, the treated old lands are intermediate in terms of ground cover and species composition.

Table 5.2: A summary of the total and site-specific number of detections of the 22 reptile species recorded between 18 November 2009 and 26 March 2010. Sites names are as per Table 5.1 and are grouped by habitat type i.e. pristine grassland, treated old lands and untreated old lands.

Family	**Species**	**No. of detections**	**Detections Per Site**								
			1P	**2P**	**3P**	**1T**	**2T**	**3T**	**1U**	**2U**	**3U**
Lizards											
Agamidae											
	Agama aculeata distanti	17	0	0	1	0	0	2	1	0	13
Gerrhosauridae											
	Gerrhosaurus flavigularis	134	27	42	8	10	13	8	4	18	4
Lacertidae											
	Nucras lalandii	3	0	1	2	0	0	0	0	0	0
Scincidae											
	Afroablepharus wahlbergii	2	2	0	0	0	0	0	0	0	0
	Trachylepis capensis	239	16	29	19	33	29	23	33	40	17
	Trachylepis varia	10	0	0	2	3	2	1	2	0	0
Snakes											
Leptotyphlopidae											
	Leptotyphlops sp.	3	0	1	0	0	0	1	0	0	1
Typhlopidae											
	Afrotyphlops bibronii	3	1	0	1	1	0	0	0	0	0
Lamprophiidae											
	Aparallactus capensis	1	0	0	1	0	0	0	0	0	0
	Boaedon capensis	1	0	1	0	0	0	0	0	0	0
	Duberria l. lutrix	1	0	0	0	0	0	0	0	1	0
	Lamprophis aurora	16	1	7	1	0	0	2	2	1	2
	Lycodonomorphus inornatus	1	0	0	0	1	0	0	0	0	0
	Lycophidion c. capense	15	2	5	1	0	0	3	0	1	3
	Psammophis crucifer	19	4	3	2	4	0	0	3	0	3
	Psammophylax r. rhombeatus	45	3	8	4	7	5	8	6	2	2
	Pseudaspis cana	7	1	0	0	0	2	1	1	1	1
Colubridae											
	Crotaphopeltis hotamboeia	4	4	0	0	0	0	0	0	0	0
	Dasypeltis scabra	40	2	6	8	3	1	4	1	5	10
Elapidae											
	Hemachatus haemachatus	19	3	3	0	4	3	0	4	1	1
Viperidae											
	Bitis a. arietans	14	3	0	2	1	3	0	4	0	1
	Causus rhombeatus	26	4	3	2	2	5	4	2	2	2
All species		**620**	73	109	54	69	63	57	63	72	60

Table 5.3: A summary of the model-estimated means for occurrence and detection probability for each reptile species recorded between 18 November 2009 and 26 March 2010. Mean estimates for the pristine grassland (P), treated old lands (T) and untreated old lands (U) are given. Estimates with > 95% probability of differing from the mean estimate in pristine grasslands are indicated with an asterisk (*).

Family	**Species**	**Detection Probability**			**Occurrence Probability**		
		P	**T**	**U**	**P**	**T**	**U**
Lizards							
Agamidae							
	Agama aculeata distanti	0.002	0.006	0.053	0.989	0.999	0.945
Gerrhosauridae							
	Gerrhosaurus flavigularis	0.231	0.092*	0.077*	0.999	0.999	0.999
Lacertidae							
	Nucras lalandii	0.008	0	0	0.988	0.68	0.76
Scincidae							
	Afroablepharus wahlbergii	0.006	0	0	0.941	0.456	0.482
	Trachylepis capensis	0.193	0.255*	0.271*	0.999	0.999	0.999
	Trachylepis varia	0.005	0.015	0.005	0.994	0.999	0.999
Snakes							
Leptotyphlopidae							
	Leptotyphlops sp.	0.002	0.001	0.001	0.997	0.999	0.999
Typhlopidae							
	Afrotyphlops bibronii	0.005	0.002	0	0.996	0.999	0.949
Lamprophiidae							
	Aparallactus capensis	0.003	0	0	0.975	0.653	0.773
	Boaedon capensis	0.003	0	0	0.979	0.845	0.785
	Duberria l. lutrix	0.001	0	0.001	0.72	0.162	0.999
	Lamprophis aurora	0.026	0.005*	0.013	0.999	0.999	0.999
	Lycodonomorphus inornatus	0.002	0.001	0	0.704	0.999	0.209
	Lycophidion c. capense	0.023	0.011	0.011	0.998	0.999	0.999
	Psammophis crucifer	0.025	0.021	0.018	0.997	0.966	0.999
	Psammophylax r. rhombeatus	0.044	0.058	0.028	0.999	0.999	0.999
	Pseudaspis cana	0.002	0.007	0.006	0.998	0.999	0.999
Colubridae							
	Crotaphopeltis hotamboeia	0.021	0.001	0	0.624	0.054	0.077
	Dasypeltis scabra	0.046	0.022	0.046	0.999	0.999	0.999
Elapidae							
	Hemachatus haemachatus	0.018	0.022	0.016	0.995	0.999	0.999
Viperidae							
	Bitis arietans	0.014	0.011	0.014	0.997	0.999	0.999
	Causus rhombeatus	0.025	0.031	0.016	0.999	0.999	0.999

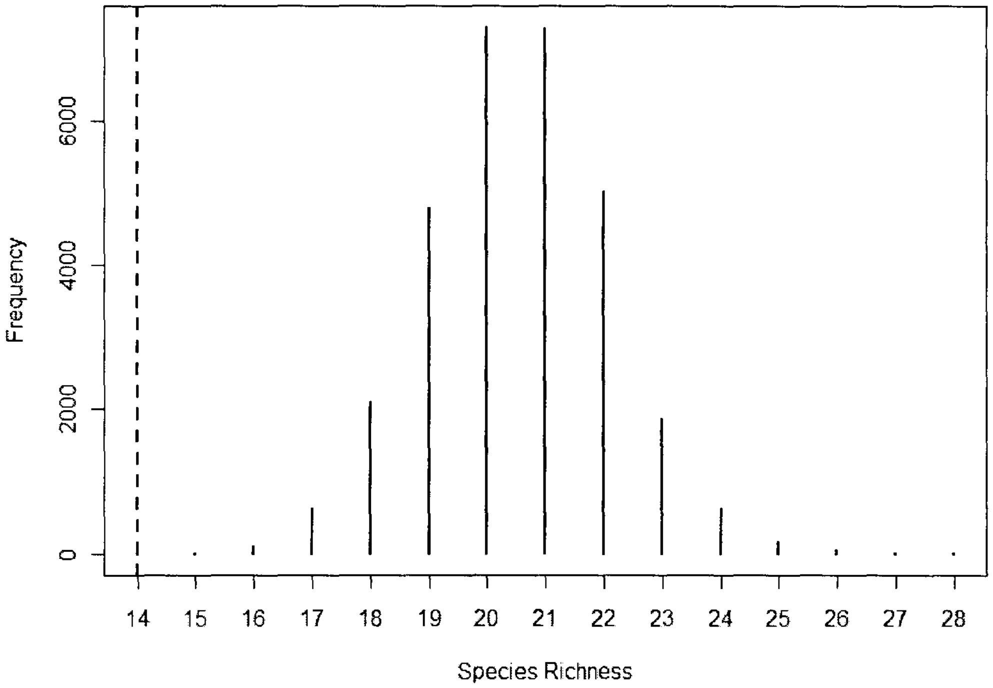

Fig. 5.4: Frequency plot of the posterior-predictive distribution of species richness at site 1P. The dashed line indicates the number of species actually detected during sampling i.e. 14.

Table 5.4: A comparison of the number of species detected (S_{obs}) with the mean number of species estimated to occur at each site (N_{est}) and in total. Sample completeness is the calculated as the percentage of species detected at each site relative to the estimated species richness.

Site ID	**S_{obs}**	**N_{est} ± 1 SE**	**Sample Completeness (%)**
1P	14	20.5 ± 1.6	68.3
1T	11	18.6 ± 1.8	59.1
1U	12	18.9 ± 1.8	63.5
2P	12	19.5 ± 1.7	61.5
2T	9	17.8 ± 1.9	50.6
2U	10	17.7 ± 1.9	56.5
3P	14	19.8 ± 1.6	70.7
3T	11	18.3 ± 1.8	60.1
3U	13	18.9 ± 1.8	68.8
All sites	22	27.5 ± 3.8	80

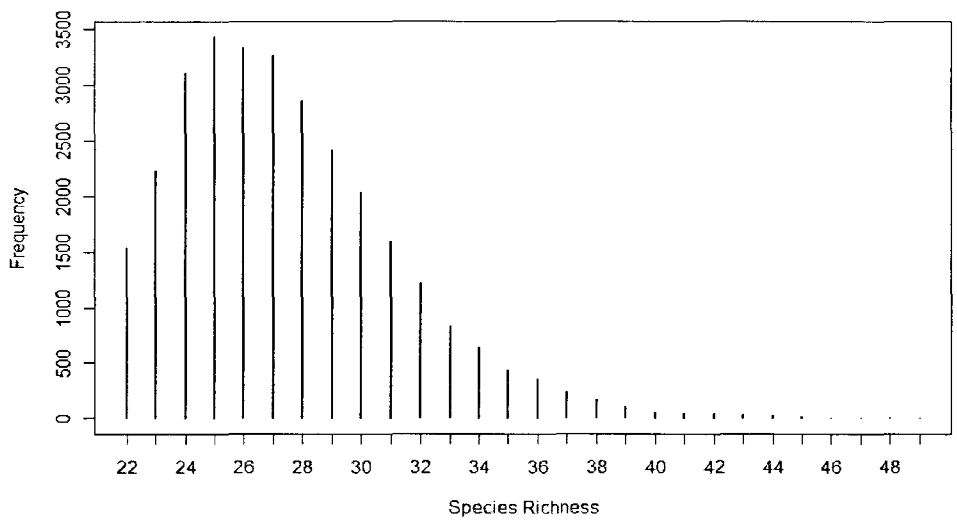

Fig. 5.5: Posterior-predictive distribution of total species richness of the reptile assemblage in the northern grasslands of Suikerbosrand Nature Reserve.

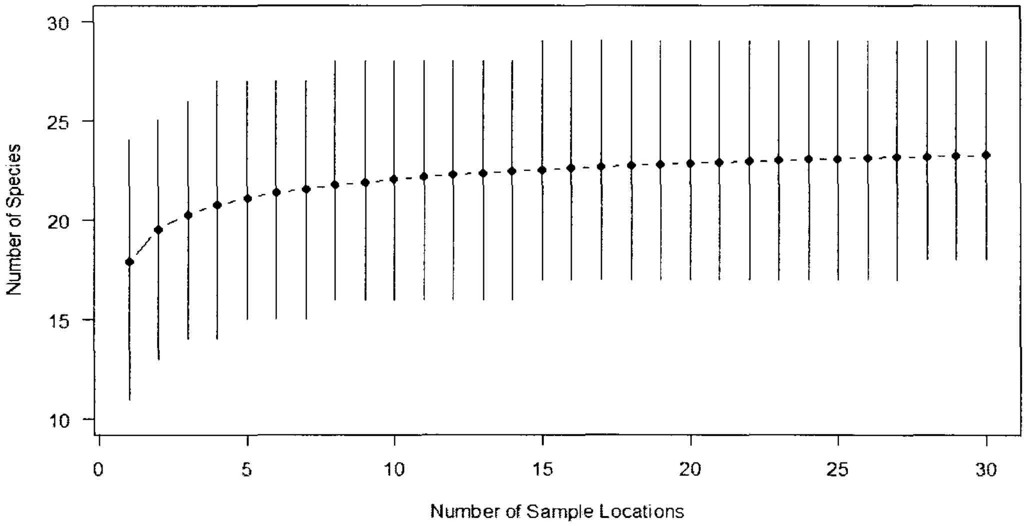

Fig. 5.6: Predicted species accumulation curve for the reptile assemblage in the northern grasslands of Suikerbosrand Nature Reserve from 1-30 sample locations. Each point represents the mean estimate of the posterior-predictive distribution for the number of sample locations. Error bars indicate 95% credible intervals.

5.4. Discussion

Data from my reptile survey indicate that the reptile assemblages in treated and untreated old lands are neither depauperate, nor lacking in any of the common reptile species found in pristine grassland. Despite detecting more reptile species in pristine grassland than in either the treated or untreated old lands, my analyses demonstrate limited statistical support for the hypothesis that reptile species richness is greater in pristine grassland than in the treated and untreated old lands. Model-based estimates suggest that species richness at sites in pristine grasslands is higher than those of the treated or untreated old lands. The model predicts that failures to detect species at sites in the treated or untreated old lands are generally the result of low detection probability and not the absence of the species. Tests of the effects of habitat type on detection probability found significant differences for only three of the 22 reptile species. *Gerrhosaurus flavigularis* has a higher detection probability in the pristine grassland than in either treated or untreated old lands, while *T. capensis* displays the opposite trend. There was no evidence of an effect of habitat type on species occurrence but the power of these tests was no doubt limited by the low detection probability of the majority of reptile species. This is not an illogical outcome of the analysis, as

Table 5.5: Ground cover and dominant grass species at each of the nine sites surveyed between 18 November 2009 and 26 March 2010. Dominant grass species were classified according the Braun-Blanquet scale and are shown in descending order of dominance per site.

Habitat Type	Site ID	Ground Cover (%)	Dominant Grass Species (> 5% cover)
Pristine grassland	1P	85	*Themeda triandra*$^{+}$; *Eragrostis chloromelas*$^{+}$; *Brachiaria serata*$^{+}$; *Hyparrhenia hirta**
	2P	85	*Setaria nigrirostris*$^{+}$; *Hyparrhenia hirta**; *Elionurus muticus*$^{+}$; *Brachiaria serata*$^{+}$
	3P	90	*Themeda triandra*$^{+}$; *Eragrostis curvula**; *Brachiaria serata*$^{+}$; *Hyparrhenia hirta**
Treated old lands	1T	80	*Paspalum dilatatum*^{a}; *Hyparrhenia hirta**; *Eragrostis curvula**; *Heteropogon contortus*$^{+}$
	2T	60	*Heteropogon contortus*$^{+}$; *Hyparrhenia hirta**; *Eustachys paspaloides*$^{+}$; *Paspalum dilatatum*^{a}
	3T	75	*Eragrostis curvula**; *Themeda triandra*$^{+}$; *Heteropogon contortus*$^{+}$; *Pogonarthria squarrosa*^{p}

Untreated old lands	1U	60	Hyparrhenia hirta*; Eragrostis curvula*; Aristida congesta*; Setaria pallide-fusca*
	2U	75	Cynodon dactylon*; Hyparrhenia hirta*; Aristida congesta*; Heteropogon contortus[+]
	3U	55	Eragrostis curvula*; Hyparrhenia hirta*; Urochloa mosambicensis*; Aristida congesta*

[+] Species that feature prominently in climax or sub-climax grassland

* Species that dominate in heavily disturbed grassland and old lands

[p] Pioneer species

[a] Alien invasive species originally from South America

species that are very difficult to detect at sites at which they do occur i.e. are detected at least once, are likely to go undetected at other sites rather than be truly absent. As the detection probability of a species increases the power to discriminate between its non-detection and absence increases. My results are a good example of the challenges that arise from a combination of the cryptic habits of reptiles and sampling limitations. The positive finding of my survey and analysis is that the impacts of low detection probability appear to be most pronounced at the site level, but diminish when the focus is shifted to the assemblage as a whole.

Comparisons of the estimated sample completeness show that overall the survey performed very well – detecting 80% of the mean number of reptile species predicted to comprise the total assemblage (Table 5.4). Sample completeness at the site level is lower with predictions ranging from 50.6 – 70.7% for my survey (Table 5.4). Consequently my analysis suggests that it is much harder to census the reptile assemblage at a single site than it is to census the broader reptile assemblage. This model prediction is supported by the predicted species accumulation curve (Fig. 5.6). The curve predicts that the sampling of an additional 21 sites will not increase the total number of reptile species exposed to sampling to an extent that would merit the increased cost and effort. However, if the relationship between sample locations and accumulation holds true for each habitat type, then increasing the number of sites in each habitat type might be able to overcome the challenges posed by low detection probability. A failure to detect a species at any of nine sites in a given habitat type could be sufficient evidence for an effect of habitat type on occurrence. This hypothesis could be tested using simulation where the model-estimated detection probabilities from this survey are used as the true values for the parameters of the test model.

The vegetation of pristine grassland sites was dominated by climax, sub-climax and disturbance-favouring species, indicating that these sites are in better floristic condition than the old lands. Untreated old lands were, without exception, dominated by grass species that favour frequently disturbed sites and are indicative of poorly managed grassland (Van Wyk & Malan 1998). Treated old lands exhibited a slight reduction in the dominance of weedy and disturbance-favouring species and slightly greater soil cover than the untreated old lands but cannot be considered equivalent to primary grassland in their current state. My vegetation data support earlier findings that the restoration efforts are having a positive effect of the condition of the vegetation in the treated old lands (du Toit & Koen, 2006; 2007; 2008). However, the intermediate nature of the vegetation characteristics in the treated old lands is not supported by the data from the reptile survey, as the reptile assemblage at treated old lands is indistinguishable from that of the untreated sites.

The reptile assemblage in the treated old lands is most similar to the reptile of the assemblage of the untreated old lands. This is evident from the patterns in the detection probabilities of *G. flavigularis* and *T. capensis* in the three habitat types (Table 5.3). *Gerrhosaurus flavigularis* is significantly more likely to be detected in pristine grassland than in either the treated or untreated old lands. This finding is in line with that of Masterson *et al.* (2009), who both captured and recaptured a greater number of *G. flavigularis* individuals in the 'unmodified' habitats of their 2005-2006 survey. The observations for *T. capensis* were an exception to this general trend (Masterson *et al.* 2009), and this survey has produced a similar result. *Trachylepis capensis* was significantly more likely to be detected in the old lands than in the pristine grassland (Table 5.3). The statistical support for the pattern in these two species, coupled with the observations of Masterson *et al.* (2009), suggest that while certain changes in the condition of the vegetation are evident, these changes have had no discernible impact on the 'suitability' of the treated old lands for either *G. flavigularis* or *T. capensis*.

The concept of habitat suitability is derived from the concept of a niche in ecological theory. A niche may be defined as a closed, *n*-dimensional space in which all conditions suitable for the indefinite persistence of a species are met (Hutchinson 1957). The 'suitability' of a habitat is determined by the degree of overlap between the conditions of the habitat and the requirements of a given species. For the majority of species it is not possible to map the *n*-dimensional space in which the conditions suitable for their indefinite persistence occur, thus the concept of a niche (*sensu* Hutchinson 1957) remains more of an ecological theory than a measurable quantity. However, when considering the suitability of a habitat in light of persistence, it is not just the occupancy of a site that is important but also the abundance of the species at the occupied sites. Abundance is directly linked to persistence in that the greater the size of the local population, the lower the probability of extirpation (Dorazio 2007). Abundance has obvious links to both occupancy and detection probability (Royle & Nichols 2003; Mackenzie 2006; Royle 2008; McCarthy *et al.* 2013) as a site can only be occupied when a species' abundance is greater than zero. Spatial variation in abundance can be expected to lead to spatial variation in detection probability (Royle & Nichols 2003; Dorazio 2007; Royle & Dorazio 2008; Kéry & Royle 2010) in the same way that large groups or clusters of animals are more likely to be detected than small clusters e.g. surveys of avifauna or ungulates (Royle 2008). Using the data already collected in this survey, I could test the hypothesis that differences in abundance in the three habitats could result in the observed differences in the probability of detecting at least one *G. flavigularis* or *T. capensis* at a site on any day of trapping (see Royle & Nichols 2003). In such an analysis, 'abundance' would refer to the number of individuals active at a site per day. Greater numbers of active individuals at sites in particular habitats are a certain indication of differences in the interaction of a species and habitat, and a possible indication of differences in the suitability of the habitat for the species concerned (Driscoll *et al.* 2012). The findings of Masterson *et al.* (2009) and this survey demonstrate consistent patterns in the relationships of *G. flavigularis* and *T. capensis* with modified and unmodified sites in the grassland of SNR, which could be further investigated.

From a conservation perspective, the similarities and dissimilarities of the reptile assemblages found in the three habitat types can be interpreted as either positive or negative depending on the management objectives of the reserve and the desired outcomes of the restoration efforts (Block *et al.* 2001). From a pure biodiversity perspective, differences in the relative abundances of species in two assemblages represent increased diversity even if the species comprising the assemblages are identical. My model suggests that the reptile assemblages in the three habitat types contain the same species, but may differ in terms of the abundance of these species. From a restoration perspective, the structure of an assemblage can be as important as the species comprising it and differences may represent a failure to 'return' the assemblage to the state observed in the reference areas i.e. pristine grassland. One of the major challenges for restoration projects is the 'shifting baseline' resulting from changes in the composition of species assemblages over time (e.g. Dornelas *et al.* 2014). With evidence that the composition of communities is changing, how does one set goals for a 'restoration' project, particularly in poorly sampled areas? The primary objectives of the restoration efforts in SNR aim to restore the vegetation communities of old lands to a state similar to that of surrounding, unploughed areas of grassland and to increase soil cover in old lands through an increase in the number of climax grassland species. The additional objective of stimulating an increase in the biodiversity in the treated old lands appears moot from a reptile perspective as the richness of the assemblages is equivalent between all three habitat types I surveyed. From the results of my survey, there are no indications that attempts to restore the vegetation in the old lands of SNR have led to specific changes in the reptile assemblage. Treated old lands support a reptile assemblage that is broadly similar to old lands that have been left to recover without assistance over the past 10 years or more.

Masterson *et al.* (2009) considered the removal of rocks from previously cultivated areas an important factor in the differences between the reptile assemblages in the modified and unmodified habitat types they surveyed. Their hypothesis is supported by observations that the availability of refugia can sustain reptile assemblages in the face of transformation and disturbance. Using an experimental design, Márquez-Ferrando *et al.* (2009) demonstrated the negative impacts of refuge removal on reptile richness following a mine-tailing spill in south-western Spain. Natural refuges e.g. logs, were removed during a soil and vegetation restoration programme and reptile richness remained low in these areas following the programme's completion. The reptile assemblage recovered more rapidly at sites that were provisioned with artificial refuges as compared with control sites (Márquez-Ferrando *et al.* 2009). Michael *et al.* (2008) found that increased rock cover associated with granite inselbergs had a positive effect on reptile diversity in agricultural landscapes of south-eastern Australia. Kanowski *et al.* (2006) suggest that the value of restored sites for reptiles can be improved by adding key habitats that are not likely to be restored by natural processes. Rocks removed from the old lands of SNR during cultivation have been piled at the boundaries of the old lands (Fig. 5.7). The redistribution of these rocks may improve the habitat in old lands by providing refugia for reptiles in an otherwise open habitat (see Márquez-Ferrando *et al.* 2009). An experimental approach to the redistribution of the removed rocks could be used to test this hypothesis.

The cryptic nature of reptiles is one of the most significant challenges restricting an understanding of their ecology and their effective conservation. In this study, I calculated that the mean of species-specific detection probabilities in the reptile assemblage of the pristine grassland is 0.025. Using a single trap array at a site at which an average reptile species occurs, we would expect to detect it approximately three times in 100 days (> 3 months) of trapping. Few surveys have this sort of duration as the costs of such an exercise are prohibitive. Many of the estimated detection probabilities for species in the pristine grassland or old lands are lower than 0.025, meaning that these species require even greater sampling effort to determine their presence or absence with a high level of certainty. Thus conventional reptile survey methods fall woefully short of their stated goals. Unfortunately, the detection probabilities associated with alternate sampling methods e.g. active searching or distance sampling are not widely reported in studies of reptile assemblages (but see East, East & Daugherty 1995 and Kéry 2002). Consequently it is difficult to evaluate whether or not alternate methods of sampling reptile assemblages provide greater precision in the estimates of species occurrence via improved detection probability. Further to the consideration of additional sampling methods, the customisation of the observation model when using trap arrays remains to be explored. Specifically trap arrays are passive sampling apparatus that rely on the activity of a reptile in order to have non-zero detection probabilities during sampling. The observation model specified in this analysis followed the form of MacKenzie *et al.* (2003) and Royle & Kéry (2007) in that the observation of the species depends upon the latent indicator variable for occurrence. Detections of species in trap arrays can only occur if an individual of a species is active near the trap array and creates additional ambiguity in the interpretation of zeroes in the detection dataset. The presence of zeroes resulting from inactivity will cause estimates of detection probability to be biased low and motivates for the further inclusion of a latent indicator variable for the activity of the species during each day of trapping. Whether or not the indicator variable for activity is identifiable without additional information is not clear but would most likely require a third level of sub-sampling (M. Kéry, pers. comm.). Such an additional level of sampling could in theory be created by breaking the sampling data into the three calendar categories of day, week and month. In such a case, the month is the primary sampling period, the week is the secondary sampling period and the day is

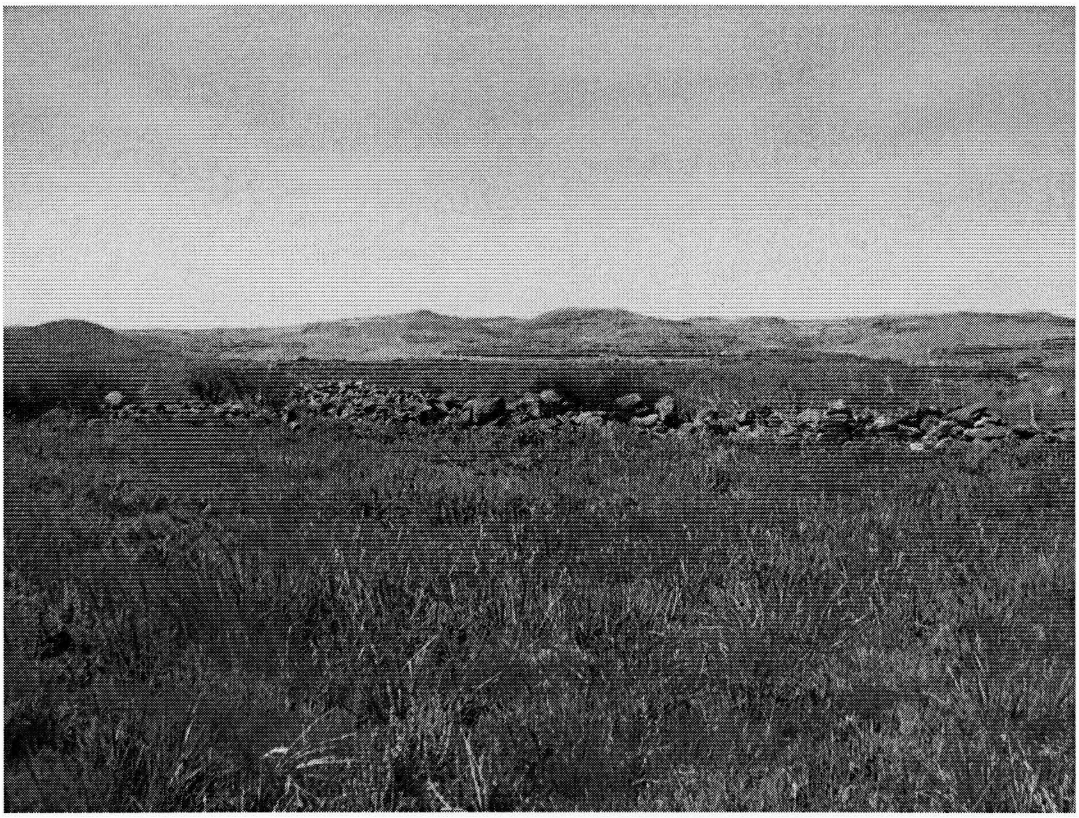

Fig. 5.7: Evidence of rock removal from areas that were ploughed prior to the acquisition of the northern extension to Suikerborand Nature Reserve. The Suikerbosrant plateau for which the reserve is named can be seen in the background.

the tertiary sampling period. The 'activity' of a reptile species in a given week might then be estimable. The ecological relevance of the sampling periods would need careful consideration but in theory, a reasonable restructuring of the data might allow for improved estimation of the true detection probability and consequently greater precision in the estimates of site occupancy (McCarthy *et al.* 2013).

In conclusion, habitat rehabilitation has, to this point, been only partially successful in re-establishing natural reptile assemblages in SNR. The estimated species richness of sites in the three habitat types did not differ significantly due to the uncertainty with which I was able to predict the absence of a given reptile species. This lack of certainty is induced by the general difficulty associated with detecting species that have a wide range of life history strategies (e.g. fossorial or terrestrial) and where the number of individuals present and active at each site is also certain to play an important role in determining the probability of detection. Despite these challenges the combination of an observation model to estimate detection probability with a process model for individual species occurrence represents an improvement on previous methods of analysing data collected during reptile surveys at SNR i.e. Masterson *et al.* (2009). The coherence of the hierarchical framework for the analysis of ecological datasets does certainly highlight the challenges associated with understanding the interactions of cryptic species and the environment. The hierarchical framework is also sufficiently flexible to accommodate further refinements which can only improve the ecological understanding gained through surveys of this type in the future.

CHAPTER 6

So What Now?

At times during this project, I have felt as though its contribution to the research topic I set out to investigate has been miniscule. While it would be far more satisfying to conclude this thesis with statements such as "species X is negatively affected by ..." or "species richness is dramatically reduced at sites that have previously been ploughed for cultivation purposes", the simplicity of these statements would contrast strongly with the complexity of the ecological process that underpins the thesis: site occupancy. While certain findings in this thesis are conclusive e.g. funnel traps are a valuable complement to pitfall traps for sampling reptile assemblages (Chapter 2), I believe that the major contribution of this thesis lies in the refinements that it proposes for future studies of reptiles in managed or transformed landscapes of southern Africa. The widespread application of hierarchical occupancy models in this thesis is one that has not been attempted for many reptile studies, both locally and globally. The consideration of the challenge that reptile crypsis will be necessary if we are to progress in our understanding of the relationship between reptiles and their local habitats (Gardner, Barlow & Peres 2007) in order to protect them. This thesis also demonstrates that trap surveys can contribute to our understanding of the distribution of species e.g. the discovery of a *Nucras lalandii* population in northern SNR, and shed new light on species we might consider widespread and abundant e.g. *Agama aculeata distanti.* It is also important to realise that the improvements in Bayesian techniques for modelling hold great promise that the information gained in each successive survey can be used as but one additional piece in a growing library of data. For these reasons, I look forward to seeing what additional questions we will be able to tackle with the information collected for SNR by this project.

6.1. Sampling Methods and Efficacy

The choice of sampling method to achieve a study's objectives is not a trivial decision. Firstly the method needs to be effective for the collection of data in the study habitat types. Secondly the method must be efficient in terms of cost, time or both, specifically considering replication at the spatial resolution at which sampling will be conducted. Methods for sampling reptile assemblages generally meet one of the two criteria listed previously, but not both. The utility of active searching is affected by the number of observers, observer effort, observer skill in identifying reptiles detected, the habitat in which searching takes place and the size of the study area. The advantages of active searching are reduced costs, observer-driven sampling intensity and time-table, and the ability to target sample microhabitats in which reptiles are likely to be found. Sampling with trap arrays is affected by the substrate on which sampling is conducted, the types of traps used, the layout of the trap array, and the abundance or activity of reptile species during the sampling period (Driscoll & Henderson 2008). The benefits of trapping are the simultaneous sampling of multiple sites, the continuous presence of an 'observer' in all weather conditions (except where weather conditions impair trap function e.g. flooding), and reduced demand for observer skill as trapped reptiles can be identified in a rigorous, unhurried fashion.

In Chapter 1, I argued that trapping is a useful method for sampling reptile assemblages at Suikerbosrand Nature Reserve (SNR). Having analysed the data collected during 37 206 trap days (Table 6.1) across SNR, I can now qualify the argument in favour of trapping over active searching. The analysis of trap efficacy in Chapter 2 offered strong evidence of the benefit gained by using both pitfall and funnel traps at each trap array. The complementary nature of the two trap types resulted in a greater number of species detections than would have been achieved using either of the trap types in isolation. As a result of the findings in Chapter 2, pitfall and funnel traps have been used in every subsequent trap-based survey or monitoring exercise of reptiles in SNR. While the applicability of the findings in Chapter 2 will vary across habitat types, the use of pitfall and funnel traps is recommended for sampling reptile species in structurally simple habitats, particularly when substrate type means that pitfalls are necessarily small. Studies that focus on a single species can make use of the trap type that best samples them, in order to employ more of these traps at equivalent cost. While many authors have argued that multiple methods of sampling should be employed to survey reptiles, I caution against a blanket approach to this, as certain methodological choices may complicate the achievement of study objectives e.g. using coverboards to assess use of modified habitats by refuge-seeking species (see Chapter 1).

The analysis conducted in Chapter 3 showed that if one uses an explicit model of detection probability to estimate species richness, then sampling efficacy is a key constraint of the precision of the estimate. This is not to say that a species' detection probability must be very high, but it needs to be sufficient when compared with the number of samples. For trap arrays that were checked on 104 occasions, precise estimates of site occupancy were achieved for species with detection probabilities greater than 0.06 sample^{-1}. Estimates of site occupancy for species with a detection probability of less than 0.01 sample^{-1} were understandably less precise and I would not use them for inference.

Unfortunately, modifications to passive methods of sampling such as trapping can only focus on the trap array itself. Trap array layout, the use of efficient trap types, the use of durable drift fence materials, the length of the drift fences, trap maintenance and the timing of sampling represent the majority of options available for increasing trap efficacy. There is no way for a researcher to modify species activity or species abundance so that a species is more frequently detected. Despite this challenge, it is important to note that the efficacy of trapping has increased with each successive survey conducted in SNR (Table 6.1). Identifying the causes of the improvement in trap efficacy require detailed analysis to be fully understood, but appear to have been associated with (1) changes to materials used to construct drift fences (changing from plastic to ceiling board), (2) an emphasis on trapping from late spring to late summer (avoiding early spring months i.e. September and October) and (3) the immediate replacement of funnel traps that are damaged by weathering or animals. One modification for future studies of microhabitat or site selection in SNR is the use of two or more trap arrays per site, or the separation of drift fences such that they cover a larger area with the same amount of material (e.g. Thompson *et al.* 2003). Another option would be to make use of longer drift fences. Ellis & Bedward (2014) suggest that the gains in sampling are not proportional to the increase in fence length yet even small increases in efficacy might result in sample data from which more confident inference can be made.

Table 6.1: Survey details for all trapping conducted within Suikerbosrand Nature Reserve showing the year of the survey, the numbers of trap arrays and types of trap used per array, trap visits during the survey period and the numbers of reptile individuals and species captured.

Survey	Year	Trap Arrays	Traps per array		Trap visits	Trap days	Reptiles captured	
			Pitfall	Funnel			Individuals	Species
Masterson, Maritz & Alexander (2008)	2004	10	8	8	30	4 800	63	13
Chapter 4	2005/6	12	5	8	156	24 336	551	20
Masterson *et al.* (2009)	2005/6	9	5	8	141	16 497	443	22
Koen & du Toit (2007)	2006/7	16	5	8	365	75 920	1960	31
Chapter 5	2009/10	9	5	8	110	12 870	750	22

* continuous sampling for one year (1 May 2005 – 30 April 2006) was conducted by D. Koen and L. du Toit.

6.2. Detection Probability

Detection probability, defined as the success rate of the sampling conducted, is a nuisance parameter in ecological investigations. Ideally all sampling should be conducted in such a way that the presence or absence of target species is perfectly observed in a single sample i.e. $p = 1$. In practice detection probability is never perfect and may also vary through time (Royle *et al.* 2010; Chapter 4). Species may advertise their presence by calling, or may be active in ways or at times such that time-based searches have a high probability of detecting them. The habitat in which sampling is conducted also influences the ease with which individuals of the target species are captured e.g. fossorial, tropical species (Maritz & Alexander 2008) vs. terrestrial, semi-desert species (Maritz 2011), and sampling strategies should be tailored accordingly.

In this thesis, I used passive trapping to sample reptiles in SNR, with no additional forms of sampling such as active, time-constrained searches. While some studies do make use of multiple sampling methods, they are typically of very short duration i.e. five days of pitfall trapping per survey (Nichols & Nichols 2003; Fischer, Lindenmayer & Cowling 2004). Surveys of longer duration for the study of reptile assemblages generally make exclusive use of passive trapping. Few of these studies have estimated the success rate of trapping explicitly but, even if available, comparisons of detection probability or trap success rates would be further complicated by structural differences in the reptile assemblages compared. Rigorous comparisons of alternatives, such as the ones by Greenberg, Neary & Harris (1994a) and Hobbs *et al.* (1994), are invaluable contributions to the methodological discussion and should be conducted prior to or as part of the drafting of a sampling framework for Environmental Impact Assessments (EIA). Current EIA methods for sampling reptiles at prospective development sites in South Africa are far less intensive than the sampling conducted in this thesis (G.J. Alexander, pers. comm.). As my results show, it is difficult to reliably detect all species at a single site even with months of trapping. How much more biased is the number of species detected by methods that are less intensive? When one considers that EIA typically focus on rare or Threatened species, which may be expected to have low detection probabilities, the question becomes even more pertinent.

The scale at which detection probability is estimated can vary dramatically and depends upon the goals of the study e.g. detection by trap types (Chapter 2), or by entire trap arrays (Chapters 3, 4 and 5). In Chapter 2, the effect of trap type on detection probability was demonstrable, with important consequences for sampling. Snake species made up the bulk of the species richness in the sites surveyed during this thesis. Thus the use of funnel traps, with the consequent increase in sampling efficacy was both a cost-saving feature of the sampling and vital to my attempts to estimate characteristics of the reptile assemblage, including detected and undetected species (Chapters 3 and 5). I also found differences in detection probability of reptile species through time (Chapter 4), which raises important questions about survey timing and duration. Analytical methods that do not allow for variation in detection probability within a survey period or study will be at greatest risk of bias under these circumstances. This is what motivated my analysis in Chapter 3, which confirmed the benefits of a hierarchical modelling approach for inference.

The detection probabilities estimated for reptiles in SNR in this thesis represent the first estimates of detection probability published for any southern African reptile assemblage. The only prior work on detection probability of southern African works is that of Gardner, Baard & le Roux (1999), who used a controlled field trial to estimate the detection probability of geometric tortoise models when walking transects through suitable habitat. Gardner, Baard & le Roux (1999) estimated the probability that each individual present in a transect is detected during searching i.e. population size data, which differs from the probability that any individual is detected during searching i.e. presence-absence data. Gardner, Baard & le Roux (1999) reported that no observer detected more than 50% of the models in a transect, and that vegetation density and detection probability were inversely proportional. Additionally, their data indicate that at least one model tortoise was detected in every transect searched, whether by groups or individuals (Gardner, Baard & le Roux 1999). Thus the presence of the 'species' was perfectly represented by the detection data, with no false absences resulting from non-detection. For this reason, and the fact that tortoises are quite large and do not move off at the approach of an observer as they tend to rely on the protection of their shells, these data are not comparable with those of my thesis.

In the absence of estimates for comparison, two questions cannot be answered: (1) how do the detection probabilities of reptile species at SNR compare with those of other species assemblages in southern Africa?; and (2) is active searching a more cost-effective method when confirmation of site occupancy is the objective of sampling? Hutchens & DePerno (2009) compared multiple sampling methodologies and reported that primary techniques (which included trapping) were more costly than other methods in terms of cost-per-capture measures and recommended the use of multiple methods to determine species richness. Unfortunately Hutchens & DePerno (2009) did not estimate detection probability explicitly, preferring to use the Chao2 estimator (Chao 1987) to estimate the number of species not detected. Pending a re-analysis of their data to estimate the detection probability of each species using each method, another study comparing active searching and trapping methods in a simultaneous survey of the same sites is recommended. Variables such as habitat type, vegetation density, cost, and time spent on trap installation and maintenance vs. time spent active searching could be controlled for in such a setting. Data from a study such as this would be invaluable for comparing the efficacy of the two methods for surveying an entire reptile assemblage. I strongly recommend that future studies of reptile assemblages in southern Africa include an explicit assessment of detection probability (regardless of the method of sampling) so that efficacy of each method can be improved, better sampling methods can be selected to meet study objectives and costs saved. The diversity of reptiles in southern Africa is too great to take a 'one-size-fits-all' approach or to utilise costly and inefficient methods when cheaper alternatives exist. This is a risk if the success rate of the chosen sampling method is not assessed.

6.3. The Site Occupancy Metric

In this thesis my analyses have focussed on the presence or absence of reptile species at my sample sites. Since the introduction of the metapopulation concept of Hanski (1998), the use of site or patch occupancy as a metric in animal studies has increased in frequency (Royle, Nichols & Kéry 2005). While passive trapping is very useful for detecting the presence of rare species (Chapter 5), it is not an efficient method for generating count data. Even if one uses mark-recapture methods to identify novel individuals from previously captured individuals, the time frame of trapping in this survey means that there is always a likelihood that new individuals will immigrate into the site population. For example, I marked individuals of the most common lizard species at SNR. The goal of marking these species was to determine if individuals moved between trap sites that were in close proximity to one another. Only a single adult *Gerrhosaurus flavigularis* was captured at two sites. The individual was first caught at site 2B (date unknown as marks were site- but not individual-specific) and recaptured on a single occasion at site 2A (date: 27 March 2006). My data confirmed that the inter-site movement of individuals of these lizard species had a negligible effect on trapping both because it is exceptional (occurring only once) and because these species were readily detected i.e. migrating individuals did not result in the only detection of the species. The use of site occupancy as a metric for each species was thus a simpler way to represent population status of each species across the study area (Royle, Nichols & Kéry 2005), however the fact that many species were not repeatedly detected at the site where they occurred led to increased uncertainty about the status of sites at which they were not detected (Chapters 3, 4 and 5).

As was noted in Chapter 4, the occupancy state of a site can be quite resilient to changes in the abundance of the species considered. While a decrease in the abundance of the species, or even the apparent abundance of the species via reduced activity at the site, can be expected to lead to a decrease in the probability of detecting the species (Royle & Nichols 2003), the site remains occupied until the population size decreases to zero and the species is locally extirpated. As the detection probability of a species decreases, the inclusion of factors that cause variation in detection probability is critical to discriminate between the true and false absence of a species. However, decreased detection probability leads to biased estimates of the relationship between site occupancy and causal factors, which then inhibits our ability to relate real declines to threatening processes and to respond effectively to them. This was a consequence that I did not foresee during the planning of my fieldwork and I cannot be certain that this 'negative-feedback loop' did not affect the results of my surveys for Chapter 4 and Chapter 5. I suggest that in the future, studies using site occupancy as the metric of population status should use multiple trap arrays, of any suitable arrangement e.g. Hobbs *et al.* (1994), such that the site-specific detection probability of 'rarer' reptile species increases to levels suitable for discriminating between occupied and unoccupied sites with high confidence. I would also, cautiously, recommend the use of active searching (time-constrained or time-measured). The use of active searching would need to be conducted in ways which did not destroy, modify or otherwise impact upon microhabitat suitability for species occurring at the site. For example, lifting rocks which are replaced as found is acceptable, but the destruction of termitaria – which many species of reptile utilise as refugia (Lynch 1988) – is not recommended for general practice.

6.4. Reptiles and Habitat Characteristics

The goal of my thesis was to study the relationship between habitat modification and the reptiles experiencing the changes. From the data collected, reptiles appear to be relatively resilient to changes in their habitat (Chapters 4 and 5). This is not to say that all reptile species responded to habitat modifications in the same way. The two most common species of lizard in SNR, *G. flavigularis* and *Trachylepis capensis* responded differently (see chapters 4 and 5). Despite no effect of fire or grass cutting on the occupancy of sites for both species, individuals of *G. flavigularis* were more frequently detected at cut sites than at either control or burnt sites, whereas individuals of *T. capensis* were less frequently detected at burnt sites compared with control or cut sites (Chapter 4). A similar dichotomy in the response of these two species was observed in Chapter 5. *Trachylepis capensis* was less likely to be detected at undisturbed grassland sites as compared with treated or untreated old lands, while *G. flavigularis* had a much higher detection probability in undisturbed sites than in both old land types. From a site occupancy perspective, the causes of these differences are inconsequential to their conservation at SNR because both species were recorded at nearly every site surveyed in both studies.

Two species of lizard that merit further consideration in future studies are (1) *Agama aculeata distanti* and (2) *Nucras lalandii*. In the case of *A. a. distanti*, it appears that the species is patchily distributed across SNR, with small population sizes at occupied sites. In combination, these two conditions make *A. a. distanti* vulnerable to localised threats, with reduced likelihood of re-colonisation (Chapter 4). In the case of *N. lalandii*, the population at SNR is the only known extant population of the species within the Gauteng Province, and the species has been recorded only in undisturbed grassland sites during surveys by Masterson *et al.* (2009), D. Koen and L. du Toit (reported in Masterson 2010), and Chapter 5. The additional concern regarding the status of *N. lalandii* in SNR is that the species has only been recorded in the grasslands north of the reserve's main plateau. Whether this is due to microclimatic differences between the northern and southern grasslands (the latter are exposed to the cold winds blowing north east off the Lesotho mountains) or due to the exclusion of large herbivores or some other factor is not known. Nevertheless, the decline of *N. lalandii* in Gauteng Province and its apparent exclusive use of undisturbed grassland sites motivate strongly for further study and careful management.

6.5. Conclusion

In the development of our understanding of the natural world, we typically progress with small steps. While this does not always seem a satisfactory outcome for the effort invested, the truth is that each step takes us closer to the goal. Perhaps that must sometimes be enough. Despite the challenges encountered during trapping at SNR since 2004, the sum total of the information collected about reptiles within the reserve boundary is impressive and invaluable for future studies in southern Africa. Suikerbosrand Nature Reserve is now one of the most intensively surveyed areas in southern Africa with regards to its reptile fauna and I expect many more interesting findings as the data continue to be analysed.

REFERENCES

Abensperg-Traun, M. (2009) CITES, sustainable use of wild species and incentive-driven conservation in developing countries, with an emphasis on southern Africa. *Biological Conservation*, **142**, 948–963.

Adalsteinsson, S.A., Branch, W.R., Trape, S., Vitt, L.J. & Hedges, S.B. (2009) Molecular phylogeny, classification, and biogeography of snakes of the Family Leptotyphlopidae (Reptilia, Squamata). *Zootaxa*, **2244**, 1–50.

Akani, G.C., Luiselli, L., Wariboko, S.M., Ude, L. & Angelici, F.M. (2002) Frequency of tail autotomy in the African Olive Grass Snake, *Psammophis "phillipsii"* from three habitats in southern Nigeria. *African Journal of Herpetology*, **51**, 143–146.

Andrews, K.M. & Gibbons, J.W. (2005) How Do Highways Influence Snake Movement? Behavioral Responses to Roads and Vehicles. *Copeia*, **2005**, 772–782.

Archer, E.R.M. (2004) Beyond the "climate versus grazing" impasse: using remote sensing to investigate the effects of grazing system choice on vegetation cover in the eastern Karoo. *Journal of Arid Environments*, **57**, 381–408.

Atauri, J.A. & de Lucio, J. V. (2001) The role of landscape structure in species richness distribution of birds, amphibians, reptiles and lepidopterans in Mediterranean landscapes. *Landscape Ecology*, **16**, 147–159.

Attum, O., Covell, C. & Eason, P. (2004) The comparative diet of three Saharan sand dune skinks. *African Journal of Herpetology*, **53**, 91–94.

Attum, O.A. & Eason, P.K. (2009) Effects of Vegetation Loss on a Sand Dune Lizard. *The Journal of Wildlife Management*, **70**, 27–30.

Bates, M.F., Branch, W.R., Bauer, A.M., Burger, M., Marais, J., Alexander, G.J. & De Villiers, M.S. (2014) *Atlas and Red List of the Reptiles of South Africa, Lesotho and Swaziland*, Suricata 1 (eds MF Bates, WR Branch, AM Bauer, M Burger, J Marais, GJ Alexander, and MS De Villiers). South African National Biodiversity Institute, Pretoria.

Bled, F., Royle, J.A. & Cam, E. (2011) Hierarchical modeling of an invasive spread: the Eurasian Collared-Dove *Streptopelia decaocto* in the United States. *Ecological Applications*, **21**, 290–302.

Block, W.M., Franklin, A.B., Ward Jr., J.P., Ganey, J.L. & White, G.C. (2001) Design and Implementation of Monitoring Studies to Evaluate the Success of Ecological Restoration on Wildlife. *Restoration Ecology*, **9**, 293–303.

Block, W.M., Morrison, M.L. & Scott, P.E. (1998) Development and Evaluation of Habitat Models for Herpetofauna and Small Mammals. *Forest Science*, **44**, 430–437.

Böhm, M., Collen, B., Baillie, J.E.M., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., Rhodin, A.G.J., Stuart, S.N., van Dijk, P.P., Young, B.E., Afuang, L.E., Aghasyan, A., García, A., Aguilar, C., Ajtic, R., Akarsu, F., Alencar, L.R.V., Allison, A., Ananjeva, N., Anderson, S., Andrén, C., Ariano-Sánchez, D., Arredondo, J.C., Auliya, M., Austin, C.C., Avci, A., Baker, P.J., Barreto-Lima, A.F., Barrio-Amorós, C.L., Basu, D., Bates, M.F., Batistella, A., Bauer, A., Bennett, D., Böhme, W., Broadley, D., Brown, R., Burgess, J., Captain, A., Carreira, S., Castañeda, M.D.R., Castro, F., Catenazzi, A., Cedeño-Vázquez, J.R., Chapple, D.G., Cheylan, M., Cisneros-Heredia, D.F., Cogalniceanu, D., Cogger, H., Corti, C., Costa, G.C., Couper, P.J., Courtney, T., Crnobrnja-Isailovic, J., Crochet, P.-A., Crother, B., Cruz, F., Daltry, J.C., Daniels, R.J.R., Das, I., de Silva, A., Diesmos, A.C., Dirksen, L., Doan, T.M., Dodd, C.K., Doody, J.S., Dorcas, M.E., Duarte de Barros Filho, J., Egan, V.T., El Mouden, E.H., Embert, D., Espinoza, R.E., Fallabrino, A., Feng, X., Feng, Z.-J., Fitzgerald, L., Flores-Villela, O., França, F.G.R., Frost, D., Gadsden, H., Gamble, T., Ganesh, S.R., Garcia, M.A., García-Pérez, J.E., Gatus, J., Gaulke, M., Geniez, P., Georges, A., Gerlach, J., Goldberg, S., Gonzalez, J.-C.T., Gower, D.J., Grant, T., Greenbaum, E., Grieco, C., Guo, P., Hamilton, A.M., Hare, K., Hedges, S.B., Heideman, N., Hilton-Taylor, C., Hitchmough, R., Hollingsworth, B., Hutchinson, M., Ineich, I., Iverson, J., Jaksic, F.M., Jenkins, R., Joger, U., Jose, R., Kaska, Y., Kaya, U., Keogh, J.S., Köhler, G., Kuchling, G., Kumlutaş, Y., Kwet, A., La Marca, E., Lamar, W., Lane, A., Lardner, B., Latta, C., Latta, G., Lau, M., Lavin, P., Lawson, D., LeBreton, M., Lehr, E., Limpus, D., Lipczynski, N., Lobo, A.S., López-Luna, M.A., Luiselli, L., Lukoschek, V., Lundberg, M., Lymberakis, P., Macey, R., Magnusson, W.E., Mahler, D.L., Malhotra, A., Mariaux, J., Maritz, B., Marques, O.A.V., Márquez, R., Martins, M., Masterson, G., Mateo, J.A., Mathew, R., Mathews, N., Mayer, G., McCranie, J.R., Measey, G.J., Mendoza-Quijano, F., Menegon, M., Métrailler, S., Milton, D.A., Montgomery, C., Morato, S.A.A., Mott, T., Muñoz-Alonso, A., Murphy, J., Nguyen, T.Q., Nilson, G., Nogueira, C., Núñez, H., Orlov, N., Ota, H., Ottenwalder, J., Papenfuss, T., Pasachnik, S., Passos, P., Pauwels, O.S.G., Pérez-Buitrago, N., Pérez-Mellado, V., Pianka, E.R., Pleguezuelos, J., Pollock, C., Ponce-Campos, P., Powell, R., Pupin, F., Quintero Díaz, G.E., Radder, R., Ramer, J., Rasmussen, A.R., Raxworthy, C., Reynolds, R., Richman, N., Rico, E.L., Riservato, E., Rivas, G., da Rocha, P.L.B., Rödel, M.-O., Rodríguez Schettino, L., Roosenburg, W.M., Ross, J.P., Sadek, R., Sanders, K., Santos-Barrera, G., Schleich, H.H., Schmidt, B.R., Schmitz, A., Sharifi, M., Shea, G., Shi, H.-T., Shine, R., Sindaco, R., Slimani, T., Somaweera, R., Spawls, S., Stafford, P., Stuebing, R., Sweet, S., Sy, E., Temple, H.J., Tognelli, M.F., Tolley, K., Tolson, P.J., Tuniyev, B., Tuniyev, S., Üzüm, N., van Buurt, G., Van Sluys, M., Velasco, A., Vences, M., Veselý, M., Vinke, S., Vinke, T., Vogel, G., Vogrin, M., Vogt, R.C., Wearn, O.R., Werner, Y.L., Whiting, M.J., Wiewandt, T., Wilkinson, J., Wilson, B., Wren, S., Zamin, T., Zhou, K. & Zug, G. (2013) The conservation status of the world's reptiles. *Biological Conservation*, **157**, 372–385.

Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E. & Pollock, K.H. (1998) Estimating Species Richness: The Importance of Heterogeneity in Species Detectability. *Ecology*, **79**, 1018–1028.

Bowers, C.F., Hanlin, H.G., Guynn, D.C., McLendon, J.P. & Davis, J.R. (2000) Herpetofaunal and vegetational characterization of a thermally-impacted stream at the beginning of restoration. *Ecological Engineering*, **15**, 101–114.

Branch,W.R. (1998) *Field Guide to Snakes and Other Reptiles of Southern Africa*. Struik Publishers, Cape Town.

Branch, W.R. (2001) The conservation status of South Africa's threatened reptiles. In: *The State of South Africa's Species*. Verdoorn G.H., le Roux J. (eds), Endangered Wildlife Trust and World Wildlife Fund.

Branch, W.R., Tolley, K.A. & Tilbury, C.R. (2006) A new Dwarf Chameleon (*Sauria: Bradypodion* Fitzinger, 1843) from the Cape Fold Mountains, South Africa. *African Journal of Herpetology,* **55**, 123-141.

Brook, B.W., Sodhi, N.S. & Bradshaw, C.J.A. (2008) Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, **23**, 453–460.

Brose, U., Martinez, N.D. & Williams, R.J. (2003) Estimating Species Richness: Sensitivity To Sample Coverage and Insensitivity To Spatial Patterns. *Ecology*, **84**, 2364–2377.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immingration on extinction. *Ecology*, **58**, 445–449.

Burnham, K.P. & Overton, W.S. (1978) Estimation of the Size of a Closed Population when Capture Probabilities vary Among Animals. *Biometrika*, **65**, 625–633.

Campbell, H.W. & Christman, S.P. (1982) Field techniques for herpetofaunal community analysis. *Herpetological Communities* pp. 193–200.

Castellano, M.J. & Valone, T.J. (2006) Effects of livestock removal and perennial grass recovery on the lizards of a desertified arid grassland. *Journal of Arid Environments*, **66**, 87–95.

Cavitt, J.F. (2000) Fire and a Tallgrass Prairie Reptile Community: Effects on Relative Abundance and Seasonal Activity. *Journal of Herpetology*, **34**, 12–20.

Chao, A. (1984) Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, **11**, 265–270.

Chao, A. (1987) Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, **43**, 783–91.

Chao, A. (2005) Species richness estimation. *Encyclopedia of Statistical Sciences* (eds N. Balakrishnan, C.B. Read & B. Vidakovic), pp. 7909–7916. Wiley, New York.

Chao, A., Chazdon, R.L., Colwell, R.K. & Shen, T.-J. (2005) A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, **8**, 148–159.

Chao, A., Colwell, R.K., Lin, C.-W. & Gotelli, N.J. (2009) Sufficient sampling for asymptotic minimum species richness estimators. *Ecology*, **90**, 1125–33.

Chao, A. & Shen, T.-J. (2004) Nonparametric prediction in species sampling. *Journal of Agricultural, Biological, and Environmental Statistics*, **9**, 253–269.

Chao, A., Shen, T.-J. & Hwang, W.-H. (2006) Application of Laplace's Boundary-Mode Approximations To Estimate Species and Shared Species Richness. *Australian & New Zealand Journal of Statistics*, **48**, 117–128.

Cherry, S., White, G.C., Keating, K.A., Haroldson, M.A. & Schwartz, C.C. (2007) Evaluating estimators of the numbers of females with cubs-of-the-year in the yellowstone grizzly bear population. *Journal of Agricultural, Biological, and Environmental Statistics*, **12**, 195–215.

Chiarucci, A., Enright, N.J., Perry, G.L.W., Miller, B.P. & Lamont, B.B. (2003) Performance of nonparametric species richness estimators in a high diversity plant community. *Diversity and Distributions*, **9**, 283–295.

Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M. & Hormiga, G. (2009) Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*, **78**, 573–584.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S.-Y., Mao, C.X., Chazdon, R.L. & Longino, J.T. (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *Journal of Plant Ecology*, **5**, 3–21.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society Series B*, **345**, 101–118.

Colwell, R.K., Mao, C.X. & Chang, J. (2004) Interpolating, Extrapolating and Comparing Incidence-Based Species Accumulation Curves. *Ecology*, **85**, 2717–2727.

Cunningham, S.C., Babb, R.D., Jones, T.R., Taubert, B.D. & Vega, R. (2002) Reaction of lizard populations to a catastrophic wildfire in a central Arizona mountain range. *Biological Conservation*, **107**, 193–201.

Doak, D.F. & Cutler, K. Re-evaluating evidence for past population trends and predicted dynamics of Yellowstone grizzly bears. *Conservation Letters*.

Donnelly, M.A., Chen, M.H. & Watkins, G.G. (2005) Sampling amphibians and reptiles in the Iwokrama Forest. *Proceedings of the National Academy of Sciences of Philadelphia*, **154**, 55–69.

Dorazio, R.M. (2007) On the Choice of Statistical Models for Estimating Occurrence and Extinction from Animal Surveys. *Ecology*, **88**, 2773–2782.

Dorazio, R.M. & Royle, J.A. (2003) Mixture models for estimating the size of a closed population when capture rates vary among individuals. *Biometrics*, **59**, 351–64.

Dorazio, R.M. & Royle, J.A. (2005a) Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. *Journal of the American Statistical Association*, **100**, 389–398.

Dorazio, R.M. & Royle, J.A. (2005b) Estimating Size and Composition of Biological Communities by Modeling the Occurrence of Species. *Journal of the American Statistical Association*, **100**, 389–398.

Dorazio, R.M., Royle, J.A., Söderström, B. & Glimskär, A. (2006) Estimating Species Richness and Accumulation by Modeling Species Occurrence and Detectability. *Ecology*, **87**, 842–854.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, a. E. (2014) Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science*, **344**, 296–299.

Driscoll, D.A. & Henderson, M.K. (2008) How many common reptile species are fire specialists? A replicated natural experiment highlights the predictive weakness of a fire succession model. *Biological Conservation*, **141**, 460–471.

Driscoll, D.A., Smith, A.L., Blight, S. & Maindonald, J. (2012) Reptile responses to fire and the risk of post-disturbance sampling bias. *Biodiversity and Conservation*, **21**, 1607–1625.

East, K.T., East, M.R. & Daugherty, C.H. (1995) Ecological restoration and habitat relationships of reptiles on Stephens Island, New Zealand. *New Zealand Journal of Zoology*, **22**, 249–261.

Eccard, J.A., Walther, R.B. & Milton, S.J. (2000) How livestock grazing affects vegetation structures and small mammal distribution in the semi-arid Karoo. *Journal of Arid Environments*, **46**, 103–106.

Edwards, D. (1983) A broad-scale structural classification of vegetation for practical purposes. *Bothalia*, **14**, 705–712.

Ellis, M. V & Bedward, M. (2014) A simulation study to quantify drift fence configuration and spacing effects when sampling mobile animals. *Ecosphere*, **5**, 55.

Ellis, E.C., Klein Goldewijk, K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, no–no.

Enge, K.M. (2001) The Pitfalls of Pitfall Traps. *Journal of Herpetology*, **35**, 467–478.

Fabricius, C., Burger, M. & Hockey, P.A.R. (2003) Comparing biodiversity between protected areas and adjacent rangeland in xeric succulent thicket, South Africa: arthropods and reptiles. *Journal of Applied Ecology*, **40**, 392–403.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits Jr., W.J., van Buskirk, J. & McCollum, S.A. (1996) Simplifying the Jargon of Community Ecology: A Conceptual Approach. *The American Naturalist*, **147**, 282–286.

Fischer, J., Lindenmayer, D.B., Barry, S. & Flowers, E. (2005) Lizard distribution patterns in the Tumut fragmentation "Natural Experiment" in south-eastern Australia. *Biological Conservation*, **123**, 301–315.

Fischer, J., Lindenmayer, D.B. & Cowling, A. (2004) The challenge of managing multiple species at multiple scales: reptiles in an Australian grazing landscape. *Journal of Applied Ecology*, **41**, 32–44.

Ford, W.M., Menzel, M.A., Mcgill, D.W., Laerm, J. & Mccay, T.S. (1999) Effects of a community restoration fire on small mammals and herpetofauna in the southern Appalachians. *Forest Ecology and Management*, **114**, 233–243.

Galán, P. (1997) Colonization of spoil benches of an opencast lignite mine in northwest Spain by amphibians and reptiles. *Biological Conservation*, **79**, 187–195.

Gardner, S., Baard, E.H.W. & le Roux, N.J. (1999) Estimating the detection probability of the geometric tortoise. *South African Journal of Wildlife Research*, **29**, 62–71.

Gardner, T.A., Barlow, J. & Peres, C.A. (2007) Paradox, presumption and pitfalls in conservation biology: The importance of habitat change for amphibians and reptiles. *Biological Conservation*, **138**, 166–179.

Gaston, K.J. & Lawton, J.H. (1990) Effects of scale and habitat on the relationship between regional distribution and local abundance. *Oikos*, **58**, 329–335.

Gelfand, A.E., Schmidt, A.M., Wu, S., Silander, J. a., Latimer, A. & Rebelo, A.G. (2005) Modelling species diversity through species level hierarchical modelling. *Journal of the Royal Statistical Society: Series C (Applied Statistics)*, **54**, 1–20.

Gelman, A. & Rubin, D.B. (1992) Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science*, **7**, 457–472.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S. & Winne, C.T. (2000) The global decline of reptiles, deja-vu amphibians. *BioScience*, **50**, 653–666.

Gibbons, J.W. & Semlitsch, R.D. (1981) Terrestrial drift fences with pitfall traps: an effective technique for quantitative sampling of animal populations. *Brimleyana*, **7**, 1–16.

Goode, M.J., Swann, D.E. & Schwalbe, C.R. (2004) Effects of destructive collecting practices on reptiles: a field experiment. *The Journal of Wildlife Management*, **68**, 429–434.

Gormley, A.M., Forsyth, D.M., Griffioen, P., Lindeman, M., Ramsey, D.S.L., Scroggie, M.P. & Woodford, L. (2011) Using presence-only and presence-absence data to estimate the current and potential distributions of established invasive species. *The Journal of Applied Ecology*, **48**, 25–34.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Gotelli, N.J. & Colwell, R.K. (2011) Estimating species richness. *Frontiers in Measuring Biodiversity* (eds A.E. Magurran & B.J. McGill), pp. 39–54. Oxford University Press, NY.

Govender, N., Trollope, W.S.W. & Van Wilgen, B.W. (2006) The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology*, **43**, 748–758.

Greenberg, C.H. (2001) Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. *Forest Ecology and Management*, **148**, 135–144.

Greenberg, C.H., Neary, D.G. & Harris, L.D. (1994a) A Comparison of Herpetofaunal Sampling Effectiveness of Pitfall, Single-Ended, and Double-Ended Funnel Traps Used with Drift Fences. *Journal of Herpetology*, **28**, 319–324.

Greenberg, C.H., Neary, D.G. & Harris, L.D. (1994b) Effect of High-Intensity Wildfire and Silvicultural Treatments on Reptile Communities in Sand-Pine Scrub. *Conservation Biology*, **8**, 1047–1057.

Guisan, A. & Hofer, U. (2003) Predicting reptile distributions at the mesoscale: relation to climate and topography. *Journal of Biogeography*, **30**, 1233–1243.

Hailey, A. (2000) The effects of fire and mechanical habitat destruction on survival of the tortoise Testudo hermanni in northern Greece. *Biological Conservation*, **92**, 321–333.

Hanski, I. (1998) Metapopulation dynamics. *Nature*, **396**, 41–49.

Hobbs, T.J., Morton, S.R., Masters, P. & Jones, K.R. (1994) Influence of Pit-trap Design on Sampling of Reptiles in Arid Spinifex Grasslands. *Wildlife Research*, **21**, 483–490.

Hodgkison, S., Hero, J.-M. & Warnken, J. (2006) The efficacy of small-scale conservation efforts, as assessed on Australian golf courses. *Biological Conservation*, **136**, 576–586.

Hortal, J., Borges, P.A. V & Gaspar, C. (2006) Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology*, **75**, 274–287.

Hubálek, Z. (2000) Measures of species diversity in ecology: an evaluation. *Folia Zoologica*, **49**, 241–260.

Hudak, A.T., Fairbanks, D.H.K. & Brockett, B.H. (2004) Trends in fire patterns in a southern African savanna under alternative land use practices. *Agriculture, Ecosystems & Environment*, **101**, 307–325.

Hutchens, S.J. & DePerno, C.S. (2009) Efficacy of sampling techniques for determining species richness estimates of reptiles and amphibians. *Wildlife Biology*, **15**, 113–122.

Hutchinson, G.E. (1957) Concluding Remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

IGBST. (2012) Updating and Evaluating Approaches to Estimate Population Size and Sustainable Mortality Limits for Grizzly Bears in the Greater Yellowstone Ecosystem. , 66.

James, C.D. (2003) Response of vertebrates to fenceline contrasts in grazing intensity in semi-arid woodlands of eastern Australia. *Austral Ecology*, **28**, 137–151.

James, S.E. & M'Closkey, R.T. (2003) Lizard microhabitat and fire fuel management. *Biological Conservation*, **114**, 293–297.

Jobin, B., Belanger, L., Boutin, C. & Maisonneuve, C. (2004) Conservation value of agricultural riparian strips in the Boyer River watershed, Québec (Canada). *Agriculture, Ecosystems & Environment*, **103**, 413–423.

Jones, J.P.G. (2011) Monitoring species abundance and distribution at the landscape scale. *Journal of Applied Ecology*, **48**, 9–13.

Jones, B., Fox, S.F., Leslie Jr., D.M., Engle, D.M. & Lochmiller, R.L. (2000) Herpetofaunal responses to brush management with herbicide and fire. *Journal of Range Management*, **53**, 154–158.

Kanowski, J.J., Reis, T.M., Catterall, C.P. & Piper, S.D. (2006) Factors Affecting the Use of Reforested Sites by Reptiles in Cleared Rainforest Landscapes in Tropical and Subtropical Australia. *Restoration Ecology*, **14**, 67–76.

Kearney, M., Shine, R. & Porter, W.P. (2009) The potential for behavioral thermoregulation to buffer "' cold-blooded '" animals against climate warming. *Proceedings of the National Academy of Sciences*, **106**, 3835–3840.

Kéry, M. (2002) Inferring the Absence of a Species: A Case Study of Snakes. *Journal of Wildlife Management*, **66**, 330–338.

Kéry, M. (2010) *Introduction to WinBUGS for Ecologists*. Elsevier.

Kéry, M., Dorazio, R.M., Soldaat, L., van Strien, A., Zuiderwijk, A. & Royle, J.A. (2009a) Trend estimation in populations with imperfect detection. *Journal of Applied Ecology*, **46**, 1163–1172.

Kéry, M. & Royle, J.A. (2008) Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys. *Journal of Applied Ecology*, **45**, 589–598.

Kéry, M. & Royle, J.A. (2010) Hierarchical modelling and estimation of abundance and population trends in metapopulation designs. *The Journal of animal ecology*, **79**, 453–61.

Kéry, M., Royle, J.A., Plattner, M. & Dorazio, R.M. (2009b) Species richness and occupancy estimation in communities subject to temporary emigration. *Ecology*, **90**, 1279–1290.

Kéry, M., Royle, J.A. & Schmid, H. (2010) Modeling Avian Abundance from Replicated Counts Using Binomial Mixture Models. *Ecological Applications*, **15**, 1450–1461.

Kéry, M. & Schaub, M. (2011) *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*.

Kéry, M. & Schmid, H. (2004) Monitoring programs need to take into account imperfect species detectability. *Basic and Applied Ecology*, **5**, 65–73.

Kéry, M. & Schmidt, B.R. (2008) Imperfect detection and its consequences for monitoring for conservation. *Community Ecology*, **9**, 207–216.

Kjoss, V.A. & Litvaitis, J.A. (2008) Comparison of two methods to sample snake communities in early successional habitats. *Wildlife Society Bulletin*, **29**, 153–157.

Klein Goldewijk, K., Beusen, A., Van Drecht, G. & De Vos, M. (2011) The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Global Ecology and Biogeography*, **20**, 73–86.

Lehohla, P.J. (2008) *Statistical Release P0302: Mid-Year Population Estimates*.

Lehohla, P.J. (2012) *Statistical Release P0441: Gross Domestic Product.*

Letnic, M., Dickman, C.R., Tischler, M.K., Tamayo, B. & Beh, C.-L. (2004) The responses of small mammals and lizards to post-fire succession and rainfall in arid Australia. *Journal of Arid Environments*, **59**, 85–114.

Lillywhite, H.B. & North, F. (1974) Perching Behavior of Sceloporus occidentalis in Recently Burned Chaparral. *Copeia*, **1974**, 256–257.

Lindenmayer, D.B., Wood, J.T., MacGregor, C., Michael, D.R., Cunningham, R.B., Crane, M., Montague-Drake, R., Brown, D., Muntz, R. & Driscoll, D.A. (2008) How predictable are reptile responses to wildfire? *Oikos*, **117**, 1086–1097.

Link, W.A. (2003) Nonidentifiability of Population Size from Capture-Recapture Data with Heterogeneous Detection Probabilities. *Biometrics*, **59**, 1123–1130.

Longino, J.T., Coddington, J. & Colwell, R.K. (2009) The Ant Fauna of a Tropical Rain Forest: Estimating Species Richness Three Different Ways. *Ecology*, **83**, 689–702.

Luiselli, L. (2006) Testing hypotheses on the ecological patterns of rarity using a novel model of study: snake communities worldwide. *Web Ecology*, **6**, 44–58.

Lunn, D.J., Thomas, A., Best, N. & Spiegelhalter, D. (2000) WinBUGS – A Bayesian modelling framework: Concepts, structure, and extensibility. *Statistics and Computing*, **10**, 325–337.

Lunney, D., Eby, P. & O'Connell, M. (1991) Effects of logging, fire and drought on three species of lizards in Mumbulla State Forest on the south coast of New South Wales. *Austral Ecology*, **16**, 33–46.

Mackenzie, D.I. (2006) Modeling the Probability of Resource Use: The Effect of, and Dealing with, Detecting a Species Imperfectly. *Journal of Wildlife Management*, **70**, 367–374.

MacKenzie, D.I. & Kendall, W.L. (2002) How should detection probability be incorporated into estimates of relative abundance? *Ecology*, **83**, 2387–2393.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G. & Franklin, A.B. (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, **84**, 2200–2207.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A. & Langtimm, C.A. (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, **83**, 2248–2255.

Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L. & Hines, J.E. (2006) *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, San Diego, CA, USA.

Mackenzie, D.I. & Royle, J.A. (2005) Designing occupancy studies: general advice and allocating survey effort. *Journal of Applied Ecology*, **42**, 1105–1114.

Magurran, A.E. & Henderson, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature*, **422**, 714–716.

Maisonneuve, C. & Rioux, S. (2001) Importance of riparian habitats for small mammal and herpetofaunal communities in agricultural landscapes of southern Québec. *Agriculture, Ecosystems & Environment*, **83**, 165–175.

Mao, C.X. & Colwell, R.K. (2005) Estimation of species richness: mixture models, the role of rare species, and inferential challenges. *Ecology*, **86**, 1143–1153.

Mao, C.X., Colwell, R.K. & Chang, J. (2005) Estimating the Species Accumulation Curve Using Mixtures. , 433–441.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Maritz, B. (2011) *Ecology of the Namaqua Dwarf Adder, Bitis Schneideri.* University of the Witwatersrand.

Maritz, B. & Alexander, G.J. (2008) Breaking ground: quantitative ecology in South Africa. *African Journal of Herpetology*, **58**, 1–14.

Maritz, B., Masterson, G., Mackay, D. & Alexander, G. (2007) The effect of funnel trap type and size of pitfall trap on trap success : implications for ecological field studies. , **28**, 321–328.

Márquez-Ferrando, R., Pleguezuelos, J.M., Santos, X., Ontiveros, D. & Fernández-Cardenete, J.R. (2009) Recovering the Reptile Community after the Mine-Tailing Accident of Aznalcollar (Southwestern Spain). *Restoration Ecology*, **17**, 660–667.

Masterson, G.P.R., Maritz, B. & Alexander, G.J. (2008) Effect of fire history and vegetation structure on herpetofauna in a South African grassland. *Applied Herpetology*, **5**, 129–143.

Masterson, G.P.R., Maritz, B., Mackay, D. & Alexander, G.J. (2009) The impacts of past cultivation on the reptiles in a South African grassland. *African Journal of Herpetology*, **58**, 71–84.

Mazerolle, M.J., Bailey, L.L., Kendall, W.L., Royle, J.A., Converse, S.J. & Nichols, J.D. (2007) Making Great Leaps Forward: Accounting for Detectability in Herpetological Field Studies. *Journal of Herpetology*, **41**, 672–689.

McCarthy, M.A., Moore, J.L., Morris, W.K., Parris, K.M., Garrard, G.E., Vesk, P.A., Rumpff, L., Giljohann, K.M., Camac, J.S., Bau, S.S., Friend, T., Harrison, B. & Yue, B. (2013) The influence of abundance on detectability. *Oikos*, **122**, 717–726.

Meik, J.M., Jeo, R.M., Mendelson, J.R. & Jenks, K.E. (2002) Effects of bush encroachment on an assemblage of diurnal lizard species in central Namibia. , **106**, 29–36.

Metzger, K.L., Coughenour, M.B., Reich, R.M. & Boone, R.B. (2005) Effects of seasonal grazing on plant species diversity and vegetation structure in a semi-arid ecosystem. *Journal of Arid Environments*, **61**, 147–160.

Meyer, C.F.J., Aguiar, L.M.S., Aguirre, L.F., Baumgarten, J., Clarke, F.M., Cosson, J.-F., Villegas, S.E., Fahr, J., Faria, D., Furey, N., Henry, M., Hodgkison, R., Jenkins, R.K.B., Jung, K.G., Kingston, T., Kunz, T.H., Cristina MacSwiney Gonzalez, M., Moya, I., Patterson, B.D., Pons, J.-M., Racey, P. a., Rex, K., Sampaio, E.M., Solari, S., Stoner, K.E., Voigt, C.C., von Staden, D., Weise, C.D. & Kalko, E.K. V. (2011) Accounting for detectability improves estimates of species richness in tropical bat surveys. *Journal of Applied Ecology*, **48**, 777–787.

Michael, D.R., Cunningham, R.B. & Lindenmayer, D.B. (2008) A forgotten habitat? Granite inselbergs conserve reptile diversity in fragmented agricultural landscapes. *Journal of Applied Ecology*, **45**, 1742–1752.

Moseby, K.E. & Read, J.L. (2001) Factors affecting pitfall capture rates of small ground vertebrates in arid South Australia. II. Optimum pitfall trapping effort. *Wildlife Research*, **28**, 61–71.

Murtaugh, P.A. & Birkes, D.S. (2006) An empirical method for inferring species richness from samples. , 129–138.

Mushinsky, H.R. (1985) Fire and the Florida Sandhill Herpetofaunal Community: With Special Attention to Responses of Cnemidophorus sexlineatus. *Herpetologica*, **41**, 333–342.

Mushinsky, H.R. (1992) Natural History and Abundance of Southeastern Five-Lined Skinks, Eumeces inexpectatus, on a Periodically Burned Sandhill in Florida. *Herpetologica*, **48**, 307–312.

Nichols, O.G. & Nichols, F.M. (2003) Long-Term Trends in Faunal Recolonization After Bauxite Mining in the Jarrah Forest of Southwestern Australia. *Restoration Ecology*, **11**, 261–272.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, 3–135.

Parr, C.L. & Brockett, B.H. (1999) Patch-mosaic burning: a new paradigm for savanna fire management in protected areas? *Koedoe*, **42**, 117–130.

Parr, C.L. & Chown, S.L. (2003) Burning issues for conservation : A critique of faunal fire research in Southern Africa. *Austral Ecology*, **28**, 384–395.

Perrings, C. & Walker, B. (2004) Conservation in the optimal use of rangelands. *Ecological Economics*, **49**, 119–128.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *The American Naturalist*, **132**, 652–661.

Read, J.L. (1995) Subhabitat variability: A key to the high reptile diversity in chenopod shrublands. *Austral Ecology*, **20**, 494–501.

Read, J.L. (2002) Experimental trial of Australian arid zone reptiles as early warning indicators of overgrazing by cattle. *Austral Ecology*, **27**, 55–66.

Regan, H.M., Ben-Haim, Y., Langford, B., Wilson, W.G., Lundberg, P., Andelman, S.J. & Burgman, M.A. (2005) Robust decision-making under severe uncertainty for conservation management. *Ecological Applications*, **15**, 1471–1477.

Rey Benayas, J.M. & de la Montaña, E. (2003) Identifying areas of high-value vertebrate diversity for strengthening conservation. *Biological Conservation*, **114**, 357–370.

Rey Benayas, J.M., De La Montaña, E., Belliure, J. & Eekhout, X.R. (2006) Identifying areas of high herpetofauna diversity that are threatened by planned infrastructure projects in Spain. *Journal of Environmental Management*, **79**, 279–89.

Ribeiro, R., Santos, X., Sillero, N., Carretero, M.A. & Llorente, G.A. (2009) Biodiversity and Land uses at a regional scale: Is agriculture the biggest threat for reptile assemblages? *Acta Oecologica*, **35**, 327–334.

Row, J.R. & Blouin-Demers, G. (2006) Thermal quality influences habitat selection at multiple spatial scales in milksnakes. *Ecoscience*, **13**, 443–450.

Royle, J.A. (2008) Hierarchical modeling of cluster size in wildlife surveys. *Journal of Agricultural, Biological, and Environmental Statistics*, **13**, 23–36.

Royle, J.A. & Dorazio, R.M. (2006) Hierarchical Models of Animal Abundance and Occurrence. *Journal of Agricultural, Biological and Environmental Statistics*, **11**, 249–263.

Royle, J.A. & Dorazio, R.M. (2008) *Hierarchical Modeling and Inference in Ecology: The Analysis of Data From Populations, Metapopulations and Communities*, First Edit. Academic Press, London.

Royle, J.A., Dorazio, R.M. & Link, W.A. (2007) Analysis of Multinomial Models With Unknown Index Using Data Augmentation. *Journal of Computational and Graphical Statistics*, **16**, 67–85.

Royle, J.A. & Kéry, M. (2007) A Bayesian State-space Formulation of Dynamic Occupancy Models. *Ecology*, **88**, 1813–1823.

Royle, J.A., Kéry, M., Gautier, R., Schmid, H., Monographs, E. & Andrew, J. (2010) Hierarchical Spatial Models of Abundance and Occurrence from Imperfect Survey Data. *Ecological Monographs*, **77**, 465–481.

Royle, J.A. & Nichols, J.D. (2003) Estimating abundance from repeated presence-absence data or point counts. *Ecology*, **84**, 777–790.

Royle, J.A., Nichols, J.D. & Kéry, M. (2005) Modelling occurrence and abundance of species when detection is imperfect. *Oikos*, **2**, 353–359.

Russell, K.R., Guynn Jr., D.C. & Hanlin, H.G. (2002) Importance of small isolated wetlands for herpetofaunal diversity in managed, young growth forests in the Coastal Plain of South Carolina. *Forest Ecology and Management*, **163**, 43–59.

Sawadogo, L., Tiveau, D. & Nygård, R. (2005) Influence of selective tree cutting, livestock and prescribed fire on herbaceous biomass in the savannah woodlands of Burkina Faso, West Africa. *Agriculture, Ecosystems & Environment*, **105**, 335–345.

Schlaepfer, M.A., Hoover, C. & Dodd Jr, C.K. (2005) Challenges in Evaluating the Impact of the Trade in Amphibians and Reptiles on Wild Populations. *BioScience*, **55**, 256–264.

Shanas, U., Abu, Y., Alshamlih, M., Cnaani, J., Ucitel, D., Khoury, F., Mittler, S. & Nassar, K. (2006) Reptile diversity and rodent community structure across a political border. *Biological Conservation*, **132**, 292–299.

Smith, A.L., Bull, C.M. & Driscoll, D.A. (2013) Successional specialization in a reptile community cautions against widespread planned burning and complete fire suppression (ed C Dickman). *Journal of Applied Ecology*, **50**, 1178–1186.

Soberón, J., Jiménez, R., Golubov, J. & Koleff, P. (2007) Assessing completeness of biodiversity databases at different spatial scales. *Ecography*, **30**, 152–160.

Soberón, J. & Llorente, J. (1993) The Use of Species Accumulation Functions for the Prediction of Species Richness. *Conservation Biology*, **7**, 480–488.

Thompson, G. (2007) Usefulness of funnel traps in catching small reptiles and mammals, with comments on the effectiveness of the alternatives. *Wildlife Research*, **34**, 491–497.

Thompson, G.G. & Thompson, S.A. (2007a) Usefulness of funnel traps in catching small reptiles and mammals, with comments on the effectiveness of the alternatives. *Wildlife Research*, **34**, 491.

Thompson, G.G. & Thompson, S.A. (2007b) Using species accumulation curves to estimate trapping effort in fauna surveys and species richness. *Austral Ecology*, **32**, 564–569.

Thompson, G.G., Thompson, S.A., Withers, P.C. & Fraser, J. (2007) Determining adequate trapping effort and species richness using species accumulation curves for environmental impact assessments. *Austral Ecology*, **32**, 570–580.

Thompson, G.G. & Withers, P.C. (2003) Effect of species richness and relative abundance on the shape of the species accumulation curve. *Austral Ecology*, **28**, 355–360.

Thompson, G.G., Withers, P.C., Pianka, E.R. & Thompson, S.A. (2003) Assessing biodiversity with species accumulation curves; inventories of small reptiles by pit-trapping in Western Australia. *Austral Ecology*, **28**, 361–383.

Tilbury, C.R., Tolley, K.A. & Branch, W.R. (2006) A review of the systematics of the genus Bradypodion (Sauria: Chamaeleonidae), with the description of two new genera. *Zootaxa*, **38**, 23–38.

Tolley, K.A. & Burger, M. (2004) Distribution of *Bradypodion taeniabronchum* and other dwarf chameleons in the eastern Cape Floristic Region of South Africa. *African Journal of Herpetology*, **53**, 123–133.

Twigg, L.E. & Fox, B.J. (1991) Recolonization of regenerating open forest by terrestrial lizards following sand mining. *Australian Journal of Ecology*, **16**, 137–148.

Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003) The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, **72**, 888–897.

Urbina-Cardona, J.N., Olivares-Perez, M. & Reynoso, V.H. (2006) Herpetofauna diversity and microenvironment correlates across a pasture-edge-interior ecotone in tropical rainforest fragments in the Los Tuxtlas Biosphere Reserve of Veracruz, Mexico. *Biological Conservation*, **132**, 61–75.

Walther, B.A. & Martin, J.-L. (2001) Species richness estimation of bird communities: how to control for sampling effort ? *Ibis*, **143**, 413–419.

Walther, B.A. & Moore, J.L. (2005) The concepts of bias , precision and accuracy , and their use in testing the performance of species richness estimators , with a literature review of estimator performance. *Ecography*, **6**, 815–829.

Walther, B.A. & Morand, S. (1998) Comparative performance of species richness estimation methods. *Parasitology*, **116**, 395–405.

Watling, J. & Donnelly, M. (2008) Species richness and composition of amphibians and reptiles in a fragmented forest landscape in northeastern Bolivia. *Basic and Applied Ecology*, **9**, 523–532.

Webb, G.A. (1999) Effectiveness of pitfallldrift-fence systems for sampling small ground-dwelling lizards and frogs in southeastern Australian forests. *Australian Zoologist*, **31**, 118–126.

Webb, J.K., Shine, R. & Pringle, R.M. (2005) Canopy Removal Restores Habitat Quality for an Endangered Snake in a Fire Suppressed Landscape. *Copeia*, 894–900.

Webb, J.K. & Whiting, M.J. (2005) Why don't small snakes bask? Juvenile broad-headed snakes trade thermal benefits for safety. *Oikos*, **3**, 515–522.

Welsh, A.H., Lindenmayer, D.B. & Donnelly, C.F. (2013) Fitting and interpreting occupancy models. *PloS one*, **8**, e52015.

Whiting, M.J. & Alexander, G.J. (2001) Oil spills and glue: a comment on a sticky sampling problem for lizards. *Herpetological Review*, **32**, 78–79.

Whittington-Jones, C., West, S., Matabane, A., Koko, R., Molaba, W., Motsamai, J., Makola, J., Mphuti, A. & Ndzhukula, S. (2008) *The Herpetofauna of Gauteng Volume 1: Distribution and Status of Reptiles*.

Van Wilgen, N.J., Wilson, J.R.U., Elith, J., Wintle, B. a. & Richardson, D.M. (2010) Alien invaders and reptile traders: what drives the live animal trade in South Africa? *Animal Conservation*, **13**, 24–32.

Wilgers, D.J. & Horne, E.A. (2006) Effects of Different Burn Regimes on Tallgrass Prairie Herpetofaunal Species Diversity and Community Composition in the Flint Hills, Kansas. *Journal of Herpetology*, **40**, 73–84.

Woinarski, J.C.Z. & Ash, A.J. (2002) Responses of vertebrates to pastoralism, military land use and landscape position in an Australian tropical savanna. *Austral Ecology*, **27**, 311–323.

Woinarski, J.C.Z., Risler, J. & Kean, L. (2004) Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology*, **29**, 156–176.

Yamaura, Y., Royle, J.A., Kuboi, K., Tada, T., Ikeno, S. & Makino, S. (2011) Modelling community dynamics based on species-level abundance models from detection/nondetection data. *Journal of Applied Ecology*, **48**, 67–75.

Appendix 1

```
# Estimation of Chao2 species richness in Chapter 3
# By Gavin Masterson

load("....") # detection data
siteS <- vector("numeric",length=13)
siteFreq <- array(0,dim=c(13,51))
samples <- c(104, 104, 104, 77, 77, 77, 104, 104, 104, 104, 104, 104, 104)

# The number of species per (summed) incidence frequency class
allSiteFreq <-
c(7,4,2,0,2,1,0,0,0,0,0,1,0,0,0,0,0,1,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,1,1)
siteFreq[13,] <- allSiteFreq

# Generate SiteFreq array
for(j in 1:12){
 for(i in 1:20){
  ifelse(specc.site[i,j]==0,i<-i+1,(siteFreq[j,specc.site[i,j]]<-siteFreq[j,specc.site[i,j]]+1))
  }
 }

# Generate siteS vector i.e. the number of species detected at each site
for(j in 1:13){
 siteS[j]<-sum(siteFreq[j,])
 }

# Parameters estimated by Chao2
S0 <- vector("numeric", length=13) # estimated number of species not detected during sampling
varS <- vector("numeric", length=13) # variances for the estimates of S0
CIChao2<-array(NA, dim=c(13,2)); colnames(CIChao2)<-c("lower","upper")  # array for CI's for each site
SChao2

# Calculate S0, varS and CIChao2
for(i in 1:13){
 q1<-siteFreq[i,1]
 q2<-siteFreq[i,2]
 ifelse(q2>0,
   S0[i]<-((samples[i]-1)/samples[i])*((q1^2)/(2*q2)), # Equation 3 - appendix B, EstimateS user guide
(bias-corrected as shown in Colwell et al. 2012)
   S0[i]<-((samples[i]-1)/samples[i])*(q1*(q1-1)/(2*(q2+1))) # Equation 4 - appendix B, EstimateS user
guide
      )
 ifelse(q2>0,
     varS[i]<-(
      ((samples[i]-1)/samples[i])*((q1*(q1-1))/(2*(q2+1))) +
```

```
        (((samples[i]-1)/samples[i])^2)*(((q1*((2*q1)-1)^2))/((4*(q2+1)^2))) +
          (((samples[i]-1)/samples[i])^2)*(((q1^2)*q2*((q1-1)^2))/(4*(q2+1)^4))
      ),  # Equation 10 - appendix B, EstimateS user guide
    varS[i]<-(
      ((samples[i]-1)/samples[i])*((q1*(q1-1))/2) +
        (((samples[i]-1)/samples[i])^2)*(((q1*((2*q1)-1)^2))/4) -
          (((samples[i]-1)/samples[i])^2)*((q1^4)/(4*S0[i]))
        )   # Equation 11 - appendix B, EstimateS user guide
    )

  Tau <- S0[i]
  K <- exp(1.96*(sqrt(log(1+(varS[i]/(Tau^2))))))
  CIChao2[i,1]<-siteS[i]+(Tau/K)
  CIChao2[i,2]<-siteS[i]+(Tau*K)

  }

SChao2 <- siteS+S0
cbind(siteS,SChao2,varS,CIChao2)
```

Appendix 2

```
# Model specification for Chapter 3 analysis
# Acknowledgements: Marc Kéry
# Indexing parameter M = The number of species in the augmented reptile assemblage

model {

   # Prior distributions and parameter transformations
   omega ~ dunif(0,1)
   p0 ~ dunif(0,1)
   psi0 ~ dunif(0,1)
   sigmap ~ dunif(0,10)
   sigmapsi ~ dunif(0,10)
   rho ~ dunif(-1,1)

   taup <- (1/(sigmap*sigmap))
   taupsi <- (1/(sigmapsi*sigmapsi))
   mup <- log(p0/(1-p0))
   mupsi <- log(psi0/(1-psi0))
   var.eta <- taup/(1.-pow(rho,2))

   # Likelihood
   for(i in 1:M){                              # Process model
           w[i] ~ dbin(omega,1)
          lpsi[i] ~ dnorm(mupsi,taupsi) I(-16,16)
          mu.lp[i] <- mup +(rho*sigmap/sigmapsi)*(lpsi[i]-mupsi)
          lp[i] ~ dnorm(mu.lp[i], var.eta) I(-16,16)
                   for(j in 1:nsites){
                           z[i,j] ~ dbern(mu.psi[i,j])
                           mu.psi[i,j] <- psi[i,j]*w[i]
                          psi[i,j] <- 1/(1+exp(-lpsi[i]))       # Avoid WinBUGS logit function
                   }
          }

   # Observation model
   for(i in 1:M){
          for (j in 1:nsites) {
                   # The observed, augmented data array
                   y[i,j] ~ dbin(mu2[i,j], samples[j])
                   mu2[i,j] <- z[i,j]*mu[i,j]
                   mu[i,j] <- 1/(1+exp(-lp[i]))
                   }
          }

   # Species-richness N as a derived parameter
```

```
   for(j in 1:nsites){
          Nsite[j] <- sum(z[1:M,j])
          }
   n0<-sum(w[(nspecies+1):M])
   Ntotal<-nspecies+n0

}
```