DYNAMICS OF GRAND SKINK (Oligosoma grande, Gray 1945) METAPOPULATIONS IN INDIGENOUS TUSSOCK GRASSLANDS AND EXOTIC PASTURE GRASSLANDS IN SOUTHERN NEW ZEALAND

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A major threat to biodiversity worldwide is human land-use change which increases habitat fragmentation and reduces landscape connectivity leading to species extinctions. For conservation biologists it is essential to understand the underlying factors that influence the population dynamics of species occurring in fragmented and isolated habitat. In this thesis, I investigate the impact of land-use change on the metapopulation dynamics of the endangered New Zealand grand skink (*Oligosoma grande*) which inhabits schist-rock outcrops scattered through indigenous tussock grasslands and exotic pasture grasslands in central South Island, New Zealand. In particular, I explore the influence of habitat patch characteristics and the type of surrounding grassland type (matrix) on the metapopulation dynamics of the grand skinks by using a spatially explicit metapopulation simulation model.

To develop a spatially explicit simulation model distinct habitat patches have to be defined. Therefore, I attached VHF-radio transmitters to 57 grand skinks to estimate their habitat use and movements. Individual grand skinks inhabited predominantly a single rock-outcrop. However, home ranges were smaller when the matrix surrounding the outcrop was pasture grasslands, and the rare between-outcrop movements were mostly recorded when the matrix was dominated by tussock grasslands. Therefore, individual rock-outcrops were considered habitat patches in the metapopulation models.

I also investigated if land-use change impacted on the body condition of grand skinks using a long-term data-set. Especially in autumn, grand skinks on outcrops in pasture grasslands had a better body condition compared to grand skink inhabiting outcrops in tussock grasslands. However, the probability of being pregnant was lower for grand skinks inhabiting rock-outcrops in the pasture matrix than for grand skinks on outcrops in the tussock matrix. Lower pregnancy probabilities could directly affect grand skink population dynamics.

At the population-level the analysis of a 3-year data-set of grand skink occupancy of rock-outcrops in both matrix grassland types using methods to account for incomplete detectability of the grand skinks, revealed that habitat patch quality
(outcrop structure and vegetation cover on the outcrop), habitat patch size and matrix grassland type strongly influenced colonisation and extinction probabilities. Grand skink populations on rock-outcrops surrounded by a matrix of pasture grasslands had higher probability of extinction and, once extinct, a lower probability of being re-colonised. Simulating the occupancy of outcrops on a landscape scale showed that grand skink populations in pasture grasslands are likely to go extinct while tussock grassland populations were stable or even increasing. Using the simulation model to investigate which outcrop in an un-inhabited landscape provides the most appropriate translocation site, revealed that rock-outcrop density was the most important factor for grand skinks, not outcrop quality.

This study showed that indirect and direct effects from the matrix surrounding the habitat patches can have strong influence on metapopulation dynamics. For successful conservation management, these effects need to be taken into consideration in the design of conservation strategies. I demonstrated how simulation models can be used to decide on appropriate translocation sites for grand skinks. Using species-specific information, and integrating habitat-patch and landscape attributes, metapopulation simulations can be useful tools in conservation research.
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CHAPTER ONE

Introduction

Landscape at Macraes Flat, New Zealand. Schist-rock outcrops surrounded by tussock grasslands in the foreground, and pasture grasslands in the background.
Chapter one: Introduction

Habitat fragmentation and extinctions

The destruction and modification of natural landscapes by humans is one of the greatest threats to biodiversity worldwide (Tilman et al. 2001, Travis 2003, Foley 2005) with one-third to one-half of all terrestrial ecosystems altered to varying degrees by human use (Vitousek et al. 1997). It is estimated that by 2050 agricultural land alone will have increased by a further 18%, driven by the demand from an increasing human population (Tilman et al. 2001). The modification of natural landscapes leads to species extinctions in two ways: firstly through the direct impact of converting the landscape, killing organisms in the process and reducing the available habitat; and secondly by creating isolated patches of natural habitat with small populations in an otherwise uninhabitable landscape (termed “matrix”, Fahrig 1997, 2003). Additionally, with continuing development the number and size of these natural habitat fragments become increasingly smaller and more isolated (Donald and Evans 2006). The fragmentation of natural habitat affects ecosystem structure and function, and can cause species extinctions (Foley 2005).

The complex interactions between matrix properties and habitat fragment properties (size, shape, number and spatial distribution), with biodiversity, population size and extinction risk, have been the focus of research for many decades (Saunders et al. 1991, Dunning et al. 1992). Habitat destruction directly contributes to significant decreases in wildlife population sizes (Fahrig 2003). However, rapid habitat loss and high levels of fragmentation can result in delayed future extinctions of species which occur without additional habitat degradation, generations after the original habitat fragmentation occurred. The time between disturbance of the ecosystem and extinction of the species or, when looking at ecological communities, the time until the establishment of a new equilibrium of species has been termed “relaxation time” (Diamond 1972, Saunders et al. 1991). Additionally, the term “extinction debt” (Tilman et al. 1994) was introduced to describe the proportion of species in ecological communities, or, in the single species context, the proportion of populations that becomes eventually extinct (Kuussaari et al. 2009). For example,
Bulman et al. (2007) found such an “extinction debt” in several extant metapopulations of the marsh fritillary butterfly (*Euphydryas aurinia*) which were estimated to go extinct in the range from 15 to 126 years. The extinction debt of a species increases with its longevity, and the reduction of size and connectivity of the remnant populations (Tilman et al. 1994, Malanson 2008, Krauss et al. 2010).

Because the size and quality of habitat fragments determines the availability of resources, such as food and shelter, the population size of any species inhabiting the habitat fragment is similarly constrained (Saunders et al. 1991, Hanski 1994). Smaller populations experience an increased risk of extinction because of the natural fluctuations of demographic and environmental factors, whereas larger populations can better withstand demographic accidents or catastrophic events (Pimm et al. 1988). Furthermore, small populations experience increased extinction risk through the Allee effect (Allee 1931) whereby with low numbers of individuals and/or decreasing population densities, per capita productivity and therefore population growth dramatically declines (Courchamp et al. 1999). The Allee effect is caused by genetic inbreeding, demographic stochasticity and/or decreasing cooperative interactions such as finding mates for reproductions (Courchamp et al. 1999).

For specialised species, the remaining area of undisturbed habitat may be even smaller than the size of the habitat fragment. The fragment edge may not provide suitable conditions thus restricting the species to the core of the fragment, a phenomenon labelled the “edge effect” (Wilcove 1985, Bender et al. 1998, Ewers and Didham 2007). How far the edge effect penetrates into the habitat fragment often is species-specific, and the strength of the edge effect depends on the size and shape of the habitat patch and the characteristics of the surrounding matrix (Laurance and Yensen 1991, Saunders et al. 1991, Ries et al. 2004). A fragment’s edge habitat may experience different microclimatic conditions and allow matrix species to penetrate the habitat fragment, increasing competition and predation (Fischer and Lindenmayer 2007, Laurance 2008). For example, Wilcove (1985) demonstrated this edge effect on forest birds in woodland patches, recording higher
rates of nest-predation along forest edges compared to core areas of woodland patches. However, habitat edges are not always detrimental and in some cases they can increase biodiversity and provide habitat for species preferring edge conditions (Bender et al. 1998).

Populations of species inhabiting habitat fragments may be connected through dispersing individuals. The ability of animals to move between fragments depends on their physical ability and their propensity to move from their current location, the suitability of the landscape to be traversed, and the distance between habitat fragments (Fischer and Lindenmayer 2007). Although some species occur naturally in fragmented habitat, changes in matrix quality can have profound effects on their dispersal ability (Fahrig 2001, Ricketts 2001). Dispersal of individuals through the matrix enables the colonisation of empty habitat fragments and the reduction of the extinction risk through dispersers settling into already occupied habitat fragments, an occurrence named the rescue effect (Brown and Kodric-Brown 1977, Gotelli 1991). Through immigrating individuals existing populations in habitat patches are enhanced in size and genetic diversity, which in turn leads to reduced extinction rates (Brown and Kodric-Brown 1977). Habitat fragments of low habitat quality where mortality exceeds population growth can be inhabited by large proportion of a species population (sink populations) when these populations are maintained by immigrants coming from high quality habitat fragments (source populations). The proportion of the population able to exist in sink habitat depends on the reproductive success of source and sink populations (Pulliam 1988). The degree of movement of individuals between habitat fragments can be used to classify the populations along a gradient from patchy populations (high migration rate) to classic metapopulations (low migration rate, Harrison 1991). Patchy populations occupy all available habitat fragments in the landscapes and individuals regularly move between them (Driscoll 2007), whereas in classic metapopulations only a proportion of the available habitat fragments is occupied and each population has a probability of becoming extinct. Unoccupied habitat patches can be recolonised by migrating individuals.
Modelling fragmented populations

The first concept recognising the influence of isolation and habitat size on the probability of species occurrence and persistence, and acknowledging turnover processes of colonisation and extinction, was Island Biogeography Theory (IBT) formulated when MacArthur and Wilson (1967) investigated the variation in the number of inhabiting species on islands compared to the mainland. The IBT states that the number of species on an island increases with the size of the island and decreases with its distance to the mainland. Furthermore, individual species on the islands can become extinct with a probability that decreases with increasing island size, or islands where a species was originally absent can be colonised by migrants from the mainland (MacArthur and Wilson 1967). Similarly, in fragmented landscapes where one or several very large habitat fragments provide the migrating individuals to colonise smaller surrounding habitat fragments, species can also occur in form of mainland-island populations (e.g., Harrison et al. 1988, MacPherson and Bright 2011). Populations in small habitat fragments have high extinction probabilities because they are vulnerable to stochasticity, while the large populations in the mainland-fragments persist. In mainland-island populations migration predominantly occurs from the mainland population to the island populations.

Richard Levins (1969) coined the term metapopulation, defined as a population of populations that occurs in discrete habitat patches within a landscape that is unsuitable to support the species. Levins (1969) developed his metapopulation model when working on strategies of biological pest control in an agricultural landscape with scattered habitat (fields of focal crop species). In the metapopulation model, local populations experienced independent population dynamics and potentially went extinct, however, empty habitat patches became colonised by migrating individuals from other populations (Levins 1969). In the late 1980s, twenty years after Levins’ research, conservation biologists applied the metapopulation concept to species in fragmented habitats (Hanski and Gilpin 1991). Hanski (1991) developed a spatially explicit metapopulation model which adjusted
extinction and colonisation probabilities according to habitat patch size and distance to occupied habitat patches, respectively, and additionally included the rescue effect (Brown and Kodric-Brown 1977) by adjusting extinction probabilities according to the number of occupied habitat patches. Further research led to the development of individual-based metapopulation models that followed the fate of individuals in each local population (e.g., Akcakaya 2000, Franklin 2010). To better understand the effects of fragmentation on species, the influence of habitat patch size (Hill et al. 1996), isolation of habitat patches (Moilanen et al. 1998, Moilanen 1999) and habitat patch quality (Dennis and Eales 1997, Thomas et al. 2001) on the metapopulation parameters have been a focus in conservation biology.

Although dispersal through the matrix is a key process of metapopulation dynamics by directly influencing colonisation and extinction probabilities, many metapopulation studies classify the matrix as homogeneous landscape and the isolation (or connectivity) measures are based on habitat patch characteristics rather than matrix attributes or species-specific behaviour (Tischendorf and Fahrig 2000, Moilanen and Hanski 2001, Baguette and Dyck 2007). On the other hand, landscape ecology and dispersal behaviour research have a long history of measuring the heterogeneity of the landscape to estimate dispersal routes, speeds and distances of species (Tischendorf and Fahrig 2000). Taylor et al. (1993) defined landscape connectivity as “the degree to which the landscape facilitates or impedes movements among resource patches”. Landscape elements such as smaller habitat patches suitable as stepping stones, or habitat corridors define the structural connectivity of a landscape (Beier and Noss 1998, Tischendorf and Fahrig 2000, Donald and Evans 2006). However, not always do corridors or stepping stones increase movements of animals between habitat patches. Potential dangers of connecting fragmented habitat such as spread of diseases, invasion of exotic species or settling of animals in areas with high mortality have been pointed out (Hobbs and Huenneke 1992, Simberloff et al. 1992). Furthermore, some species also migrate through types of matrix which reduces the need of structural connectivity (Ricketts 2001, Carroll et al. 2004, Donald and Evans 2006). Functional connectivity is influenced by how animal move through the landscape which is often positively
correlated with the structural connectivity of a landscape. However, functional connectivity is species-specific, linking information on animal movements in different landscape types with the composition of the landscape (Belisle 2005, Fahrig 2007, Kadoya 2009, Doerr et al. 2011). Despite the repeated call to integrate functional connectivity into metapopulation models and therefore connecting metapopulation research with landscape ecology and dispersal behaviour research (Hanski and Gilpin 1991, Tischendorf and Fahrig 2000, Baguette and Dyck 2007) only recently studies emerged which accounted for heterogeneity of the matrix (Ricketts 2001, Jepsen et al. 2005, Vögeli et al. 2010).

No consensus has been reached on the degree of importance of habitat patch quality, habitat patch size, isolation or matrix characteristics on metapopulation dynamics and persistence (eg., Hodgson et al. 2009, Doerr et al. 2011, Hodgson et al. 2011). Because habitat is a species-specific concept, the parameters influencing metapopulation dynamics will differ between species. Therefore, successful conservation management must be based on a species-specific foundation of scientific knowledge.

The grand skink (*Oligosoma grande*) as a model system

The aim of this thesis is to investigate how changes in the matrix landscape surrounding habitat patches affects species which occur naturally in metapopulations, using the threatened New Zealand grand skink (*Oligosoma grande*) as a model system. Grand skinks inhabit schist rock outcrops surrounded by indigenous tussock grasslands and exotic pasture grasslands, resembling a classic metapopulation. Historically, the grand skink occurred throughout most of the Otago region in South Island, New Zealand; however, today it occupies only 8% of its historic range (Whitaker and Loh 1995). Large parts of the indigenous tussock grassland have been converted into pasture grasslands by burning, ploughing, fertilizing and oversowing (Whitaker 1996). Additionally, grazing by introduced herbivores, such as domestic stock and the European rabbit (*Oryctolagus*
cuniculus), has contributed to the degradation of existing tussock grasslands (Whitaker 1996). Along with the modification of the tussock grasslands, the introduction of mammalian predators has been identified as a major threat to the grand skink. At Macraes Flat (45°28’S, 170°28’ E) the New Zealand Department of Conservation has been monitoring grand skink populations for over two decades and has put in place a large-scale predator control programme to ensure the persistence of the species (Reardon et al. 2012). Although a number of research projects have been conducted on the grand skink, much of their large-scale population dynamics, essential to making informed management decisions, remains unknown. In this thesis, I construct a spatially explicit metapopulation model for grand skink metapopulations, and investigate how the model can aid decision making by conservation managers to ensure the persistence of this critically endangered species. In order to develop the model it is important to understand the habitat use by grand skinks. I obtained and analysed information on grand skink body condition, and on the home range size and daily movements of grand skinks inhabiting outcrops in indigenous tussock and exotic pasture grasslands. I used occupancy modelling to derive colonisation and extinction probabilities taking patch-specific characteristics and incomplete detectability of grand skinks into consideration. I then applied these patch-specific vital rates in spatially explicit metapopulation models to investigate the possible long-term impacts of land-use change on grand skink demographics.

Thesis structure

To facilitate future publication the thesis consists of a series of chapters, hence some degree of repetition may occur but was minimised where possible by cross-referencing previous chapters. The main objectives of the chapters are as follows.

To model grand skink populations as metapopulations discrete habitat patches have to be defined. The Chapter 2 presents the analysis of data on the home range size and daily movements of grand skinks in spring, summer and autumn. It provides an
insight into the habitat use of grand skinks as well as indications of differences in the population dynamics between populations in tussock grassland and in pasture grasslands. I aimed to address following questions: Do home range sizes differ between (1) grand skinks on outcrops in tussock grasslands and pasture grasslands, (2) sexes and (3) seasons? (4) Does movement length and frequency differ between grand skinks on outcrops in tussock grasslands and pasture grasslands, (5) between sexes, and (6) between seasons?

In Chapter 3, I analyse factors influencing the body condition of grand skink populations in tussock and pasture grasslands because population parameters such as survival and reproduction are dependent on the individual’s body condition. By using a long-term dataset and mixed effects model analysis differences in grand skink body condition between (1) grasslands types can be investigated, as well as changes in body condition (2) over time, (3) between sexes, (4) mature and immature individuals and (5) between seasons. The chapter provides an indication of the influence of tussock grassland conversion into pasture grasslands on the body condition of grand skinks.

In Chapter 4, I use presence-absence data to estimate the extinction and colonisation probabilities of habitat patches in pasture and tussock grassland grand skink metapopulations. I incorporate habitat patch characteristics to obtain habitat patch specific extinction and colonisation probabilities and account for the incomplete detectability of grand skinks during presence-absence surveys. I investigate which patch attributes affects colonisation and extinction probabilities, and how the matrix type influences these two parameters.

In Chapter 5, I utilize the estimated metapopulation parameters from Chapter 4 to develop a spatially explicit metapopulation simulation model for the grand skinks. The model is used to investigate the influence of deviations of colonisation and extinction probabilities from the estimated values and various distances of maximum grand skink dispersal. Furthermore, I demonstrate the application of the
simulation model to answer questions concerning conservation management of grand skinks particularly how to determine an appropriate translocation site.

The findings of the thesis are summarized in Chapter 6. Here I also provide recommendation for future research and the conservation of the grand skink.
CHAPTER TWO

Home range size and movements of grand skinks

Locating grand skinks (*Oligosoma grande*) fitted with VHF radio transmitters.
INTRODUCTION

The patterning of animal behaviour in a landscape is seldom random: their spatial distribution is dependent on the availability of food, mates, shelter, nesting sites and intra- and inter-specific interactions. Burt (1943) defined the area that an animal uses for foraging, shelter and reproduction as the animal’s home range (Burt 1943). It is ‘an area repeatedly traversed by an animal’ and therefore different from unidirectional dispersal excursions (Kenward 2001). The size and shape of home ranges and the pattern of utilisation of space are important factors when addressing questions of ecology, behaviour and conservation of species. For threatened and endangered species conservation, biologists investigate how fragmentation, reduction and destruction of habitat through anthropogenic processes influence the use of habitat and movements within and between habitat patches by animals (Dunning et al. 1992). The attributes of home ranges are affected by a range of parameters, most importantly the animal’s sex, age, reproductive status and the spatial and temporal distribution of resources (Harris et al. 1990, Laver et al. 2008). In addition, the sampling period and sampling method used to identify an animal’s location can significantly affect detection, tracking and resulting behavioural description (Harris et al. 1990). Therefore Kernohan et al. (2001) suggested that the home range definition should be extended to include a temporal component so that the home range is ‘the extent of an area with a defined probability of occurrence of an animal during a specific time period.’

The decision by an animal to undertake a certain behaviour including movements through an environment is made by balancing costs and benefits for the animal (Lima and Dill 1990), and any decision to move or not to move will influence the home range used. For lizards, the need to thermoregulate to achieve optimal body temperatures has a strong influence on the decision process (Huey and Slatkin 1976). Costs of movements for lizards include risk of predation, and the loss of access to mates, shelter or food, especially in territorial species. Benefits for lizards include finding more optimal places for thermoregulation, with higher food availability, and access to mates and shelter. Studies on home ranges in lizards have
looked at the various factors influencing size, shape, overlap and utilisation of home ranges. In their review of 60 species of lizards, Perry and Garland (2002) found that male lizards had consistently larger home ranges than female lizards, which they presumed was related to access to females in the predominantly polygamous mating systems of lizards. During the breeding season, increased movements by male lizards looking for females have been found to result in larger home ranges and distances travelled in some species (Rose 1982, Thompson et al. 1999, Perry and Garland Jr. 2002, Wone and Beauchamp 2003, Stark et al. 2005, Kerr and Bull 2006). However, no home range size differences between sexes were found for the earless dragon (Tympanocryptis pinguicolla, Stevens et al. 2010) or the sleepy lizard (Tiliqua rugosa) which has been found to be socially monogamous (Bull et al. 1998, Bull and Freake 1999). Further, changes in home range sizes were related to seasonal changes in lizard behaviour caused by differences in food availability and temperatures between seasons (Avery and Bond 1989, Pinch and Claussen 2003, Stevens et al. 2010). Additionally, differences in activity levels during the day because of changes in temperature have been recorded (Irwin 1965). Changes in the natural environment, such as grazing and fragmentation of habitats, have been shown to influence lizard behaviour and even morphology (Sumner et al. 2001, Wasiolka et al. 2009a, Wasiolka et al. 2009b). Furthermore, the presence of predators in the environment leads to behavioural adaptations in many animal species (Lima and Dill 1990). In environments with increased predation risk lizards have been found to reduce movement duration and even change their diet composition (Eifler et al. 2007, Hawlena and Perez-Mellado 2009).

The threatened grand skink (Oligosoma grande) is one of New Zealands largest lizard species that reaches a snout-vent length (SVL) of up to 113 mm (Cree 1994, Tocher 2003), and individuals known to be 19 years of age live in the wild (N. Whitmore, Department of Conservation, New Zealand, pers. comm., 2012). It has been estimated that the current range of this species only encompasses 8% of their historic occurrence (Whitaker and Loh 1995). Introduced mammalian predators and the conversion of indigenous tussock grasslands into pasture have been identified as the biggest threats to grand skinks. The New Zealand Department of Conservation
(DoC) has been monitoring grand skinks for over two decades, and has established a captive breeding programme and large scale predator control and monitoring programme to ensure the species survival (Reardon et al. 2012).

The omnivorous grand skink inhabits schist-rock outcrops both in indigenous tussock and exotic pasture grasslands and uses crevices in the rock outcrops as retreats. Remnant, predominantly native vegetation on outcrops provides shelter, food in the form of plant fruits, and serves to attract invertebrates (Tocher 2003). Occasionally, grand skinks have been reported in vegetation surrounding rock outcrops (Murphy 1994, Eifler and Eifler 1999a, Marshall 2000) but no information is available on the extent of the use of vegetation surrounding rock outcrops.

Murphy (1994), in her study of grand skink home ranges in tussock and pasture grasslands, reported that home ranges were mostly delimited by rock-outcrop size. Similarly, core areas of activity were located only on rock areas in a study by Marshall (2000). Home range size did not differ between tussock and pasture grasslands (Murphy 1994, Whitaker 1996, Houghton 2000), but male grand skinks had larger home ranges than females (Murphy 1994, Coddington and Cree 1997, Marshall 2000). Until now there have been no studies investigating seasonal differences in movements and home range size of grand skinks. Seasonal analysis was not possible in the study conducted by Marshall (2000) because of lack of data. However, Murphy (1994) suggested that home ranges in other seasons (outside the mating season) could be different in size. Furthermore, Eifler and Eifler (1999b) reported differences in grand skink home range size between sexes when natural invertebrate prey availability was artificially increased, while they found no differences between sexes when not influencing the invertebrate abundances. The diet composition of grand skinks changes between seasons from predominantly invertebrates in spring and summer to high proportions of fruit in autumn (Tocher 2003) which could result in changes of home range size.

Although previous studies on grand skinks have investigated both home range sizes and movement distances, small sample sizes and a lack of comparable studies in
different seasons or habitat types still prevent conservation biologists from developing a clear picture of daily movements and activity, and robust home ranges sizes and their potential change between seasons. Additionally, all previous studies used mark-resight/recapture techniques to identify the location of grand skinks. In these studies, grand skinks were observed using binoculars to find the skinks on the rock-outcrops. Dense vegetation on and around outcrops and the complex structure of the rock-outcrops themselves limits observations of grand skinks by eye and leads to location data biased towards skinks on rock-outcrops which in turn could lead to false identification of habitat use and home range size (Weatherhead and Charland 1985, Griffiths and Christian 1996). Therefore, extensive and unbiased locations of grand skinks were collected through the use of radio-telemetry to allow for realistic and accurate home range estimates in this study, which had two main aims: Firstly, to investigate if home ranges differed between (a) grand skinks inhabiting outcrops in pasture grassland and tussock grasslands, (b) female and male grand skinks, (c) outcrops of different size, and (d) seasons. Secondly, to investigate if grand skink activity differed between (a) habitat types, (b) sexes, (c) in accordance with the time of the day, (d) the size of the rock-tor, (e) the temperature and (f) the season.

METHODS

Study location

The research was conducted near the township of Macraes Flat, New Zealand (45° 28’ S, 170° 28’ E; Fig. 2.1). The ‘Redbank’ study site consisted of indigenous tussock grasslands protected by the New Zealand Department of Conservation and private farmland consisting predominantly of exotic pasture grasslands used for sheep and cattle grazing. The tussock grasslands are dominated by narrow-leaved snow tussock (Chionochloa rigida) and red tussock (C. rubra) which grow up to 1.5 m high, while the exotic pasture grasslands are dominated by rye grass (Lolium
perenne) and white clover (*Trifolium repens*) which are grazed to less than 5 cm high.

The schist rock-outcrops that grand skinks inhabit in both grassland types vary in shape and structure from monolithic outcrops to clusters of outcrops. A definition for the delineation of a rock-outcrop (termed ‘Rock’ in this chapter) is all rock-outcrops which are separated by less than 10 m of grasslands, as suggested by Whitaker (1996) and used by the Department of Conservation for monitoring purposes at the study site, and in all studies subsequent to Whitaker (1996).

**Figure 2.1:** ‘Redbank’ study site. Study areas are visualised by dashed lines: spring (I), summer (II) and autumn (III), in indigenous tussock grasslands (a) and exotic pasture grasslands (b). Black filled polygons are outlines of Rocks.
Data collection

To collect unbiased location data on grand skink movements, radio-telemetry equipment was used. The radio-transmitters (BD-2 and LB-2, Holohil Systems LTD, Ontario, Canada) weighed 0.6–0.9 g which made it necessary to choose only adult grand skinks (SVL > 75 mm, weight > 12 g) since a requirement of the research permit was that the transmitter would not exceed 5% of a grand skink’s body weight.

The presence of large grand skinks on several Rocks within an area which could be traversed by the observer within an hour was confirmed before any skinks were caught. Within on season it was endeavoured to use only one grand skink on each Rock but because of the scarcity of the species and the limitations of the study area, occasionally two grand skinks were captured and fitted with radio-transmitters which occupied opposite sides of a large Rock and were unlikely to use the same area. Several reasons contributed to the decision to use different study areas for each season within the study site opposed to choosing Rocks randomly or repeated measures on the same animals: a) because the radio-transmitters lasted for 4–5 weeks due to size restrictions, repeated captures of grand skinks to replace transmitters might result in behavioural changes (see Germano 2007 for capture effects on sympatric O. otagense, Gebauer, pers. observation); b) additionally the rarity of the species made it necessary to use different sites for each season because one area containing all required animals would be too large to be traversed by the observer within one hour and therefore reduce location estimations per day and animal. Although statistically sites are now confounded with season, there are arguments that the site effect is not likely to mask behavioural changes of grand skinks between seasons: a) The study areas are located geographically close enough and along the same ridge line that they would not experience different climatic effects; b) vegetation was very homogenous with habitat types across the overall study site, and all pasture sites were stocked with sheep; c) predator control measures were equal throughout the whole study site. Therefore, any differences in
predator pressure that could impact grand skink behaviour are assumed to be differences between habitat types; d) in all study areas grand skinks that inhabit a rock-outcrop of various sizes were transmittered to reduce a potential confounding site effect. However, the possibility of a confounding effect between season and site should be taken into consideration when interpreting the statistical results.

After selecting an appropriate study area (Fig. 2.1, dashed line polygons), grand skinks were captured with a thin nylon noose run through a thin hollow aluminium tube. Transmitters were attached to the side of the base of the tail with sensitive-skin Leucopore® bandage tape (Fig. 2.2, Neilson et al. 2006, Germano 2007). The position of the transmitter was chosen to avoid skinks being hindered in their movements and so that they were still able to seek refuge in narrow rock-crevices. The height of the transmitter did not exceed the thickness of grand skinks to avoid them being stuck in crevices. The antenna of the transmitter ran along the side of the tail avoiding entanglement in vegetation. Additionally, animals were marked with a non-toxic golden marker on their back close to the head to make identification easier when transmitters where not visible while skinks were partly sitting in a crevice (Fig. 2.2). During this study, 57 grand skinks were fitted with transmitters: 10 grand skinks were caught on Rocks in tussock grasslands and nine skinks in pasture in spring (October/November 2009), while in summer (January/February 2010) and autumn (March/April 2010) nine skinks were caught on Rocks in tussock and 10 on Rocks in pasture grasslands.

The influence of serial autocorrelation on home range estimates has been widely discussed in the literature. Most studies are conducted over a fixed time period which will result in a trade-off between large sample sizes for more robust home range estimates and increased serial autocorrelation of the location data. As a rule of thumb, time sufficient for an animal to move to another point in its home range between observations should be allowed for independent location data, using prior knowledge about the mobility of the species as guidance (Kenward et al. 2001, Kernohan et al. 2001, Fieberg 2007). Swihart and Slade (1985) suggested
estimating the ‘time to statistical independence’ (TTSI) for adequately designing the sampling strategy to avoid negatively biased home range estimates. However, for a fixed-term study the estimated TTSI could lead to small numbers of observations which in turn lead to biased home range estimates (Otis and White 1999).

Furthermore, Fieberg (2007) and Otis and White (1999) argued that it is important to design the sampling regimes by taking into consideration that location data is collected in a way that represents the relative amount of time spent by animals in different parts of the home ranges. Consequently, in fixed-term studies autocorrelated locations can provide better estimates for home range size than independent data (Reynolds and Laundre 1990, Otis and White 1999).

No information is available on the distance that grand skinks move in short time periods. However, during a pilot study (Appendix 1) grand skinks were observed to move across large areas of a Rock in short amounts of time (Gebauer, pers. obs.). Therefore, for each skink, up to three consecutive locations at intervals of one hour were recorded every day using a 3-element Yagi antenna (Sirtrack, Havelock North, New Zealand) and a TR4 receiver (Telonics Inc., Arizona, USA). Although it was endeavoured to track grand skinks three times per day, logistics, weather conditions, transmitter battery failure and loss of transmitters by skinks shedding their skin,
resulted in one to three realised location records for each grand skink per day. The start time and location of the surveys were varied every day to minimise the effect of time of day on the location; for example observations for the day were recorded in the tussock grassland study area first and the observer then moved to the pasture. The following day the pasture site would be monitored first followed by the tussock site and so on. Before every hourly survey, the air-temperature was measured in the shade using a digital thermometer. A pilot study revealed that triangulation procedures to identify the location of a skink did not result in the required precision and accuracy (Appendix 1). Therefore each Rock was surveyed for the transmittered skink with binoculars from a distance of more than 20 m. If the transmittered skink could not be visually located, the radio-transmitter signal was used to identify the direction of the location of the skink. The outcrop was then approached slowly until the focal skink was sighted or its location within a rock-crevice could be estimated. Each location was marked on a map and identified as new when the skink was approximately 50 cm from any previously marked location. To minimise the disturbance to the grand skinks during the tracking period, coordinates of marked locations were taken with a GPS (GeoExplorer® 3, Trimble Navigation Ltd., Sunnyvale, USA) after transmitters were removed from the skinks. All GPS points were differentially corrected using the PathFinder® software (Trimble Navigation Ltd., Sunnyvale, USA) and base station data (Land Information NZ Dunedin, New Zealand) to increase precision.

**Home range analysis**

**Home range estimation**

Previous studies have estimated grand skink home range size and shape using minimum convex polygons (MCP), an approach which has been suggested to be comparable between studies (Rose 1982, Harris et al. 1990, Perry and Garland Jr. 2002). MCPs are one of the most frequently used and simplest techniques for home-
range calculations (Harris et al. 1990, Laver and Kelly 2008). The home range estimate is derived by establishing a minimum convex polygon which encompasses all locations of an animal (Kenward et al. 2001). However, criticism of the MCP home range estimates has been accumulating. Laver & Kelly (2008) suggested that MCPs should not be used as a home range estimator because including all locations in the home range estimate is likely to be overestimated home range size and to include areas which are not used by the animal at all (Worton 1987, Harris et al. 1990), whereas removing seldom use locations will strongly underestimate the home range size (Perry and Garland Jr. 2002). Indeed, estimates of home range size using MCP have been found to be sensitive to the number of locations, especially outliers (Harris et al. 1990), and the frequency of recording the locations (Swihart and Slade 1985). Furthermore, Home range estimates using the MCP method provide no indication of the frequency of use of different areas by the animal within the estimated home range (Worton 1987). However, techniques using probabilistic methods are able to overcome such disadvantages. Kernel density estimators (KDE) assess the animal’s probability of occurrence at each location and can be used to estimate the distribution of home range utilisation (Worton 1987, Marzluff et al. 2004, Laver and Kelly 2008).

To use KDEs for home range estimation, several choices have to be made concerning the smoothing parameter which controls the probability density function over each location used to estimate the home range (Worton 1989). The same smoothing parameter can be applied to all locations, resulting in so-called fixed KDE estimates, or smoothing parameters can be optimized for individual locations within the home range which will result in adaptive KDE estimates. Fixed KDE estimates have smaller bias than adaptive KDE and reach the most accurate home range estimates (size and position) with lower sample size (n > 50, Seaman et al. 1999), but the bias of inner contours is greater than for 95% contours whereas this trend is reversed with adaptive KDE estimates (Seaman et al. 1999). Furthermore various methods have been developed to find the optimal smoothing parameter with the least-square cross-validation (LSCV) method and the reference method being the most commonly used (Laver and Kelly 2008). The method of determining the
smoothing parameter can have a large influence on the home range estimate (Worton 1989). Seaman and Powell (1996) showed in their simulation models that fixed KDE using LSCV generally performed better than fixed KDE using the reference method, whereas Boerger et al. (2006) reported robust and unbiased estimates with both LSCV and the reference method for estimating the smoothing parameter (Fig. 2.3). To estimate home range sizes of grand skinks in this study I used fixed kernel analyses with smoothing parameters estimated by the reference method on a 1 m grid because LSCV would not converge on this small scale with the number of locations available. As suggested by Laver (2008), I used 95% kernel estimates as home range estimates, excluding 5% of the outermost locations to avoid overestimation. The 50% kernel area was used as the core area estimate, describing an area of high grand skink activity within the home range (Seaman and Powell 1990). The differentially corrected GPS points of the mapped locations were imported into Ranges 8 Software (Anatrack Ltd., Wareham, UK).

Independent of the method used for establishing reliable estimates of home range sizes, adequate sample sizes have to be collected. Seaman et al. (1999) suggested generally >30 to >50 locations are necessary for fixed KDE estimates. To identify the minimum number of locations to cover the home range of the animal the number of locations are plotted versus the estimated home range size which results in an asymptotic curve where additional samples do not increase the home range estimate significantly (Rose 1982, Laver and Kelly 2008). The number of locations where the curves reach the asymptote is used as the minimum number of locations necessary to describe the home range. Marshall (2000) found asymptotes after 16 sightings for grand skinks, similar to Rose (1982) who found 18 sightings were needed in her study of the Sceloporus virgatus in North America, and Wasiolka et al. (2009b) who reported 21 locations for spotted sand lizard (Pedioplanis l. lineoocellata). However, Stevens et al. (2010) deemed less than 50 samples inadequate for their study of earless dragons. For this study, a pilot study determined that 20 locations of grand skinks were appropriate to estimate robust home range sizes (Appendix 1). Therefore home range estimates were only calculated for grand skinks with more than 20 recorded locations.
Figure 2.3: Home range from a single grand skink (Oligosoma grande) estimated with five different methods. Displayed are 50% and 95% contours for each method: a) Kernel Density Estimator (KDE) with a fixed smoothing parameter estimated with the reference method, b) KDE with a fixed smoothing parameter estimated with the Least Square Cross-Validation (LSCV) method c) KDE with adaptive smoothing parameters estimated with the reference method d) KDE with adaptive smoothing parameters estimated with LSCV method, e) Minimum Convex Polygon. Locations are depicted by grey points (n = 62)
Analysis

The relationship between home range estimates (95% kernels) and core area size (50% kernels), and grand skink sexes (Sex), seasons (Season), Rock size (RockSize) and grassland types (Habitat) was analysed with linear regression models. As an index for Rock size, the two dimensional footprint of the Rock was calculated as the area of a polygon drawn around the borders of rock-outcrop clusters located through the use of Google Earth satellite imagery. The polygon was then imported into ArcGIS 10 (ESRI, Redlands, USA) to calculate the area (RockSize).

The distribution of home range and core area estimates was highly skewed. A square root transformation of the estimates did not provide a satisfying correction of the distribution and therefore log-transformed home range and core area estimates were used. The log transformation has a stronger effect on reducing the y-axis (area estimates) for outliers, which was necessary in this data set to more closely resemble a symmetric distribution to meet the assumptions of linear regression models. A model set was created using all combinations of the fixed factors and the interaction terms Sex:Season, Season:Habitat, Sex:Habitat and RockSize:Sex. Differences in the behaviour of male and female grand skinks between seasons because of different foraging strategies (Eifler and Eifler 1999b, Tocher 2003) and reproductive behaviours (suggested by Murphy 1994) were investigated by including the Sex:Season interaction term. Similarly differences in movements between the sexes across different grassland types could result in different home range sizes. These possible differences were investigated by including the Sex:Habitat and Habitat:Season interaction. The RockSize:Sex interaction was included into the models to investigate if grand skinks males and females utilize the space available differently on the outcrop. All statistical analyses were performed with R version 2.12.0 (R Development Core Team 2010).
Activity analysis

*Movements of grand skinks*

The characteristics of animal movements and behaviour will determine the factors that influence home range size and the appropriate location sampling regime. To identify daily activity patterns in grand skinks, Murphy (1994) counted individuals on rock-outcrops at a given time of the day, and reported the lowest numbers in the early morning with a wide peak from mid-morning to afternoon. In accordance with these findings, Marshall (2000) reported that grand skinks in gully habitats were more likely to move in the middle of the day. Spatial attributes of animal movements include the distance and location of the movement. When investigating grand skink movements it is important to differentiate between movements within the boundaries of a Rock (Coddington and Cree 1997) and movements between Rocks (Whitaker 1996, Berry et al. 2005). Overall, only a low proportion of grand skinks have been reported to move between Rocks (Whitaker 1996, Coddington and Cree 1997, Houghton 2000). However, grand skinks might have knowledge of the surrounding beyond their Rocks. Stanley (1998) found that grand skinks successfully returned to their home Rock after being displaced distances up to 60 – 70 m indicating that homing is most likely to occur only from familiar territory (Spoecker 1967, Thompson et al. 1999, Morales et al. 2010). Using a long-term data set, Houghton (2000) analysed the distances between re-sightings of grand skinks (the distance between the different Rocks where they were observed), and found that adult grand skinks predominantly moved within 0 – 50 m whereas juveniles moved 100 – 200 m (time between re-sightings 0 days to 10 years). Furthermore, research showed that male grand skinks moved larger distances than females both within and between Rocks (Murphy 1994, Coddington and Cree 1997, Marshall 2000). A number of studies reported that the distances moved by grand skinks did not differ between tussock and pasture grasslands (Murphy 1994, Whitaker 1996) and Houghton (2000) concluded that grand skinks disperse equally in both habitat types. Contrary to these findings, genetic and population occupancy studies found that grand skink populations on Rocks in pasture grasslands were more isolated
from each other than on Rocks in tussock grasslands (Berry et al. 2005, Seddon et al. 2011), and several researchers suggested that a matrix of tussock grassland was important for movements between Rocks (Marshall 2000, Berry et al. 2005, Seddon et al. 2011).

**Analysis**

To investigate the temporal and spatial characteristics of grand skink movements, the distance moved between consecutive observations of the same day (1 hour apart) was calculated, and defined as a movement if the distance was greater than 1 m. Movements were then categorized as occurring on rock surfaces only or including a distance of at least 1 m across grassland. Because grand skinks were often observed at the same position, the data set contained many distances of 0 m. Fletcher et al. (2005) recommended for the analysis of count data that include a large proportion of zeros to split the analysis into two parts and analyse presence data and log-abundance data separately. Because of the high proportion of non-movements (zeros) in the data set, the two part approach recommended by Fletcher et al. (2005) was also used in this study. The first step investigates the presence (1) or absence (0) of a movement where the first category (presence) includes all sampling points where skinks moved a distance larger than 1 m between observations and the second group (absences) contained all points where skinks did not move at all or less than 1 m. These data were then analysed using a set of generalised linear mixed models which accounted for the binomial distribution of the data.

The fixed factors Sex and Season were included in the models to investigate differences in movements between male and female grand skinks, and between different seasons caused by changes in foraging and reproductive behaviour. The interaction term Sex:Season accounted for disproportional differences in movements between grand skink sexes and seasons.
Habitat and RockSize were entered as fixed factors in the models to investigate differences in movements of grand skinks caused by changes in behaviour when crossing different grassland types and utilisation of Rocks of different sizes, respectively. Because RockSize was entered as continuous variable and during each season grand skinks inhabiting outcrops of various sizes were used, confounding effects with the categorical variable Season are not expected. Habitat:Sex interaction term was included in models to investigate if variation in movements between Habitats differed between sexes. Furthermore, because the activity of thermoregulating skinks is highly dependent on the surrounding temperature, the fixed factor temperature (Temp) was included. Grand skinks will not emerge until air temperatures reach approximately 4 °C, and highest number of skinks were seen at temperatures between 10 – 22 °C (Patterson 1992, Murphy 1994). However, at relatively high temperatures (>25 °C) grand skinks will move into the shade to avoid overheating (eg., Patterson 1992, Murphy 1994). Therefore, models were fitted with a quadratic temperature term (Temp+Temp²) to investigate possible effects of high temperatures on movements. Furthermore, previous studies have found that grand skink activity also depended on the time of the day with low activity in the morning, high activity during midday and low activity again in the late evening (Murphy 1994, Marshall 2000). Therefore the fixed factor ‘Time of the day’ (ToD) was included in the models. The length of the day was divided into five sections (ToD): morning (8 am – 10 am), mid-morning (10 am – 12 am), mid-day (12 am – 2 pm), afternoon (2 pm – 4 pm) and evening (4 pm – 6 pm). Because differences in climatic factors between seasons could influence movements of grand skinks during the day the interaction term Season*ToD was also included in models. To account for repeated measures from the same individuals and same days, the variables SkinkID and JulianDay (day of observation), respectively, were used as random factors in all models.

In the second step of the analysis, only the presence of movements, identified in the first step, was analysed using linear mixed models with the distance travelled during the movement as the response variable. A log-transformation of the distance moved allowed a Gaussian distribution of the data to be used in the modelling process.
Similarly to previous analyses a model set was created using all combinations of the fixed factors Sex, Habitat, Temp (and Temp\(^2\)), ToD, Season, RockSize and Surface. Differences of movement distances between sexes caused by differences between habitat types, and in foraging or/and reproductive behaviour between the sexes have been recorded for lizards (Eifler and Eifler 199b, reviewed by Perry and Garland Jr. 2002). Therefore the interaction terms Habitat:Sex and Season:Sex were also included in models. Furthermore differences between movement distances of male and grand skink on Rocks of different size or across different surfaces were investigated through the interaction terms RockSize:Sex and Surface:Sex. The random intercept terms SkinkID and JulianDay were added into all models to account for repeated measures of individual skinks and during the same day, respectively.

Model selection for each of the model sets of the home range, core area and both parts of the movement analysis was performed using the corrected Akaike Information Criterion (AICc, Burnham and Anderson 2002). In this study, the highest ranked model(s) with a $\Delta$AICc < 2 were selected as the most parsimonious (Anderson 2008). All statistical analyses were performed with R version 2.12.0 (R Development Core Team 2010) and the packages ‘lme4’ (Bates and Maechler 2010) and ‘MuMIn’ (Barton 2010).

**RESULTS**

A total of 2227 grand skink locations was recorded with the majority being located on rock surfaces and only six locations (0.3%) occurring in grassland. On average, each grand skink was tracked for 22.7 (SE = 6.1) days (range 7 – 33). The mean number of locations recorded per animal were 39.1 (SE = 11.7, range 10 – 60). Eight grand skinks (six in tussock, two in pasture habitat) were observed moving between Rocks up to four times during the monitoring period.
Home range analysis

There were less than 20 locations collected for four grand skinks which were therefore removed from the home range and core area analysis. One animal did move a large distance after several days of monitoring and established a new home range at the new location without returning to the old activity centre. An asymptote of the area-location plot was not reached for this skink and it was also removed from the analysis. All other animals exhibited an asymptote. The mean home range and core area size for grand skinks was 146.6 m$^2$ (SE = 210.9 m$^2$) and 35.3 m$^2$ (SE = 46.4 m$^2$), respectively (Fig. 2.4). On average the core area constituted 27.9% (SE = 8.0) of the home range area.

Of the model set analyzing home range size, four models received a $\Delta$AICc < 2 and a summed model weight of 0.55. The other models received little support (Table 2.1). The fixed factor Habitat was included in all four top models. Additionally, the selected models included the factors Sex and/or RockSize. Similar results were obtained for the core area size analysis (Table 2.2). Neither the variable Season nor any of the interaction terms were included in the four top models in either analysis. Home range estimates and core area were larger for male skinks and skinks on Rocks in tussock grasslands. Male home ranges were on average 213 m$^2$ (SE = 274 m$^2$) compared to average female home ranges of 90 m$^2$ (SE = 113m$^2$). Mean home range in tussock grasslands was 176 m$^2$ (SE = 196 m$^2$) and in pasture grasslands 118 m$^2$ (SE = 225 m$^2$). There was a weak positive relationship between RockSize and home range and core area size.
Table 2.1: The 10 highest ranked models explaining home range size of grand skinks.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat + Sex</td>
<td>4</td>
<td>75.316</td>
<td>175.684</td>
<td>0.00</td>
<td>0.24</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>79.262</td>
<td>175.988</td>
<td>0.30</td>
<td>0.21</td>
</tr>
<tr>
<td>Habitat + RockSize + Sex</td>
<td>5</td>
<td>73.822</td>
<td>177.095</td>
<td>1.41</td>
<td>0.12</td>
</tr>
<tr>
<td>Habitat + RockSize</td>
<td>4</td>
<td>78.103</td>
<td>177.574</td>
<td>1.89</td>
<td>0.09</td>
</tr>
<tr>
<td>Sex</td>
<td>5</td>
<td>82.836</td>
<td>178.282</td>
<td>2.60</td>
<td>0.07</td>
</tr>
<tr>
<td>Null</td>
<td>4</td>
<td>86.782</td>
<td>178.446</td>
<td>2.76</td>
<td>0.06</td>
</tr>
<tr>
<td>Habitat + RockSize * sex</td>
<td>3</td>
<td>73.621</td>
<td>179.516</td>
<td>3.83</td>
<td>0.04</td>
</tr>
<tr>
<td>RockSize + Sex</td>
<td>2</td>
<td>81.746</td>
<td>179.944</td>
<td>4.26</td>
<td>0.03</td>
</tr>
<tr>
<td>RockSize</td>
<td>6</td>
<td>85.974</td>
<td>180.215</td>
<td>4.53</td>
<td>0.03</td>
</tr>
<tr>
<td>Habitat + Season + Sex</td>
<td>6</td>
<td>74.993</td>
<td>180.476</td>
<td>4.79</td>
<td>0.02</td>
</tr>
</tbody>
</table>

k = number of estimated parameters

Table 2.2: The 10 highest ranked models explaining core area size of grand skinks.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat + Sex</td>
<td>4</td>
<td>65.157</td>
<td>168.150</td>
<td>0.00</td>
<td>0.26</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>69.272</td>
<td>168.983</td>
<td>0.83</td>
<td>0.17</td>
</tr>
<tr>
<td>Habitat + RockSize + Sex</td>
<td>5</td>
<td>64.378</td>
<td>169.977</td>
<td>1.83</td>
<td>0.11</td>
</tr>
<tr>
<td>Sex</td>
<td>3</td>
<td>70.822</td>
<td>170.134</td>
<td>1.98</td>
<td>0.10</td>
</tr>
<tr>
<td>Null</td>
<td>5</td>
<td>74.937</td>
<td>170.815</td>
<td>2.67</td>
<td>0.07</td>
</tr>
<tr>
<td>Habitat + RockSize</td>
<td>2</td>
<td>68.733</td>
<td>170.928</td>
<td>2.78</td>
<td>0.07</td>
</tr>
<tr>
<td>Habitat + RockSize * sex</td>
<td>4</td>
<td>63.806</td>
<td>172.075</td>
<td>3.93</td>
<td>0.04</td>
</tr>
<tr>
<td>RockSize + Sex</td>
<td>4</td>
<td>70.291</td>
<td>172.094</td>
<td>3.94</td>
<td>0.04</td>
</tr>
<tr>
<td>RockSize</td>
<td>4</td>
<td>74.599</td>
<td>172.836</td>
<td>4.69</td>
<td>0.03</td>
</tr>
<tr>
<td>Habitat + Season + Sex</td>
<td>6</td>
<td>64.998</td>
<td>173.038</td>
<td>4.89</td>
<td>0.02</td>
</tr>
</tbody>
</table>

k = number of estimated parameters
To investigate if the differences in home range and core area size between habitat types were predominantly caused by a few animals moving between Rocks, I excluded the seven home ranges of animals using more than one Rock (five in tussock grasslands, two in pasture grasslands; six male, one female) and repeated the analysis. The model selection process for the home range analysis resulted in one model with $\Delta \text{AIC}_c < 2$ and revealed that Habitat and RockSize were the most important variables to explain differences in home range size (Table 2.3). The same model was also ranked highest in the core area analysis, however, three more models, including the intercept-only model, received $\Delta \text{AIC}_c < 2$ (Table 2.4). In

**Figure 2.4:** The distribution of the home range sizes (95% kernel estimate) for female and male grand skinks on outcrops in tussock and pasture grasslands.
contrast to the analysis including grand skinks that use more than one Rock, Sex was not included in the top models for home range or core area analysis. Grand skinks in tussock habitats again had larger home ranges and core areas than grand skinks in pasture habitat, and home range and core area size increased with increasing Rock size.

Table 2.3: The 10 highest ranked models explaining home range size of grand skinks which did only utilise one Rock (= all rock outcrops that are separated by less than 10 m of vegetation).

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat + RockSize</td>
<td>4</td>
<td>39.2</td>
<td>130.463</td>
<td>0.00</td>
<td>0.54</td>
</tr>
<tr>
<td>RockSize</td>
<td>3</td>
<td>43.3</td>
<td>132.568</td>
<td>2.10</td>
<td>0.19</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>43.6</td>
<td>132.871</td>
<td>2.41</td>
<td>0.16</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>47.7</td>
<td>134.577</td>
<td>4.11</td>
<td>0.07</td>
</tr>
<tr>
<td>Habitat + Season</td>
<td>5</td>
<td>43.1</td>
<td>137.317</td>
<td>6.85</td>
<td>0.02</td>
</tr>
<tr>
<td>Season</td>
<td>4</td>
<td>47.1</td>
<td>138.764</td>
<td>8.30</td>
<td>0.01</td>
</tr>
<tr>
<td>Habitat + RockSize + Season*Sex</td>
<td>9</td>
<td>35.4</td>
<td>140.030</td>
<td>9.57</td>
<td>0.00</td>
</tr>
<tr>
<td>Habitat*Season + RockSize</td>
<td>8</td>
<td>38.4</td>
<td>140.569</td>
<td>10.11</td>
<td>0.00</td>
</tr>
<tr>
<td>Habitat*Season</td>
<td>7</td>
<td>41.6</td>
<td>141.226</td>
<td>10.76</td>
<td>0.00</td>
</tr>
<tr>
<td>Habitat + Season*Sex</td>
<td>8</td>
<td>39.6</td>
<td>141.945</td>
<td>11.48</td>
<td>0.00</td>
</tr>
</tbody>
</table>

k = number of estimated parameters

Table 2.4: The 10 highest ranked models explaining core area size of grand skinks which only occupy one Rock (= all rock outcrops that are separated by less than 10 m of vegetation).

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat + RockSize</td>
<td>4</td>
<td>34.6</td>
<td>124.887</td>
<td>0.00</td>
<td>0.30</td>
</tr>
<tr>
<td>RockSize</td>
<td>3</td>
<td>37.2</td>
<td>125.771</td>
<td>0.88</td>
<td>0.19</td>
</tr>
<tr>
<td>Habitat</td>
<td>3</td>
<td>37.4</td>
<td>125.948</td>
<td>1.06</td>
<td>0.18</td>
</tr>
<tr>
<td>Null</td>
<td>2</td>
<td>40.0</td>
<td>126.654</td>
<td>1.77</td>
<td>0.13</td>
</tr>
<tr>
<td>Habitat + RockSize + Sex</td>
<td>5</td>
<td>34.5</td>
<td>127.281</td>
<td>2.39</td>
<td>0.09</td>
</tr>
<tr>
<td>Habitat + RockSize*Sex</td>
<td>6</td>
<td>34.3</td>
<td>129.738</td>
<td>4.85</td>
<td>0.03</td>
</tr>
<tr>
<td>Habitat + Season</td>
<td>5</td>
<td>36.9</td>
<td>130.327</td>
<td>5.44</td>
<td>0.02</td>
</tr>
<tr>
<td>RockSize*Sex</td>
<td>5</td>
<td>37.0</td>
<td>130.429</td>
<td>5.54</td>
<td>0.02</td>
</tr>
<tr>
<td>Season</td>
<td>4</td>
<td>39.5</td>
<td>130.809</td>
<td>5.92</td>
<td>0.02</td>
</tr>
<tr>
<td>Habitat + RockSize + Season*Sex</td>
<td>9</td>
<td>30.0</td>
<td>132.657</td>
<td>7.77</td>
<td>0.01</td>
</tr>
</tbody>
</table>

k = number of estimated parameters
Movement analysis

Calculating the distance moved between consecutive observations on the same day (1 hour difference) from the location data resulted in 1131 data points of 57 animals. Of these, 737 were for distances of $<1$ m which were categorized as no movement (0). Of the 394 that resulted in distances of $>1$ m (categorized as movements (1)), 290 were across rock surfaces only and 104 included $\geq 1$ m of grassland. Only nine movements across more than 10 m of grassland were observed during the study. Because of the low sample size of this group, movements across more than 10 m of grassland were combined with movements across more than 1 m of grassland in the analysis. The average distance moved by grand skinks in tussock habitat and pasture habitat was 6.9 m (SE = 0.6) and 4.8 m (SE = 0.4, Fig. 2.5), respectively.

Figure 2.5: Distribution of distances moved by grand skinks inhabiting outcrops in pasture or tussock grasslands within one hour.
The model set analysing the probability of grand skinks movement occurrence resulted in four top models with $\Delta AICc < 2$ (Table 2.5). The two highest ranked models included a negative quadratic relationship between the presence or absence of a movement and temperature. One of those models also included an interaction between sex and season. The third and fourth highest ranked models received similar weights but modelled a linear relationship between the probability of a movement and temperature. Season was included in all four models, Sex only in two models within an interaction term with season. Furthermore, the time of day (ToD) was included in all high ranked models. The probability of occurrence of movements was highest mid-morning and at mid-day and lowest in the morning, afternoon and evening (Fig. 2.6c). Grand skinks had the highest probability of moving in spring and the lowest in autumn. However, the interaction term Sex:Season indicate that males moved the most in summer, less in spring and the least in autumn, while female grand skinks moved the most in spring and the least in autumn (Fig. 2.6a). In the models that include the quadratic term for temperature, the probability of moving increased with increasing temperatures at first, the reached a wide peak around 12 – 18 °C and for temperatures >18 °C decreased slightly (Fig. 2.6b). The four highest ranked models did not reveal a difference in the presence or absence of movements between grassland types. The interaction terms Sex:Habitat and ToD: Sex were also not included.

**Table 2.5:** The 10 highest ranked models estimating the probability of grand skink movements.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Temp^2 + Temp + Season^* Sex + ToD$</td>
<td>14</td>
<td>1255.647</td>
<td>1284.023</td>
<td>0.00</td>
<td>0.22</td>
</tr>
<tr>
<td>$Temp^2 + Temp + Season + ToD$</td>
<td>11</td>
<td>1261.966</td>
<td>1284.202</td>
<td>0.18</td>
<td>0.20</td>
</tr>
<tr>
<td>$Temp + Season * Sex + ToD$</td>
<td>13</td>
<td>1258.031</td>
<td>1284.357</td>
<td>0.33</td>
<td>0.19</td>
</tr>
<tr>
<td>$Temp + Season + ToD$</td>
<td>10</td>
<td>1264.323</td>
<td>1284.520</td>
<td>0.50</td>
<td>0.17</td>
</tr>
<tr>
<td>Season * Sex + ToD</td>
<td>12</td>
<td>1262.992</td>
<td>1287.272</td>
<td>3.25</td>
<td>0.04</td>
</tr>
<tr>
<td>$Temp^2 + Temp + Season^* Sex + Habitat^*Sex + ToD$</td>
<td>16</td>
<td>1254.808</td>
<td>1287.296</td>
<td>3.27</td>
<td>0.04</td>
</tr>
<tr>
<td>Season + ToD</td>
<td>9</td>
<td>1269.235</td>
<td>1287.395</td>
<td>3.37</td>
<td>0.04</td>
</tr>
<tr>
<td>$Temp + Season^* Sex + Habitat^*Sex + ToD$</td>
<td>15</td>
<td>1257.093</td>
<td>1287.523</td>
<td>3.50</td>
<td>0.04</td>
</tr>
<tr>
<td>$Temp^2 + Temp + ToD$</td>
<td>9</td>
<td>1272.013</td>
<td>1290.174</td>
<td>6.15</td>
<td>0.01</td>
</tr>
<tr>
<td>Season * Sex + Habitat^*Sex + ToD</td>
<td>14</td>
<td>1262.138</td>
<td>1290.514</td>
<td>6.49</td>
<td>0.01</td>
</tr>
</tbody>
</table>

$k$= number of estimated parameters
Figure 2.6: Distribution of the movement probability (P) of grand skinks across (a) seasons, (b) temperatures, and (c) the length of the day. Probabilities were predicted by the model $P \sim \text{Temp} + \text{Temp}^2 + \text{Season} \times \text{Sex} + \text{ToD}$ including the random factors SkinkID and JulianDay. (a) and (b) are estimated probabilities with standard errors denoted by error bars, in (b) open circles denote samples ($n = 1131$).
Chapter two: Home range and movements

The analysis of the distances moved by grand skinks resulted in two models with \( \Delta \text{AICc} < 2 \) (Table 2.6). The highest ranked model had a model weight of 0.48 and included the fixed term Habitat and the interaction term Sex:Surface. The next highest ranked model gained a model weight of 0.28 including only the Sex:Surface interaction term, but not the Habitat variable. All other models received little support. Grand skinks moved further in tussock habitats than in pasture grasslands. Both sexes moved larger distances when crossing grassland compared movements only occurring on rock surfaces. However, male grand skinks moved longer distances across grasslands than females (Fig. 2.7). There was no support for a quadratic or linear relationship between temperature and the distances moved.

The analysis of movement distances was repeated after excluding movements which occurred across more than 10 m of grassland (between Rocks), investigating the effect of the large inter-Rock movements. The highest ranked models with \( \Delta \text{AICc} < 2 \) included again the variable Habitat and the Sex:Surface interaction term (Table 2.7). The distances moved were again larger from grand skinks on Rocks in tussock grasslands and by males crossing grasslands when moving.

Table 2.6: The 10 highest ranked models estimating the distance moved by grand skinks if movements (1) occurred.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>( \Delta \text{AICc} )</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat + Sex*Surface</td>
<td>8</td>
<td>762.771</td>
<td>779.145</td>
<td>0.00</td>
<td>0.48</td>
</tr>
<tr>
<td>Sex*Surface</td>
<td>7</td>
<td>765.936</td>
<td>780.226</td>
<td>1.08</td>
<td>0.28</td>
</tr>
<tr>
<td>Habitat* Sex + Sex* Surface</td>
<td>9</td>
<td>763.899</td>
<td>782.368</td>
<td>3.22</td>
<td>0.10</td>
</tr>
<tr>
<td>Habitat<em>Surface + Sex</em>Surface</td>
<td>9</td>
<td>764.088</td>
<td>782.556</td>
<td>3.41</td>
<td>0.09</td>
</tr>
<tr>
<td>Habitat* Sex + Sex<em>Surface + Habitat</em>Surface</td>
<td>10</td>
<td>765.229</td>
<td>785.804</td>
<td>6.66</td>
<td>0.02</td>
</tr>
<tr>
<td>Habitat + Sex*Surface + Season</td>
<td>10</td>
<td>766.532</td>
<td>787.106</td>
<td>7.96</td>
<td>0.01</td>
</tr>
<tr>
<td>Sex*Surface + Season</td>
<td>9</td>
<td>769.582</td>
<td>788.050</td>
<td>8.91</td>
<td>0.01</td>
</tr>
<tr>
<td>Habitat* Sex*Surface + Temp</td>
<td>9</td>
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<tr>
<td>Sex*Surface + Temp</td>
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<td>789.731</td>
<td>10.59</td>
<td>0.00</td>
</tr>
</tbody>
</table>

k= number of estimated parameters
Table 2.7: The 10 highest ranked models estimating distances moved by grand skinks after excluding movements across more than 10 m of grassland (between Rocks).

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
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<td>8</td>
<td>722.8</td>
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</tr>
<tr>
<td>Sex * Surface</td>
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<tr>
<td>Habitat * Surface</td>
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<td>740.267</td>
<td>1.13</td>
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</tr>
<tr>
<td>Surface</td>
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<td>741.553</td>
<td>2.42</td>
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</tr>
<tr>
<td>Habitat<em>Sex + Sex</em>Surface</td>
<td>9</td>
<td>723.8</td>
<td>742.261</td>
<td>3.13</td>
<td>0.07</td>
</tr>
<tr>
<td>Habitat<em>Surface + Sex</em>Surface</td>
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<td>724.4</td>
<td>742.900</td>
<td>3.76</td>
<td>0.05</td>
</tr>
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<td>730.8</td>
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<tr>
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</tr>
<tr>
<td>Sex + Surface</td>
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<td>734.1</td>
<td>746.330</td>
<td>7.19</td>
<td>0.01</td>
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k= number of estimated parameters

Figure 2.7: Mean distance moved by grand skinks across rock surfaces only, and surfaces which included a distance of 1 m of grassland. Bars denote standard errors.
DISCUSSION

To establish successful management plans for the conservation and protection of species detailed information is required on their behaviour and ecology. Using radio-telemetry equipment has allowed studying movements of grand skinks in greater detail than previous studies. More locations were collected in this study which increased the robustness of the home range estimates and identified grand skink location independent of the visibility of the skink.

The activity of lizards is highly dependant on their body temperature which they regulate through basking or retreating into shade (Avery et al. 1982). For grand skinks the previously reported importance of air temperature for activity and movements (Murphy 1994, Coddington and Cree 1997, Marshall 2000) has been confirmed in this study with reduced movement probabilities estimated for temperatures below approx. 13 °C and above 20 °C. Furthermore, activity patterns during the day observed by Murphy (1994) and Marshall (2000) were similar to what the models in the present study predicted. Predominantly basking in the morning would lead to the low movement probabilities estimated by the models in the morning followed by a period of high activity over mid-morning and mid-day, and a slowing down of activity in the afternoon with basking in the evening.

I also found differences in the probability of movements for female and male grand skinks between seasons. Asynchronous seasonal activities between sexes have been reported by Bull et al. (1991) for the sleepy lizard (*Tiliqua rugosa*). The differences in activity of the sleepy lizard were related to different costs of reproductive activities for the sexes in the different seasons. Female lizards adjust their behaviour during pregnancy for optimal thermoregulation to support the development of embryos (Beuchat 1986), avoidance of predators (Amo et al. 2007a) and to remedy reduced mobility (Shine 1980, Schwarzkopf and Shine 1992). Therefore pregnancy could explain the decrease of movement probability of grand skink females from spring to autumn found in this study. In spring, grand skink females in their early stages of pregnancy might move more often to adjust basking sites for optimal...
thermoregulation, while in summer the temperatures are higher which reduces the need to find perfect basking sites. Additionally, females in their late stages of pregnancy (late summer/autumn) might stay closer to refuges and have reduced mobility which impairs their ability to hunt for large flighty prey (Amo et al. 2007b). Unlike results from studies of other lizard species (Dubas and Bull 1992, Perry and Garland Jr. 2002), male grand skinks did not show increased activity in the mating season (autumn). There is little information available on the mating behaviour of grand skinks (Murphy 1994). It is possible that male grand skinks identify possible mating partners during higher activity in summer and spend time nearby female skinks during autumn when mating occurs, reducing the need for movement.

The lower probability of female movements compared to male movements in summer and autumn found in this study, appears to contradict findings by Eifler and Eifler (1999a) that female grand skinks display a higher movement frequency. However, female grand skinks predominantly complete short movements to glean small invertebrates of the rock-surface and only occasional long movements to fruit bearing shrubs, whereas male grand skinks move longer distances to hunt large flying invertebrates (Eifler and Eifler 1999a). Although the season variable could be partially confounded with site due to restrictions in the experimental design, no differences in climate, predator pressure or food availability are expected between sites that could explain differences in movement probabilities of grand skinks, especially between sexes. Another likely explanation could be the definition of movements in the present study. For the analysis grand skinks were required to move at least 1 m to make a movement, which might have led to less movements being recorded for female grand skinks which move predominantly very short distances according to Eifler and Eifler (1999a).

During this study grand skinks occurred predominantly on the rock-outcrops, with only a very small number of sightings of grand skinks in vegetation. Furthermore, those sightings were always in connection with movements of grand skinks between rock-outcrops. Potential utilisation of grassland around outcrops for foraging was
not observed in this study. In agreement with Murphy (1994), Marshall (2000) and Coddington and Cree (1997), I found that males moved larger distances, especially across grasslands, than females and hence had larger home ranges. Murphy (1994) found that home ranges of males overlap that of several females and concluded that males in the search of mates move further and therefore hold larger home ranges. Similar results have been found with numerous lizard species (reviewed by Perry and Garland Jr. 2002). However, Eifler and Eifler (1999a) reported no differences in home range size between male and female grand skinks. Excluding grand skinks which were observed on more than one Rock, from my analysis also resulted in no differences between sexes because most of the animals which included several Rocks in their home range were males (six out of eight grand skinks). In Eifler and Eiflers’ (1999a) study no individuals were reported moving between Rocks which were isolated by more than 100 m grasslands, distances that have rarely been reported being crossed by adult grand skinks (Houghton 2000). For several species of lizards seasonal differences in home range size and movement distances have been reported, caused by reproductive behaviour or changes in diet (Thompson et al. 1999, Wone and Beauchamp 2003, Stark et al. 2005). However, grand skinks did not display such a difference. Due to the experimental design there is a small possibility of site effects masking season effects. However, grand skinks were located almost exclusively on rock surfaces and did not seem to use surrounding vegetation for foraging. Also, most skinks were found occupying only one Rock, especially in pasture habitats. Being limited to the rock surface of one Rock would reduce the ability of grand skinks to extend their home ranges between seasons.

Behavioural adaptations of lizards to differences in predator or food densities in the environments can lead to differences in their home range size (Kerr and Bull 2006, Hawlena and Perez-Mellado 2009, Wasiolka et al. 2009a). Hawlena & Perez-Mellado (2009) observed that lizards in natural environments, where predator numbers were artificially increased, did reduce the time moving but not the frequency of movements or microhabitat use. Similarly, the present study resulted in no differences between habitat types for movement probabilities but longer movements and larger home ranges in tussock habitat compared to pasture habitat.
A factor influencing the differences in distances moved and home range size between habitat types could be a behavioural adjustment to higher perceived predation risk by grand skinks travelling across short vegetation in pasture habitats and rock surfaces where there is no shelter from predators. Although there are no data available on the actual predator numbers in both habitat types at the study site, Norbury (2001) suggested a higher number of predators in pasture habitats because predator populations were bottom up regulated by the numbers of rabbits which are more abundant in pasture habitats. Furthermore, only two out of eight grand skinks that moved between Rocks were in pasture grasslands which support findings of increased genetic isolation of the populations in pasture grasslands (Berry et al. 2005) and reduced colonization probabilities of uninhabited Rocks in pasture habitat (Seddon et al. 2011).

An alternative explanation to grand skinks having smaller home ranges in pasture landscapes compared to tussock landscapes could be a higher abundance of food which would require less distance moved in pasture landscapes resulting in smaller home ranges. A varied response of lizards towards different food densities has been recorded concerning home range sizes, ranging from increased home ranges and larger movements (Simon 1975, Griffiths and Christian 1996, Wasiolka et al. 2009b), no differences in home range size (Jones et al. 1987, Guyer 1988, Eifler 1996) to reduced home range sizes (Nagy 1973, Kerr and Bull 2006). By artificially increasing invertebrate abundance on rock-outcrops, Eifler and Eifler (1999b) found that male grand skinks increased their home range while that of females decreased. Therefore, increased food densities are an unlikely explanation for smaller home ranges of both sexes in pasture landscapes, because I would expect the model selection process in the present study to favour models including the Habitat:Sex interaction terms under those circumstances.

For conservation management, the reluctance of grand skinks to move longer distances in pasture habitat is an important factor to take into consideration. Population dynamics are strongly influenced by differences in movements between habitat patches. Reduced movements will result in genetic isolation of populations
on Rocks and decreased colonisation probabilities of unoccupied Rocks as have been found in earlier studies (Berry et al. 2005, Seddon et al. 2011). The results of the present study showed that grand skinks movements depend on the vegetation type surrounding the Rocks. It is also reasonable to assume that movements between Rocks are limited by the distance of grassland to traverse. However, grand skinks that utilised several Rocks during the present study crossed on average a distance of 22 m (SE = 3.0 m) of continuous vegetation, which is not significantly different from the distance grand skinks that utilise only one Rock would have to traverse to the nearest Rock (26 m, SE = 2.5 m; Gebauer, unpublished data). Further investigation is needed on the factors influencing the movements of grand skinks between Rocks to guide future management decisions. Although this study showed that skinks do not largely rely on vegetation around the rock-tors for foraging, it is unknown to what extent the invertebrates that grand skinks feed on rely on the surrounding vegetation. Additionally, further investigation is needed to identify differences and availability of invertebrate food resources for grand skinks in the two different habitat types. Furthermore, more research is needed on the reduced movements on rock-surface of grand skinks in pasture habitat. One probability is that this is caused by increased perceived or actual predation risk; however, isolating this behavioural response is difficult.

Management strategies for protected sites should strive to retain and/or improve the tussock vegetation between Rocks to enable more frequent movements of grand skinks between the Rocks. This will likely increase genetic exchange between otherwise strongly isolated groups of grand skinks. Additionally, increased movements between Rocks will increase colonization probabilities in the grand skink metapopulation increasing its probability of persistence. A further recommendation resulting from this study is to prefer sites for protection or translocation with distances less than 40 m between Rocks to take into consideration the reluctance of grand skinks to travel larger distances through grasslands of either type. Higher Rock densities (shorter distances between Rocks) will incur in a higher frequency of movements which increases genetic diversity and metapopulation persistence.
CHAPTER THREE

Differences in body condition between populations of grand skinks in modified and native grasslands

Female and juvenile grand skink basking on a schist-rock outcrop
INTRODUCTION

In conservation biology, where limited budgets lead to managers having to prioritise strategies, it is important to know if changes in vital rates of populations (e.g., survival, reproduction and recruitment) are part of natural variation or due to management actions (e.g., Waye and Mason 2008). Slowly developing trends in population parameters due to anthropogenic effects can be masked by strong natural fluctuations (e.g., Iverson et al. 2006). Conversely, short-term trends may be incorrectly connected to human impacts when they are actually part of natural cycles in the population (Lawson 1993) which is especially important for long-lived species. Therefore, long-term data sets are required to demonstrate overall population trends over time (Pechmann et al. 1991, Blaustein 1994, Reading 2007).

For example, on Stephens Island, New Zealand, a decline in body condition of tuatara (*Sphenodon punctatus*), a species that lives for at least 61 years in the wild (Nelson et al. 2002), was only evident after >22 years of monitoring (Hoare et al. 2006, Moore et al. 2007). The decline was attributed to increased intraspecific competition for food caused when the population density increased after the successful removal of introduced predators (Moore et al. 2007). Additionally the decreased predation risk contributed to an increased use of nesting sites in open areas in pasture grasslands which increased recruitment (Moore et al. 2007).

To detect trends in population demographics, features such as population size, survival rates, reproductive success and population persistence are utilised (Van Horne 1983, Hall et al. 1997, Johnson 2007), but also of importance are indicators of population health, such as morphological variation and growth rates (Hoare et al. 2006, Johnson 2007, Benard and McCauley 2008). One indicator of population health that has been widely used amongst vertebrate taxa is the body condition index (BCI) of individuals. The BCI influences important population parameters, including reproductive output and survival of individuals, as well as dispersal of juveniles (see Stevenson and Woods 2006, Benard and McCauley 2008). Body condition indices are used to infer the fitness (health) of an animal by providing an index of their relative energy stores (Jakob et al. 1996, Green 2001, Schulte-
Hostedde et al. 2005, Stevenson and Woods 2006, Peig and Green 2010). For wild animals, individuals with a larger mass relative to their body size are generally regarded as healthier since obese animals are rarely encountered in the wild (Stevenson and Woods 2006, Connolly and Cree 2008). However, in captivity increased food availability, reduced activity and continuous favourable environmental conditions can lead to obesity, which may have detrimental effects on their fitness (Connolly and Cree 2008; but see Hare et al. in press). In the wild, lizards with higher BCI values survive longer (Henle 1989, Reading 2007) and female lizards with higher BCI values have more offspring with larger juveniles (Petren and Case 1996, Olsson and Shine 1997, Rohr 1997), which in turn often have a greater chance of survival (Hare and Cree 2011). For some species, juveniles with higher BCI values are more likely to disperse (Lena et al. 1998, Meylan et al. 2002, Le Galliard et al. 2005). In addition, female reptiles with longer bodies also tend to have higher litter/clutch sizes (Du et al. 2005).

Body condition is directly influenced by food availability, costs of maintenance (e.g., reproduction) and the behaviour of individuals. Additionally, variation in both habitat and climate influence these factors. For example, Ballinger (1977) found that drought led to reduced food availability, thus lowering body condition, which in turn led to lower reproductive output in the tree lizard (*Urosaurus ornatus*). Correspondingly, Pygmy bluetongue lizards (*Tiliqua adelaidensis*) had lower body condition in burned sites compared to unburned control sites, attributed to reduced time spent foraging in the burnt sites (Fenner and Bull 2007). Higher predation pressures between habitat types, or increasing predation pressures over time, reduce the time allocated to foraging and increases the time spent in refuges and/or fleeing from predators, which has resulted in lowered BCI in some lizard species (Pérez-Tris et al. 2004, Amo et al. 2006). High levels of intraspecific and interspecific competition for resources have been found to cause similar results (Petren and Case 1996, 1998, Hoare et al. 2006, Starr and Leung 2006). Furthermore, the cost of reproduction to females is high, and after birth/oviposition females can have much reduced body condition indices (King 1993, Waye and Mason 2008), and often
need to gain a high BCI in order to successfully reproduce (van Wyk 1991, Schwarzkopf 1993, Doughty and Shine 1998).

Habitat deterioration and increased predation by introduced mammalian predators have been identified as major threats for the lizards of New Zealand (Towns and Daugherty 1994, Whitaker 1996). The indigenous grassland regions of Otago have experienced some of the most dramatic declines of abundance and distribution of lizards, including two large skinks that are critically endangered; the grand (Oligosoma grande) and Otago skinks (O. otagense) (Patterson 1984, Towns and Daugherty 1994, Whitaker and Loh 1995). Today, both species can be found in only 8% of their estimated historic distribution (Whitaker and Loh 1995), and these declines are attributed to changes in both habitat and predation pressures (Towns and Daugherty 1994, Whitaker 1996). The New Zealand Department of Conservation (DoC) has put in place a large-scale predator control and monitoring program together with translocations, captive breeding programs and protection of 1875 ha of indigenous tussock grasslands to ensure the continued survival of both skink species in the wild (Whitaker and Loh 1995, Hutcheon et al. 2011, Reardon et al. 2012). This study uses long-term monitoring data spanning a 17-year period to explore whether natural and/or anthropogenic-induced changes in grand skink population structure and health can be seen. In particular, I explored potential changes in the body condition index, and the probability of a skink being pregnant (mature-sized females only), in both native tussock grasslands and exotic pasture grasslands.

Previous research highlighted that grand skink populations in pasture grasslands declined in numbers while populations in tussock grasslands appeared stable (net number of occupied outcrops in tussock grasslands +1.5% (SE = 1.5), in pasture grasslands -21.4% (SE = 7.9) over a 5-year period (1986 – 2001), Houghton and Linkhorn 2002). Furthermore, occupancy of outcrops in pasture grasslands was significantly lower compared to tussock grasslands (Whitaker 1996, Seddon et al. 2011). However, in a study using two years of data (1994–1995), the log(mass)/log(snout-vent length) body condition of grand skinks did not differ
between modified pasture and indigenous tussock grasslands (Whitaker 1996). Conversely, recently post-parturient females of the sympatric, smaller McCann’s skink (O. maccanni) had higher body condition indices when captured from areas with predominantly native tussock grasses, as opposed to exotic pasture, surrounding the rock outcrops (Hare and Cree 2011). However, as no data are available on the natural variability of population parameters of grand skinks, it is unclear whether the declines in numbers in exotic pastures are linked to a reduction in reproductive output and/or body condition index, and/or increased predation pressure. Therefore, using a long-term data-set, I aimed to answer the following questions, focusing on the key factors of body condition index and reproductive output in grand skinks. (1) Are there differences in BCI between males and females (including reproductive status), and between mature and immature grand skinks? (2) What is the natural short-term variation of body condition of grand skinks between seasons? (3) Are there obvious long-term trends of grand skink body condition for the 17-year period covered by the data set? (4) Have the past conservation management practices (habitat conservation and predator control) altered body condition indices and/or reproductive output? (5) Does the BCI and/or probability of mature female grand skinks being pregnant differ between indigenous tussock and exotic pasture grasslands? (6) Does the probability of being pregnant change based on size (SVL) or body condition of the mature female grand skink?

**METHODS**

**Study species**

The strongly diurnal and heliothermic grand skink is one of New Zealand’s largest lizard species reaching a snout-vent length (SVL) of up to 113 mm (Cree 1994, Tocher 2003). Grand skinks are long-lived with animals of 19 years known in the wild (N. Whitmore, DoC, pers. comm. 2012), and reach maturity at approximately 3 – 4 years (Cree 1994). Adult grand skinks mate in late autumn (March/April) and females ovulate in October/November (Cree 1994). In summer (February/March),
the females will give birth to one to three young (mean = 2.4, SE = 0.1 offspring, Cree 1994). The smallest pregnant females that have been recorded had a SVL = 78 – 81 mm (Cree 1994). Grand skinks are mostly active from spring through to autumn (September to May), but, like other NZ skinks, they do not hibernate, and instead, on warm sunny days can be seen basking during winter (June–August, Tocher 2003).

The highly saxicolous grand skinks show strong site fidelity to the outcrop they are born at, and only a small proportion (8%) of juveniles disperse to a new outcrop (Houghton 2000); even adult grand skinks rarely leave their home-outcrop (Coddington and Cree 1997, Chapter 2). Grand skinks feed on invertebrates and fruits that they find on the outcrops and use rock crevices and vegetation on the outcrop as shelter (Eifler and Eifler 1999a, Tocher 2003).

**Study site**

Data used in this analysis stems from the grand skink population occupying ca. 250 ha of a NE-SW ridge (Redbank) at 590 to 620 m elevation near the township of Macraes Flat, New Zealand (45°28′ S, 170°28′ E; Fig. 3.1). The area is divided by a property boundary with conservation land to the SW and private farmland to the NE (Whitaker 1996). The conservation land at the Redbank site was acquired by the DoC in 1993 and consists of indigenous tussock grasslands dominated by narrow-leaved snow tussock (*Chionochloa rigida*) and red tussock (*C. rubra*) which has not been burnt or fertilized since 1980. Low intensity grazing happened in the conservation area until approximately 1998. The private farmland adjacent to the conservation land was turned into pasture by ploughing and over-sowing with exotic grasses in 1980 – 82. The pastures are dominated by rye grass (*Lolium perenne*) and white clover (*Trifolium repens*) and are very closely grazed and fertilized (Whitaker 1996). Schist-rock outcrops occupied and unoccupied by grand skinks are scattered throughout both grassland types at the study area. Previous studies reported a higher abundance of invertebrates (Tocher 2003) and a lower
number of fruiting shrubs growing on schist-outcrops in pasture grasslands compared to tussock grasslands (Whitaker 1996). In 1999, the DoC started a trapping programme targeting feral cats (*Felis catus*). The tussock grasslands of the study site were located at the periphery of the programme and the pasture grasslands lay just outside the trapped area. In 2004, the predator control programme was extended to include a wider range of introduced mammalian predators including feral cats, stoats (*Mustela erminea*), ferrets (*Mustela putorius furo*), weasels (*Mustela nivalis vulgaris*) and hedgehogs (*Erinaceus europaeus*). An expansion of the trapped area followed in 2008 to increase the core of the trapped area which showed positive responses of grand skink populations to the trapping programme (Reardon et al. 2012, Fig. 3.1).

**Data**

The Grand and Otago skink recovery programme (GAOS) administered by DoC maintains a database with entries of grand skinks that have been caught and measured for research, monitoring and translocation purposes since the early 1980s. This programme has resulted in a large database including 4983 entries of morphological measures from grand skinks captured at the broader Redbank study site between the years 1983 to 2010. For the purpose of the analysis in this thesis, I used data from a subset of 13 years in the 17-year period of 1993 – 2010 which provided sufficient samples from both, tussock and pasture grasslands. A predator proof fence was built within the study site in 2007. Data of grand skinks caught inside the predator proof fence were also excluded from the analysis to avoid the inclusion of a parameter in the models with a relatively small sample size. The resulting data-set included 4636 entries for the analysis (Table 3.1). Each entry included the outcrop-ID and date of capture, the person who measured the skink, individual skink-ID (initially by toe-clip and later by photo-identification), SVL [± 1 mm], vent-tail length (VTL [± 1 mm]) and mass [± 1 g]. Like most other
Figure 3.1: New Zealand Department of Conservation reserve boundaries at Macraes Flat, including trap-lines and Redbank study site.
Chapter three: Body condition

Oligosoma skinks, sex of juveniles could not be identified, therefore, skinks <51 mm SVL were classified as neonates and between 51 – 68 mm SVL as juveniles, respectively. Grand skinks above 68 mm SVL were considered to be sexually mature skinks which were classified as males, pregnant females, non-pregnant females and, where personnel were not trained in sexing techniques, adult skinks of unknown sex.

For this study, the location information was used to assign each database entry to one of two grassland types, indigenous tussock grassland or modified pasture grassland (outcrops were fully surrounded by either tussock or pasture grassland). For the purposes of this chapter, analyses were conducted for the 12 month period from September to August, in order to have clearly incorporated the austral summer into the seasonal sequence, rather than using the calendar year (January to December). The date of capture was then used to assign each entry to a season (spring: September–November, summer: December–February, autumn: March–May, winter: June–August). The GAOS team did not capture animals in winter due to their unpredictable emergence behaviour, and not wanting to risk unnecessary stress caused by handling the animals (see Germano (2007) for capture effects on the sympatric Otago skink, Oligosoma otagense).

Statistical analysis

Accounting for tail-loss

Lizards are able to autotomise (discard) their tail in response to encounters with predators or aggressive intraspecific encounters (Arnold 1988, Vitt and Zani 1997). However, despite the immediate benefit of caudal autotomy, there are physiological and functional costs including reduced reproductive output (Chapple et al. 2002) and lowered sprinting speeds (Cooper Jr et al. 2009). Because reduced mass through
Table 3.1: Number of grand skinks (*Oligosoma grande*) captured between September 1987 and September 2010 at the Redbank study site, and management on conservation land. Only data from the years shaded in grey were used in the analyses of this thesis.

<table>
<thead>
<tr>
<th>Year</th>
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<th>Management on conservation land</th>
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</thead>
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<tr>
<td></td>
<td>N</td>
<td>J</td>
</tr>
<tr>
<td>Sept 1987 – Sept 1988</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Sept 1988 – Sept 1989</td>
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<td>Sept 2008 – Sept 2009</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Sept 2009 – Sept 2010</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

N = Neonates, J = Juveniles, F = females, M = males, U = Adults of unknown sex

significant tail-loss can have a considerable impact on the body condition index and grand skink behaviour which in turn could influence body condition, I calculated the difference of the measured tail length to an estimated original tail-length and only included individuals which had more than 50% (a majority) of their estimated original tail length (eg., Hoare et al. 2006). The 50%-mark should be regarded as a conservative threshold because losing 50% of the tail length (starting at the pointy end) would account for approximately 20% of the volume (or mass) when using a cone as a model for a lizard tail.
The original tail length was estimated using 132 entries of the total database that stated skinks had complete tails in an ordinary least square (OLS) regression analysis of log-transformed VTL against SVL. Although OLS regression does not account for measurement errors in the x-axis (SVL) it minimises the squared residuals in y-axis (VTL) and therefore was recommended for predictive purposes by Legendre (1998). The coefficient estimates were used to estimate the expected tail-length for the SVL of each skink \( VTL = e^{(0.818 \times \log(SVL) + 1.198)} \), \( R^2 = 0.81 \). Records of 62 grand skinks that were estimated to have tail length of \( \leq 50\% \) of their original tail-length were excluded from the analysis.

**Scaled mass body condition index (M)**

There has been an ongoing discussion in the literature on what constitutes a reliable body condition index (Jakob et al. 1996, Green 2001, Schulte-Hostedde et al. 2005, Stevenson and Woods 2006, Peig and Green 2009). Body condition indices range from simple ratios between body weight and a length measurement to residuals of regressions of log-transformed body weight against log-transformed length measurements. Peig and Green (2009, 2010) argued that a reliable body condition index should also account for effects of growth and proposed the scaled mass index \( M \) which computes the mass that each individual would have at a fixed length. In this study, after comparisons among different BCIs (see Appendix 2), the scaled mass index (M) was used. The scaled mass index \( M \) is calculated as follows: 

\[ M = M_i \times \frac{L_0}{L_i}^{b_{SMA}} \]

whereby \( L_0 \) is the standard value of the length measurement, \( M_i \) and \( L_i \) are the individual’s mass and length measurements, respectively, and \( b_{SMA} \) is the scaling exponent of the standard major axis (SMA) regression of the mass against the length measurements (Peig and Green 2009). The parameters used for calculating \( M \) were estimated following the description of Peig and Green (2009).

The slope of the SMA regression of log (mass) versus log (SVL) using the whole dataset excluding animals with less than 50% tail length was estimated as 3.148 (\( n = 4574, R^2 = 0.98 \)). The overall arithmetic mean of SVL for the whole dataset
was taken as $L_0 = 73.0$ mm. Consequently the scaled mass index was calculated as follows: $M = M_i \times [73.0 \text{ mm}/L_i]^{3.14}$ (Peig and Green 2009).

**Modelling body condition differences**

To investigate the influence of seasons, sexes, habitat types and time on the body condition of grand skinks, I used Linear Mixed Effect Models with a Gaussian distribution. Models were ranked according to the corrected Akaike Information Criterion for small sample sizes values (AICc, Burnham and Anderson 2002). In the model selection process, the most parsimonious model was identified by having the lowest AICc value and models which differ by $>2$ AICc from the highest ranked model are less favoured. I created 49 models with different combinations of fixed and interaction terms, but used the same four random intercept terms in all models. The random intercept terms were “SkinkID” (accounting for repeated measures), “Year” (accounting for heterogeneity in residual variances) and “Catcher” (accounting for observer bias in measurements). Additionally “OutcropID” was entered as random factor to account for microhabitat bias. Outcrops were inhabited by a varying number of skinks which show high site fidelity (Whitaker 1996, Tocher 2003). Microhabitat attributes of outcrops such as abundance of vegetation on the outcrop, population density and basking areas could influence body condition. The fixed terms and interaction terms included in the models are explained below.

a) Effects of season and sex on body condition

I entered “Season” as a fixed factor in the models to test for seasonal changes in body condition while the variable “Sex” was entered as a fixed factor to investigate growth-independent differences in body condition between the grand skink sex-classes. The Sex:Season interaction term was included in the models to account for increasing body condition due to increasing mass of pregnant females caused by
developing embryos over spring and summer, reduced mass after giving birth in autumn and sex-dependent changes in activity due to behavioural changes between seasons.

b) Effects of the grassland type surrounding outcrops

The variable “Habitat” was included as a fixed factor in the models to investigate differences in body condition between animals living on outcrops in exotic pasture grasslands and indigenous tussock grasslands. The two grassland types were assumed to provide different food resources, microclimatic conditions and predator numbers (Whitaker 1996, Norbury 2001, Tocher 2003). Therefore two interaction terms focusing on habitat-specific changes in body condition were also included: between seasons (Habitat:Season) and sex-classes (Habitat:Sex).

c) Long-term body condition trends

To model changes of grand skink body condition over time I included the variable “Year” as a fixed factor. Models including Year as a continuous variable allowed for an increase or decrease of body condition over time in a linear fashion, while models that did not include the variable Year treated body condition as constant over time. To investigate if potential linear trends of changes in body condition over time differed between the two habitat types pasture and tussock grassland, I included models with the interaction term Year:Habitat in the model set.

Modelling the probability of pregnancy

Adult female grand skinks (SVL >69 mm) captured between November and April of each nominal year (n = 1109) were identified by careful palpation as being pregnant (1) or not being pregnant (0). Generalized linear mixed models with a
binomial distribution were used and ranked according to lowest the AICc. Random factors included in all models of this model set were “SkinkID” (repeated measures), “Year” (heterogeneity of variances) and “Catcher” (observer bias). The following fixed factors and interaction terms were entered in all combinations to create a set of 26 models:

a) Effects of habitat type

To establish any differences in the probability of pregnancy in females inhabiting outcrops in tussock grasslands and outcrops in pasture grasslands, the categorical variable “Habitat” (tussock grasslands or pasture grasslands) was entered in models.

b) Morphology

The variable ‘SVL’ was included into the models to investigate the probability of pregnancy in adult grand skink females (>73 mm SVL) for different body lengths.

c) Time scale

The variable “Month” was included to control for pregnancy status at different times of capture. Grand skinks ovulate in October–November and give birth late February – March (Cree 1994), therefore fewer pregnant females were expected to be captured in March and April. To establish differences in the pregnancy probability of grand skink females of different sizes, the interaction term SVL:Month was also included in the models.

The existence of a long-term trend associated with the probability of pregnancy was tested by including “Year” as a continuous variable. Models including the Year variable would indicate a decrease or increase in pregnancy probability over time and models without the variable Year would indicate no changes in pregnancy
probability over time. The interaction term Habitat:Year was used to investigate possible differences in the long-term trend of pregnancy probability of grand skinks between the two habitat types.

All statistical analyses were performed with R version 2.12.0 (R Development Core Team 2010) and the packages ‘smatr’ version 2.1 (Warthon et al. 2011), ‘lme4’ (Bates and Maechler 2010) and ‘MuMIn’ (Barton 2010).

RESULTS

Morphology and body condition

The mean SVL differed between the adult sex classes, with pregnant females having the highest SVL (mean = 94.6 mm, SE = 0.3 mm, n = 608), followed by males (mean = 86.8 mm, SE = 0.2 mm, n = 1030) and non-pregnant females (mean = 86.9 mm, SE = 0.4 mm, n = 548). Adult skinks of unknown sex had the lowest mean SVL (mean = 77.4, SE = 0.3 mm, n = 501; Fig. 3.2). However, the mean body condition index differed only for neonates (SVL < 51 mm) but showed no significant differences for grand skinks with SVL > 50 mm (juveniles and adult grand skinks, p > 0.05, Fig. 3.3).

Modelling differences in grand skink body condition

The model that best explained the data included the fixed terms Season, Sex and Habitat as well as the interaction terms Sex:Season and Habitat:Season. All other models received only minimal or no support (Table 3.2, the five highest ranked models included only).
Effects of season and sex on body condition

The highest ranked model retained the Season:Sex interaction term, indicating large variations in body condition between seasons that differed between the sex classes. Neonate grand skinks exhibited very high body condition index values (mean = 8.1, SE = 0.05) compared to all other age classes (mean = 7.9, SE = 0.03, Fig.3.3). During their second year, grand skink juveniles had a lower body condition (mean = 7.9, SE = 0.03, Fig. 3.4), similar to that of adult grand skinks (mean = 7.9, SE = 0.03, Fig. 3.3). Body condition peaked in summer and reached slightly higher values in autumn compared to spring for all grand skink sex classes (Figs. 3.4 and 3.5). Exceptions were non-pregnant females where autumn body condition was similar to spring body condition (Fig. 3.5)

Table 3.2: The five highest ranked Linear Mixed Effects Models (out of 49 models) estimating grand skink body condition index.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>model weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex<em>Season + Habitat</em>Season</td>
<td>26</td>
<td>12857.75</td>
<td>12910.06</td>
<td>0.00</td>
<td>0.95</td>
</tr>
<tr>
<td>Sex<em>Season + Habitat</em>Season + Year</td>
<td>27</td>
<td>12862.87</td>
<td>12917.21</td>
<td>7.15</td>
<td>0.03</td>
</tr>
<tr>
<td>Sex*Season</td>
<td>23</td>
<td>12871.74</td>
<td>12917.99</td>
<td>7.93</td>
<td>0.02</td>
</tr>
<tr>
<td>Sex*Season + Habitat</td>
<td>24</td>
<td>12874.89</td>
<td>12923.15</td>
<td>13.10</td>
<td>0.00</td>
</tr>
<tr>
<td>Sex*Season + Year</td>
<td>24</td>
<td>12876.85</td>
<td>12925.11</td>
<td>15.10</td>
<td>0.00</td>
</tr>
</tbody>
</table>

Random factors for all models: skink-ID, outcrop-ID, catcher, year
k = numbers of parameters estimated
Figure 3.2: Distribution of snout-vent length (SVL) of adult grand skinks (*Oligosoma grande*) (SVL >69 mm, n = 2687) from the Redbank ridge area. Different letters refer to significant differences in mean snout-vent length at the 5% level based on Tukeys HSD post-hoc tests.

Figure 3.3: Mean body condition index M for the four age classes of grand skinks (*Oligosoma grande*): 1 - neonates (<1 year, SVL <51 mm), 2 - juveniles (1–2 years, SVL = 51 – 68 mm), 3 and 4 - adults (2–3 years, SVL = 69 – 84 mm, and >3 years, SVL >85 mm, respectively). Bars denote 95% confidence intervals. Different letters refer to significant differences in means at the 5% level based on Tukeys HSD post-hoc tests.
Influence of grassland type on body condition

The estimated parameters of the models showed that animals on outcrops in pasture grasslands had higher body condition (mean = 8.0, SE = 0.03) than animals on outcrops in tussock grasslands (mean = 7.9, SE = 0.02). The interaction term Habitat:Season revealed that this difference was most prominent in autumn (Fig. 3.6).

Linear trends in body condition

The fixed factor Year or any interaction term including Year are not included in the top model revealing that body condition, on average, stayed constant during the 17-year time-period under investigation.
Figure 3.5: Mean body condition index of adult grand skinks (*Oligosoma grande*) for each season estimated by the highest ranked model. Bars depict standard error.

Figure 3.6: Mean body condition of grand skinks (*Oligosoma grande*) caught in different habitat types estimated for different seasons with the highest ranked model. Bars are standard errors.
Models of pregnancy probability

Five of the highest ranked models had values of $\Delta\text{AIC}_c < 2$ with a combined model weight of 0.75. The variables SVL and Month were included in all of the five top-models, and the interaction term SVL:Month and the variable Habitat were included in four of the five models with a combined weight of 0.58 and 0.66, respectively (Table 3.3). The variable Year was only included in two of the top models (0.25 weight) and the Habitat:Year interaction term in only one of the highest ranked models (0.15 weight).

The highest ranked model predicted the highest probabilities of pregnancy to occur in November – February, and very low probabilities for female grand skinks caught in March and April. Additionally, larger grand skink females were predicted to have a higher probability of being pregnant. The interaction term SVL:Month indicated higher probabilities for female grand skinks of lower SVL size being identified as pregnant in November than all the other months, while large females (SVL $> 95$ mm) had a higher probability of still being pregnant in April than smaller females (Fig. 3.7). Furthermore, the model predicted pregnancy probabilities of grand skink females to be higher in tussock habitats (mean $= 0.54$, SE $= 0.01$) than in pasture habitats (mean $= 0.52$, SE $= 0.02$, Fig. 3.8).
Table 3.3: The ten highest ranked Generalised Linear Mixed Models (binary distribution) establishing the probability of pregnancy in female grand skinks. All models included the random factors SkinkID (repeated measures), Catcher (measurement bias) and Year (heterogeneity of residual variances).

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>AAICc</th>
<th>Model weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>SVL*Month + Habitat</td>
<td>17</td>
<td>832.34</td>
<td>866.90</td>
<td>0</td>
<td>0.24</td>
</tr>
<tr>
<td>SVL + Month + Habitat</td>
<td>12</td>
<td>843.27</td>
<td>867.55</td>
<td>0.65</td>
<td>0.17</td>
</tr>
<tr>
<td>SVL<em>Month + Habitat</em>Year</td>
<td>19</td>
<td>829.19</td>
<td>867.89</td>
<td>0.99</td>
<td>0.15</td>
</tr>
<tr>
<td>SVL*Month + Habitat + Year</td>
<td>18</td>
<td>832.04</td>
<td>868.67</td>
<td>1.77</td>
<td>0.10</td>
</tr>
<tr>
<td>SVL*Month</td>
<td>16</td>
<td>836.34</td>
<td>868.84</td>
<td>1.93</td>
<td>0.09</td>
</tr>
<tr>
<td>SVL + Month + Habitat*Year</td>
<td>14</td>
<td>841.07</td>
<td>869.45</td>
<td>2.55</td>
<td>0.07</td>
</tr>
<tr>
<td>SVL + Month</td>
<td>11</td>
<td>847.22</td>
<td>869.46</td>
<td>2.56</td>
<td>0.07</td>
</tr>
<tr>
<td>SVL + Month + Habitat + Year</td>
<td>13</td>
<td>843.62</td>
<td>869.95</td>
<td>3.05</td>
<td>0.05</td>
</tr>
<tr>
<td>SVL*Month + Year</td>
<td>17</td>
<td>836.01</td>
<td>870.57</td>
<td>3.67</td>
<td>0.04</td>
</tr>
<tr>
<td>SVL + Month + Year</td>
<td>12</td>
<td>846.74</td>
<td>871.02</td>
<td>4.12</td>
<td>0.03</td>
</tr>
</tbody>
</table>

k = number of parameters estimated in the model
Figure 3.7: The probability of pregnancy for female grand skink (*Oligosoma grande*) determined by snout-vent-length (SVL) and by month of capture.
Figure 3.8: The probability of pregnancy for female grand skinks of different snout-vent-length comparing between grand skinks occurring on outcrops in tussock grasslands and pasture grasslands.

DISCUSSION

The long-term monitoring programme by DoC provided a large database spanning across a 17-year time period, which allowed thorough investigation of grand skink body condition and pregnancy probabilities. The present study confirmed the size dimorphism between female and male grand skinks with female grand skinks reaching larger snout-vent-length than males, a finding that was also reported by Greer and Whitaker (2002) and Murphy (1994). Compared to other adult classes, adult grand skinks of unknown sex had a smaller average SVL, which is likely explained by immaturity of smaller individuals and difficulties associated with sexing younger animals; immature individuals of *Oligosoma* species are notoriously difficult to sex (e.g., Hare and Cree 2010, Hare and Cree 2011). This study also confirmed positive allometry (a disproportional increase of size to shape) in grand skinks. However, the scaling coefficient (b) was higher than found in previous studies (Whitaker 1996, b=3.12, Greer and Whitaker 2002, b=3.10, this study b=3.15). This difference in scaling may be due to ordinary least square regression
analysis underestimating the slope of the regression line of log (mass) against log (SVL) compared to the standard major axis regression that was used here (Legendre 1998, Green 2001).

This study revealed that body condition differences between sexes of grand skinks were dependent on season and pregnancy status of the females. Such differences can be caused by several factors including physiological and behavioural effects of reproduction, and variation in resource availability in the environment (Eifler 1996, Dickinson and Fa 2000, Amo et al. 2007b). Tocher (2003) reported similar abundances and type of invertebrate food sources throughout the entire grand skink activity season (spring – autumn) which suggested that body condition differences of sex classes between seasons may be attributed to pregnancy status and behavioural differences. The generally low grand skink body condition of all sex classes in spring may be attributed to the loss of energy stores over winter (Jameson Jr. 1974). Grand skinks do not hibernate and have been seen basking during mild winter days (Tocher 2003). However, foraging activity and food resources are likely to be reduced during winter because of the cold temperatures, which may limit food ingestion by grand skinks (Avery et al. 1982). However, metabolic rates will also be reduced in cold temperatures conserving energy stores. Reading (2007) showed that milder winters caused by climate change led to the decline of body condition and survival rates of female common toads (Bufo bufo) in England because the increased metabolism during mild winters reduced stored energy reserves and thus survival rates. Similarly, milder winters caused by climate change could also result in reduced body condition of grand skinks, leading to even lower body condition in spring.

The reproductive status of female lizards influences body condition indices because the female’s mass increases during the development of the embryos/eggs relative to its length. Murphy (1994) found female grand skinks (excluding pregnant females) to be larger, but not significantly heavier, than male grand skinks, while Greer and Whitaker (2002) found female grand skink were larger and heavier than males, but suggested that the differences in weight in their study could be due to females being
pregnant over summer. In the present study, it became apparent that pregnant females in summer exhibited especially high body condition (mass per standardized length) compared to other non-pregnant females, males and grand skinks of unknown sex.

The body condition of female lizards before and during pregnancy impacts on the number and size of offspring/clutches, the length of gestation and the success of the pregnancy (Shine 1980, Schwarzkopf and Shine 1992, Swain and Jones 2000). Female grand skinks ovulation occurs in spring (October/November) and parturition in late summer (March) and early autumn (April, Cree 1994). In spring, body condition of pregnant females was similar to that of all other adult sex classes. The disproportionately high body condition of pregnant females in summer can be attributed to developing embryos which increase body mass. However, females that were still pregnant in autumn (generally the larger females) showed a lower body condition than females that were pregnant in summer. The low body condition of the females still pregnant in autumn could be caused by several reasons: smaller or fewer offspring, or lower maternal body condition compared to females giving birth in summer. Swain and Jones (2000) found that female Metallic skinks (*Niveoscincus metallicus*) which did not have access to optimal basking opportunities had increased gestation length and smaller offspring, which was independent of maternal body condition. Similarly, Rohr (1997) reported that female water skinks (*Eulamprus tympanum*) on restricted diets produced a lower total offspring mass than females on high diets. Moreover, females with lower body condition during gestation have been shown to have fewer and smaller offspring (Doughty and Shine 1998).

Non-pregnant grand skink females showed a disproportional low body condition in autumn compared to other groups of adult grand skinks. In autumn, the non-pregnant female group includes females that had not been pregnant that year, females with failed pregnancy or females that already had given birth. Gestation is energetically costly for lizards (Doughty and Shine 1998, Olsson et al. 2001, Bleu et al. 2011) and the decrease in body condition in the non-pregnant females group
could be attributed to the decrease in body condition of the proportion of females that were pregnant and gave birth in summer and therefore experienced lower body condition than females that were not pregnant.

Reproduction does not only incur a cost on female lizards, male lizards have been found to have lower body condition during mating seasons caused by higher activity associated with mating, increased aggression and increased movements to search for females (Abell 2000). Although, grand skink males experienced also a decline in body condition during mating season (autumn, Cree 1994, Murphy 1994), male grand skinks have not been found to increased their movements (frequency or distance) during autumn (Chapter 2), and pregnant and non-pregnant females experienced similar declines in body condition. Further information on the behaviour and physiology of grand skinks is required to establish the cause for body condition decline in grand skinks in autumn.

Neonate grand skinks showed the highest body condition of all sex classes. It is possible that young grand skinks have a relatively higher mass for their size owing to additional energy stores provided during pregnancy by the maternal female to support them from birth (see Speake (2000) for review of lipid transfer to neonates). Like most other squamates, grand skinks do not display parental care (Murphy 1994) and newborns must fend for themselves, so higher body condition would provide an important energy supplement for their first few months of life.

Next to the reproductive status and associated behaviour changes, environmental factors such as modification of habitat, food availability, increased predation pressure or competition can influence the body condition of lizards (Petren and Case 1998, Amo et al. 2006, Fenner and Bull 2007). The results of this study suggest that the conversion of native tussock grasslands into exotic pasture grasslands may impact on the body condition of grand skinks inhabiting outcrops surrounded by these grasslands. The body condition of grand skinks on outcrops in tussock grasslands was lower than those captured on outcrops in pasture grasslands, driven by a large difference in body condition in autumn between the two grassland
types. Contrary to our results, Hare and Cree (2011) found body condition in post-parturient females of the smaller, sympatric McCann’s skink to be higher on outcrops in tussock grassland than in pasture, and Whitaker (1996) found no difference in body condition of grand skinks between the two habitat types in 1994–95. The differences between the results of the studies could be: 1) use of different body condition indices (Green 2001, see Appendix 2), (2) differences in time-frames of the studies; however, this explanation is not supported by the highest ranked model of this study because it did not include the Year:Habitat interaction that allowed for differences between habitats to develop over time, or (3) as in the case of McCann’s skinks (Hare and Cree 2011) — differences in body shapes, or (4) a real difference based on differences in food availability to each species in the habitats and/or behaviour of the species in different habitat types. Tocher (2003) reported higher invertebrate abundances in pasture grasslands compared to tussock grasslands. Furthermore, Tocher (2003) reported a higher proportion of food items in grand skinks scats in autumn to be fruit, and Whitaker (1996) reported a correlation of skinks occurrences with the diversity of fruit-bearing shrubs on the outcrops. Additionally, Whitaker (1996) reported lower densities of grand skinks per outcrop in pasture grasslands. Higher body condition in autumn in pasture could result from a combination of animals more likely to occupy outcrops which provide fruit-bearing shrubs and less competition on the outcrops due to lower densities. In tussock habitats larger populations of grand skinks may force skinks to occupy less optimal outcrops resulting in reduced overall mean body condition for this habitat type.

Higher densities of grand skinks (Whitaker 1996) and more movements of grand skinks between outcrops in tussock habitat (Chapter 2) would increase the probabilities of encountering mates. Higher probabilities of pregnancy for grand skinks in tussock habitats were found in this study. As pregnancy includes an energetic cost to the female and female skinks have been found to have lower body condition after giving birth (Doughty and Shine 1998), high autumn body condition found in non-pregnant grand skinks in pasture habitat could result from a lower proportion of females that gave birth late summer and autumn in this sex class.
Because resources consumed the season before have been found to strongly influence the number of offspring in the following season (Doughty and Shine 1998), grand skink females in pasture habitat having very high body condition in autumn, might produce higher numbers of offspring, which could balance the lower pregnancy probability in terms of number of offspring. Balanced offspring numbers support findings from Whitaker (1996) who reported no significant differences in the age structure of populations between grand skinks in pasture and tussock habitats. On the other hand, lower colonisation and higher extinction rates were found for sub-populations inhabiting outcrops in pasture grasslands compared to tussock habitats (Seddon et al. 2011). Those lower colonisation rates and higher extinction rates have been explained with predation by assumed higher predator numbers in pasture habitats (Norbury 2001) and avoidance of grand skinks to move across low cropped pasture grasslands between outcrops (Chapter 2). However, the lower colonisation could also be caused by a lack of dispersing offspring. The increased extinctions rates by births and immigration of individuals not replacing deaths and emigrating individuals, could have a significant influence in the overall metapopulation dynamics (Hanski 1998).

For the conservation management of grand skinks knowledge about the population health is important to understand possible decline of reproduction or survival rates. The present study revealed no decline of body condition health over the 17-year period but a previously unknown difference of body condition and pregnancy probabilities of grand skinks between pasture and tussock habitats in autumn. The possible influence on population dynamics have been discussed above and should lead to further investigations. Additionally, the study highlighted the large differences of body condition of male and female skinks between season, which should be taken into consideration when designing and analysing body condition data because of the possibility of biasing the results. This study also highlighted several areas of grand skink’s physiology and behaviour that require further investigation.
CHAPTER FOUR

Influence of Habitat patch characteristics and matrix type on metapopulation parameters: the case of the highly threatened grand skink

A large schist-rock outcrop surrounded by native tussock grasslands.
INTRODUCTION

The concept of metapopulations has gained considerable traction in conservation biology since an increasing number of animal and plant populations now inhabit fragmented landscapes, often resulting from habitat degradation and destruction (Hanski and Gilpin 1991, Dunning et al. 1995, Tischendorf and Fahrig 2000, Franklin 2010). More than four decades ago, Levins (1969) published his work on how environmental heterogeneity influences population dynamics and coined the term metapopulation. The concept, originally developed to maximise effective biological control of agricultural pest species spatially separated in the environment, is used by conservation biologists to investigate dynamics of populations in fragmented habitats. A metapopulation consists of a number of small populations that occur in spatially distinct habitat patches surrounded by a landscape that is generally unsuitable for species occupancy (termed ‘matrix’, Levins 1969, Hanski 1998). Individual populations resident in habitat patches embedded in the matrix may become extinct but migrating individuals may be able to (re-)colonise unoccupied habitat patches. For the metapopulation concept to be valid however, the level of migration of individuals between habitat patches has to be low enough to allow for independent population dynamics in individual habitat patches (Hanski and Gilpin 1997). The metapopulation framework introduces a spatial dimension to modelling population dynamics, connecting individual populations which are spatially distributed in a wider landscape. Conservation biologists and managers are thus able to investigate metapopulation responses to ecological processes at the landscape scale, the level of connectivity of individual populations, and their probabilities of extinctions or new establishment.

Levins’ classic metapopulation concept assumes equal size of habitat patches, and equal colonisation and extinction probabilities for populations on all habitat patches (Levins 1969). In reality, there are no metapopulations that have been found to meet these assumptions and models have been developed to allow for heterogeneity in patch size, colonisation and extinction probabilities. According to the “area and isolation” paradigm developed by Hanski (1998), and supported by empirical and
theoretical research, the extinction rate is inversely correlated to the size of a habitat patch (Hill et al. 1996), whereas colonisation probability is inversely correlated to the degree of isolation of the habitat patch (Thomas and Harrison 1992, Moilanen et al. 1998, Moilanen 1999). Although the discrimination of habitat patches of different size and isolation has been factored into metapopulation models in the past, more realistic models incorporating the quality of habitat patches have been called for (Dennis and Eales 1997, Thomas et al. 2001, Armstrong 2005). In recent years, empirical evidence has pointed towards the importance of habitat characteristics in metapopulation dynamics and that these influence colonisation, extinction and occupancy probabilities differently. Moilanen and Hanski (1998) accounted for habitat quality by adjusting the effective habitat patch size but found model fit did not improve with inclusion of the chosen environmental variables. On the other hand, research by Dennis and Eales (1997) and Thomas et al. (2001) showed that habitat quality strongly determined butterfly occupancy probabilities in fragmented landscapes. Similarly, Jaquiery et al. (2008) demonstrated that habitat quality significantly influenced occupancy probabilities for greater white-toothed shrew (Crocidura russula) metapopulations, although the extinction probabilities were not lowered as expected.

Many metapopulation models treat the matrix surrounding habitat patches as a homogeneous landscape, similar to an ocean surrounding a group of islands (Jules and Shahani 2003). Increasingly, research shows that the matrix is neither uniform nor ecologically separated from habitat patches, rather the matrix is heterogeneous and can affect patch populations and the migrants that move through it (Ricketts 2001, Fischer and Lindenmayer 2007). Although research in landscape ecology has demonstrated that matrix composition can influence the speed, distance and direction of dispersing animals, rarely are these factors incorporated into metapopulation models. The influence of matrix type on the dispersal of individuals has an effect on colonisation and occupancy probabilities in relation to metapopulation dynamics (Ricketts 2001, Vögeli et al. 2010). Thus, it is important to know to what extent different habitat patch and matrix characteristics can
influence the different parameters of metapopulations in order to understand changes in the overall metapopulation dynamics.

Several different approaches have been developed to model metapopulation parameters ranging from models based on the occupancy state of habitat patches, to simulation models which model the dynamics of each local population, requiring very detailed information about the demography of the study species (Akcakaya 2000, Sjögren-Gulve and Hanski 2000). On the other hand the occupancy state of a habitat patch can be described with simple presence-absence data which are used in logistic regression models or incidence function models (Hanski 1994) to estimate extinction, colonisation and occupancy parameters. An advantage of presence-absence data is the rapidity of data collection over large areas, however two types of errors have to be taken into account in the sampling design. First, false-presences occur when a species is recorded as present in a habitat patch while actually being absent, for example by misclassification of the species. This bias can be avoided with a rigorous sampling design specifically targeting the study species and using well-trained observers. Second, false-absences occur when a species is recorded as absent while being present but unobserved in a habitat patch. The detection probability of a species depends on a variety of factors: local density of the species, seasonal and diurnal behavioural patterns, how conspicuous the species is, as well as environmental variations and sampling effort (Gu and Swihart 2004, Bailey et al. 2007). Moilanen (2002) and Tyre et al. (2003) showed that incomplete detection of a species can result in biased estimation of metapopulation parameters and can reduce the predictive abilities of metapopulation models. To account for incomplete detectability in the estimation of metapopulation parameters, Mackenzie et al. (2003) developed a sampling regime including repeat surveys for each habitat patch and a statistical framework using a detection probability parameter to estimate colonisation, extinction and occupancy probabilities.

This chapter presents a study which takes into account the incomplete detectability of a species in the evaluation of the effects of habitat patch and matrix characteristics on the predictive accuracy of metapopulation models. The goal was
to quantify the degree to which habitat patch and matrix characteristics influence the underlying dynamics of a metapopulation of the highly endangered, New Zealand grand skink (Oligosoma grande). Presence-absence data were used to create models identifying the relative importance of habitat patch characteristics on metapopulation parameters (occupancy, colonisation and extinction probabilities). I investigated what effect the type of matrix between habitat patches, habitat patch size and structure, isolation and vegetation cover had on patch-specific colonisation, extinction, occupancy and detectability probabilities for the grand skink metapopulation. Additionally, I measured the ability of the final model to classify outcrops as occupied or unoccupied to provide guidance for conservation biologists as to the quality of the model for predictive purposes.

METHODS

Study species

The grand skink is an endangered large, viviparous skink occupying schist-rock outcrops scattered throughout the native tussock and exotic pasture grasslands of the central South Island, New Zealand. Today, grand skinks occur in only eight percent of their historic range (Whitaker and Loh 1995). Introduced mammalian predators and the loss of habitat have been identified as their major threats (Whitaker and Loh 1995, Reardon et al. 2012). The omnivorous grand skinks feed on insects and fruits that they find mostly on their residential outcrop (Whitaker and Loh 1995, Tocher 2003). Grand skinks show strong site fidelity, and have only occasionally been observed in vegetation away from a rock outcrop (Coddington and Cree 1997). The grassland matrix surrounding the outcrops is used primarily during dispersal. However, a very small percentage of young animals disperse to new outcrops while adult animals spend most of their life on the same outcrop (Murphy 1994, Whitaker 1996). The outcrops grand skinks occur on come in various sizes and shapes. Even relatively small outcrops can be inhabited by small populations of up to 20 grand skinks while large outcrops can be inhabited in excess of 50 individuals (Gebauer,
pers. observation). These characteristics of grand skink metapopulations (high site fidelity, and small populations even on small outcrops) make them suitable to study with presence-absence data because the proportion of outcrops occupied by passing by grand skinks will be very small and identified extinction and colonisation events are to a large extent non-trivial.

**Study area**

This study was conducted at Macraes Flat (45°28′ S, 170°28′ E; Fig. 4.1), which is a population stronghold for grand skinks, monitored and managed by New Zealand’s Department of Conservation for over two decades. When Europeans settled in New Zealand about 170 years ago, extensive indigenous tall tussock (*Chionochloa* spp.) grasslands dominated the area, with some tussock grass individuals exceeding 1.5 m in height. Over the intervening period, these indigenous grasslands have been modified to varying degrees through the application of fertiliser, over-sowing with preferred exotic forage plant species, by grazing and by burning (McGlone 2001, Wardle 2002). Today, land use for the most part comprises intensive cattle and sheep grazing. However, within the conservation reserve at Macraes Flat, the New Zealand Department of Conservation is protecting remnant indigenous tussock grassland ecosystems. Grand skinks occur on schist-rock outcrops scattered throughout the study area, surrounded by a matrix consisting of a mosaic of indigenous tussock grasslands dominated by *C. rigida* and *C. rubra*, and pasture grasslands dominated by *Lolium* spp. and *Trifolium repens* close-grazed by sheep and cattle. A property boundary divides the study site which encompasses protected tussock grasslands to the south-west and pasture grasslands of private farmlands to the north-east.
Figure 4.1: Relative location of study sites and distribution of the monitored habitat patches (black squares). In 2006–08 data was collected in study sites A (exotic pasture grasslands) and B (indigenous tussock grasslands; Seddon, unpublished data). Study site C (tussock grasslands) and D (pasture grasslands) were used for evaluation data collection as part of this thesis in 2010.
Data collection

Occupancy data were collected by surveying all schist-rock outcrops in pasture (n = 115) and tussock grasslands (n = 174) at the study site. As in ‘Rock’ in Chapter 2, an outcrop was classified as a schist-rock tor or group of schist-rock tors separated by a minimum of 10 m of matrix grassland from any other schist-rock tor (Whitaker 1996, Seddon et al. 2011). To continue with the standard terminology of metapopulation theory (Hanski and Gilpin 1997) these outcrops/Rocks are referred to as habitat patches in the present chapter. Each habitat patch was surveyed for three years (2006–2008, Seddon, unpublished data) with four surveys within a two-week time period in January each year. The habitat patch was searched until at least one grand skink was sighted or 5 minutes elapsed without a sighting, using a standard search protocol modified from Roughton and Seddon (2006). A habitat patch was recorded as having skinks present (1) when at least one skink was sighted, and as absent (0) when no skink was sighted within the 5 minute search. Each survey was undertaken in sunny, warm and low wind weather conditions when skinks are most likely to bask and forage (Patterson 1992, Coddington and Cree 1997) providing highest detection probabilities. During each set of four surveys observers were rotated so they would not monitor the same habitat patch twice. Similar weather conditions for each survey day and the rotation of observers was assumed to provide detection probabilities independent of survey specific factors.

Five categorical habitat patch characteristics that could be rapidly collected during surveys were identified, and were likely to be important for the ecology of grand skinks. Habitat patch size has been shown to be an important attribute of extinction probabilities through its assumed correlation with population size which in turn decreases the risk of extinction by stochastic events and therefore increases occupancy probability (Hanski 1998). In this study, habitat patches were categorised according to their relative size into three broad size groups: small, medium and large. Small habitat patches where large enough to be inhabited by small populations of grand skinks (Gebauer, pers. observations). The structure of a habitat patch was either categorised a distinct rock-tor (“discrete”) or a group of
rock-tors (“clustered”). A cluster of rock-tors within a habitat patch may provide more crevices of varying sizes, potentially providing more refugia for grand skinks (Murphy 1994). Cracks and crevices are also spaces for invertebrates which form a large part of the grand skink’s diet. On the other hand, a distinct rock-tor may be more likely to provide crevices with enough depth to protect grand skinks during winter. I categorised the vegetation cover in the habitat patch as “none”, “moderate” and “abundant”. Vegetation on an outcrop provides habitat for invertebrates, and flowers attract flying invertebrates from the surrounding matrix. Additionally, fruit bearing shrubs have been identified as an important factor correlated with grand skink occupancy (Whitaker 1996). Fruits are an important part of the grand skinks’ diet (Tocher 2003). Furthermore, vegetation can act as refuge for grand skinks during predatory attacks as well as shade during hot temperatures allowing for optimal thermoregulation. Different matrix types surrounding a habitat patch may influence invertebrate composition and abundance (Tocher 2003), but also movements of grand skinks between habitat patches. Habitat patches were classified as being surrounded by either pasture grasslands or tussock grasslands. Previous studies found that movements of grand skinks were predominantly less than 50 m, with only occasional movements of over 400 m (Coddington and Cree 1997, Houghton 2000). Therefore, the distance between habitat patches would significantly influence colonisation and occupancy probabilities. A large number of connectivity measures have been suggested in the literature (Tischendorf and Fahrig 2000, Prugh 2009). One of the simplest measures is the distance to the nearest neighbour habitat patch. This measure is often described as too simplistic, and Prugh (2009) reported that the distance to the nearest occupied habitat patch would perform significantly better as a predictor for species occupancy. However, because grand skinks have a low detectability (Seddon et al. 2011), recorded absences could also include presences of grand skinks introducing an error into connectivity measures based on occupancy data. Therefore, as a measure of isolation of habitat patches, I used the Euclidean distance from each habitat patch to the nearest neighbouring patch (but see Appendix 3 for post-hoc analysis). The distances were measured using aerial photographs and the GIS ArcView 10 software.
Statistical analysis

The presence-absence and habitat patch specific data were entered into the computer program PRESENCE 3.0 which was specifically developed to account for incomplete detectability in the analysis of presence-absence data (MacKenzie et al. 2003, Hines 2006). The metapopulation parameters, occupancy probability, colonisation probability and extinction probability are simultaneously estimated using a resource selection function based on logistic regression models which are simultaneously corrected for incomplete detectability using a second logistic regression-based detectability model (for details see MacKenzie et al. 2006). According to the sampling design I used the multiple season analysis to estimate occupancy, colonisation, extinction and detection probabilities (Mackenzie 2006). For each habitat patch, a survey history can be created using the presence or absence of grand skinks recorded during each of the four surveys per year utilising the detectability model. This information was used to estimate the probability of detection for each habitat patch dependent on the patch-specific characteristics. The patch-specific probability of colonisation, extinction and occupancy is then estimated for each habitat patch (MacKenzie et al. 2002, 2003).

One aim of this study was to investigate the relative importance of habitat patch characteristics on the metapopulation parameters. Since all parameters were estimated simultaneously in the models created in PRESENCE, including all biological meaningful combinations of habitat characteristics would have resulted in a large number of models. I employed a selection process to identify the most relevant habitat characteristics for each metapopulation parameter separately, as suggested by MacKenzie (2006). While creating a set of models investigating the relative importance of habitat patch characteristics for one metapopulation parameter, I used intercept only models (null-models) for the other three parameters (Mackenzie 2006). To rank the relative importance of the habitat patch characteristics I created a model set for each of the four parameters representing all combinations of the habitat patch characteristics to ensure each were represented equally in the model set (Anderson 2008). Within each model set, models were
ranked using values of the second-order bias corrected Akaike Information Criterion (AICc, Burnham and Anderson 2002). To identify the relative importance of a particular variable the Akaike weights of all models that included the focal variable were added and the variables ranked accordingly (Anderson 2008).

Using the selection process described above, the relative importance of the habitat patch characteristics (size, structure, vegetation cover and matrix type) was investigated for all metapopulation parameters (occupancy, colonisation, extinction and detection probability) while habitat patch isolation was included only in the models sets for colonisation probability and occupancy probability. Candidate model-sets for each parameter included models with a single patch characteristic and models with all combinations of the patch characteristics, resulting in 31 models for occupancy and colonisation probability, and 15 models for extinction and detection probabilities. Habitat patch characteristics which had summed weights of >0.5 were used to create models for the candidate set investigating temporal variation on the metapopulation parameter. The candidate set included the following models: (1) all parameters were allowed to vary between years, (2) only colonisation probabilities remained constant, all other parameters varied between years, (3) only extinction probabilities remained constant, (4) only detection probabilities remained constant and (5) colonisation and extinction probabilities remained constant. I allowed detection probability to vary between years in all models acknowledging the potential differences in weather conditions and observer experience between years.

**Evaluation**

A further aim of this study was to evaluate the predictive abilities of the top-ranked model to provide guidance for conservation biologists. A number of authors have requested that every model needs to be evaluated when being considered for predictive purposes (Fielding and Bell 1997, Manel et al. 2001). To measure the predictive power of logistic regression models, the continuous probabilities
predicted by the model were converted into dichotomous presence-absence data utilizing the threshold optimization method of determining the cross-point of the proportion of correctly identified presences (sensitivity) and correctly identified absences (specificity) plotted against a number of thresholds (Barbosa et al. 2003, Jimenez-Valverde and Lobo 2007, Fig.4.2). The presences and absences obtained using the optimised threshold were then compared to the validation data-set by determining sensitivity, specificity and correct classification rates ranging from 0 (no correct classification) to 1 (perfect classification, Fielding and Bell 1997). I used two evaluation measures, the threshold dependent true skill statistic (TSS) developed by Allouche et al. (2006) and the threshold independent area under the curve (AUC) of the receiver operating characteristic (ROC) function (Fielding and Bell 1997). The TSS is similar to the widely used Cohen’s kappa (Cohen 1960) but has the advantage of being unaffected by prevalence or the size of the validation set (Allouche et al. 2006). It takes into account sensitivity and specificity and ranges between -1 to +1, where values below zero indicate a performance no better than random, and +1 represents perfect agreement (Allouche et al. 2006). The AUC does not directly identify a classification rule for converting probabilities into presences and absences (Fielding and Bell 1997). It is obtained by plotting 1-specificity versus sensitivity for all thresholds with AUC values varying from 0.5 for an indiscriminate model to 1.0 for a perfect model (Hirzel et al. 2006, Cianfrani et al. 2010).

To evaluate the predictive abilities of the highest ranked model from my previous analysis I used 10-fold cross-validation (internal evaluation) and independent data (external validation). The 10-fold cross-validation procedure randomly splits the data into ten independent groups, using nine groups to train the model and the 10th group to validate the model. The training and validation process was repeated ten times, each time leaving out a different group for validation enabling the calculation of the standard deviation and variance for the AUC and TSS of the highest ranked model (Hirzel et al. 2006, Hastie et al. 2009). AUC and TSS were calculated using the software R version 2.12.0 (R Development Core Team 2010).
Using the habitat patch characteristics of the validation data-set, the individual probability of occupancy for each habitat patch in the first year was estimated using the logistic regression model for occupancy probability of the top-ranked model. The occupancy probabilities for the following two years were then estimated by calculating predicted extinction ($\varepsilon$) and colonisation ($\gamma$) probabilities for each habitat patch with the logistic regression models obtained in PRESENCE and deriving the occupancy probabilities ($\psi_{t+1}$) from the occupancy probabilities ($\psi_t$) of the previous year:

$$\psi_{t+1} = \psi_t \times (1- \varepsilon_t) + (1- \psi_t) \times \gamma_t \quad \text{(MacKenzie et al. 2006)}$$

It has been argued that cross-validation data-sets do not fully satisfy the assumption of using independent data to reduce bias in evaluation measures because they were collected at the same study site at the same time (Boyce et al. 2002). Therefore, Araujo and Guisan (2006) emphasized that to test transferability of the predictive accuracy of a model to other areas, testing data should be spatially independent from training data. To assess how well the occupancy model predicted skink occurrences in other areas I collected habitat patch characteristics and determined the presence or absence of grand skinks for 64 habitat patches surrounded by pasture and 67 habitat patches surrounded by tussock grasslands during four surveys in December 2010. The habitat patches in pasture grasslands were located 1 km east and the habitat patches in the tussock grasslands 3 km west of the original site (Fig. 4.1). The final model was trained with all available data from the years 2006–2008 and the optimized threshold identified. The data collected on habitat patch characteristics in 2010 were used to predict occupancy of grand skinks in the two new study sites and the model’s predictive abilities measured using TSS and AUC with combined presence-absence data of the four surveys from 2010.
RESULTS

During the 2006–2008 surveys, a total of 289 habitat patches, 115 in pasture grasslands and 174 in tussock grasslands, were identified at the study site. Combining all four surveys of each year and collating the proportion of patches where skinks were recorded as being present resulted in a naïve estimated occupancy rate of 0.42, 0.48 and 0.47 in 2006, 2007 and 2008, respectively. Thirty-three colonisation and 19 extinction events were recorded between 2006 and 2007, and 34 colonisations and 35 extinctions between 2007 and 2008.

Habitat and matrix characteristics

After ranking the habitat patch characteristics according to their relative importance for each metapopulation parameter, the occupancy probability model retained (in order of relative importance) size and matrix type; the colonisation probability model retained size and matrix type; the extinction probability model retained size, structure, vegetation cover and matrix type, and the detection probability model retained size, structure and matrix type (Table 4.1). Overall, size of the habitat patch was the highest ranked variable for each of the metapopulation parameters, closely followed in importance by matrix type. Larger habitat patches had higher occupancy, colonisation and detection probabilities and a lower extinction probability. Additionally, detection probabilities increased with habitat patch size (Table 4.2). Matrix type had similar combined model weights compared to habitat patch size for occupancy, colonisation and detection probabilities. Matrix type was ranked lowest for extinction probabilities but still accounted for combined model weights of 0.57 and therefore was included in the final model (Table 4.1). Habitat patches had higher occupancy and colonisation probability if surrounded by tussock grasslands compared to pasture grasslands (Table 4.2). The structure of habitat patches was included only in the models for extinction and detection probabilities (Table 4.1); habitat patches consisting of a cluster of outcrops had higher extinction
Figure 4.2: Estimating the optimised threshold for converting continuous probabilities into presences and absences by determining the corrected classification rates at all possible cut-off points at 0.1 intervals for the 2006 dataset using the final model. Identification of the cross-point between sensitivity and specificity results in an optimized threshold of 0.43 with a correct classification rate of 69%.

probabilities and lower detection probabilities than did habitat patches with one distinct outcrop (Table 4.2). High-ranked models for extinction probabilities also included vegetation cover (Table 4.1), with greater vegetation cover associated with decreased extinction probabilities (Table 4.2). Distance to the nearest habitat patch yielded only very low combined model weights and therefore was not included in the resulting models for any of the metapopulation parameters (Table 4.1).

Using all retained variables for each metapopulation parameter, the most parsimonious model describing variation in metapopulation parameters over time kept the colonisation probability constant but varied extinction and detection
probabilities between years (Table 4.2). The other models had little support with delta AICc >2.00 (Table 4.3). In the most parsimonious model, the average extinction probability increased in the period 2007/08, compared to 2006/07 while colonisation probability was constant at 0.27 (SE = 0.16) over the three year period (Table 4.4). Average occupancy probabilities were lowest in 2006 at 0.43 (SE = 0.21), but increased to 0.51 (SE = 0.22) and 0.50 (SE = 0.22) in 2007 and 2008, respectively (Table 4.5). Detection probabilities were highest in 2006 with 0.60 (SE = 0.11) and decreased to 0.51 (SE = 0.11) in 2007 and 0.53 (SE = 0.10) in 2008 (Table 4.5). The combined probability of successfully detecting skinks during all four surveys of one year was derived from the estimated detection probabilities (Stauffer et al. 2002), and ranged from 0.94 to 0.97, leaving a very small probability of 0.06 – 0.03 of recording skinks as being absent when they were actually there.

### Table 4.1: Summed Akaike weights for models including a particular variable

<table>
<thead>
<tr>
<th>Metapopulation Parameter</th>
<th>Occupancy probability</th>
<th>Colonisation probability</th>
<th>Extinction probability</th>
<th>Detection probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat patch characteristic</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size</td>
<td>1.00*</td>
<td>1.00*</td>
<td>0.97*</td>
<td>1.00*</td>
</tr>
<tr>
<td>Structure</td>
<td>0.49</td>
<td>0.29</td>
<td>0.97*</td>
<td>1.00*</td>
</tr>
<tr>
<td>Vegetation</td>
<td>0.28</td>
<td>0.33</td>
<td>0.69*</td>
<td>0.44</td>
</tr>
<tr>
<td>Isolation (distance)</td>
<td>0.40</td>
<td>0.27</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Matrix</td>
<td>1.00*</td>
<td>1.00*</td>
<td>0.57*</td>
<td>0.98*</td>
</tr>
</tbody>
</table>

* Variables included in the overall model for the corresponding parameter (Summed Akaike weight >0.5)
Chapter four: Metapopulation parameters

**Table 4.2:** Variables included in the final model for each of the metapopulation parameters, their coefficients (β) and standard errors (S.E.).

<table>
<thead>
<tr>
<th>Metapopulation parameter</th>
<th>Variable</th>
<th>β</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occupancy probability</td>
<td>Size</td>
<td>1.001</td>
<td>0.190</td>
</tr>
<tr>
<td></td>
<td>Matrix</td>
<td>1.314</td>
<td>0.288</td>
</tr>
<tr>
<td></td>
<td>intercept (2006)</td>
<td>-3.064</td>
<td>0.480</td>
</tr>
<tr>
<td>Colonisation probability</td>
<td>Size</td>
<td>0.782</td>
<td>0.235</td>
</tr>
<tr>
<td></td>
<td>Matrix</td>
<td>1.532</td>
<td>0.365</td>
</tr>
<tr>
<td></td>
<td>intercept</td>
<td>-3.654</td>
<td>0.598</td>
</tr>
<tr>
<td>Extinction probability</td>
<td>Size</td>
<td>-0.394</td>
<td>0.310</td>
</tr>
<tr>
<td></td>
<td>Structure</td>
<td>0.904</td>
<td>0.499</td>
</tr>
<tr>
<td></td>
<td>Vegetation</td>
<td>-0.645</td>
<td>0.478</td>
</tr>
<tr>
<td></td>
<td>Matrix</td>
<td>-0.540</td>
<td>0.448</td>
</tr>
<tr>
<td></td>
<td>intercept (2006/07)</td>
<td>-1.420</td>
<td>1.087</td>
</tr>
<tr>
<td></td>
<td>intercept (2007/08)</td>
<td>-0.330</td>
<td>1.089</td>
</tr>
<tr>
<td>Detection probability</td>
<td>Size</td>
<td>0.526</td>
<td>0.082</td>
</tr>
<tr>
<td></td>
<td>Structure</td>
<td>-0.529</td>
<td>0.120</td>
</tr>
<tr>
<td></td>
<td>Matrix</td>
<td>0.317</td>
<td>0.131</td>
</tr>
<tr>
<td></td>
<td>intercept (2006)</td>
<td>0.064</td>
<td>0.260</td>
</tr>
<tr>
<td></td>
<td>intercept (2007)</td>
<td>-0.333</td>
<td>0.254</td>
</tr>
<tr>
<td></td>
<td>intercept (2008)</td>
<td>-0.229</td>
<td>0.257</td>
</tr>
</tbody>
</table>

**Table 4.3:** Models investigating temporal variation of colonisation (γ), extinction (ε) and detection probability (p) for the models γ (size + matrix), ε (size + structure + veg + matrix) and p (size + structure + matrix). The model for occupancy probability was ψ (size + matrix). The models were ranked by AICc values. (.) = parameter is constant over time, only covariates included, (time) = parameter varies between years, covariates and intercepts for each year included.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>Deviance</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>ψi, γ(.), ε(time), p(time)</td>
<td>18</td>
<td>2907.01</td>
<td>2945.54</td>
<td>0.00</td>
</tr>
<tr>
<td>ψ, γ (time), ε (time), p(time)</td>
<td>19</td>
<td>2906.96</td>
<td>2947.79</td>
<td>2.24</td>
</tr>
<tr>
<td>ψ, γ (.), ε (.), p(time)</td>
<td>17</td>
<td>2912.81</td>
<td>2949.07</td>
<td>3.52</td>
</tr>
<tr>
<td>ψ, γ (time), ε (.), p(time)</td>
<td>18</td>
<td>2912.81</td>
<td>2951.34</td>
<td>5.80</td>
</tr>
<tr>
<td>ψ, γ (.), ε (.), p(.)</td>
<td>15</td>
<td>2940.15</td>
<td>2971.91</td>
<td>26.36</td>
</tr>
</tbody>
</table>

k – number of estimated parameters
Table 4.4: Mean (SE) colonisation and extinction probabilities estimated from the final model across all habitat patches.

<table>
<thead>
<tr>
<th>Year</th>
<th>Colonisation probability</th>
<th>Extinction probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006 – 2007</td>
<td>0.27 (0.16)</td>
<td>0.11 (0.07)</td>
</tr>
<tr>
<td>2007 – 2008</td>
<td>0.27 (0.16)</td>
<td>0.25 (0.12)</td>
</tr>
</tbody>
</table>

Table 4.5: Mean (SE) occupancy and detection probabilities estimated from the final model across all habitat patches.

<table>
<thead>
<tr>
<th>Year</th>
<th>Detection probability</th>
<th>Occupancy probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>0.60 (0.11)</td>
<td>0.43 (0.21)</td>
</tr>
<tr>
<td>2007</td>
<td>0.51 (0.11)</td>
<td>0.51 (0.22)</td>
</tr>
<tr>
<td>2008</td>
<td>0.53 (0.10)</td>
<td>0.50 (0.22)</td>
</tr>
</tbody>
</table>

Internal validation

For the cross-validation data-sets used to train the models, the optimized thresholds varied between 0.42 and 0.57, highlighting the differences in prevalence of presences and absences in the different data-sets. The mean of the correct classification rate from 10 cross-validation data-sets decreased from 0.70 (SE = 0.07) for the 2006 data to 0.65 (SE = 0.06) for the 2007 data and 0.64 (SE = 0.10) for the 2008 data (Table 4.6). Overall the correct classification rate ranged from 0.54 to 0.74 with an overall mean of 0.70 (SE = 0.07). The cross-validation procedure for the top model estimated an overall mean AUC of 0.74 (SE = 0.06) which indicated “satisfying to good” predictive abilities (Hosmer and Lemeshow 1989, Fig. 4.3). The AUC of the model stayed relatively constant for grand skink occupancy predictions for all three years. The mean TSS was 0.38 (SE = 0.13) suggesting a predictive ability of the model that was better than
random. Similar to the correct classification rate, the TSS revealed a better predictive ability for the first year (2006) compared to the following two years (2007, 2008) and showed an increase in the associated standard error (Table 4.6; Fig. 4.4).

Table 4.6: Accuracy measures for the predictive abilities of the final model. Mean (SE) of 10 cross-validation sets using optimised classification thresholds. The correct classification rate ranges from 0 for no correctly classified cases to 1.0 for perfect classification by the model. The true skill statistic (TSS) values range from -1 indicating predictive abilities no better than random, to +1 for a perfect model. The AUC values range from 0.5 for indiscriminate models to +1 for perfect predictive abilities.

<table>
<thead>
<tr>
<th>Year</th>
<th>optimised threshold</th>
<th>correct classification rate</th>
<th>TSS</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>0.46 (0.05)</td>
<td>0.70 (0.07)</td>
<td>0.38 (0.13)</td>
<td>0.74 (0.06)</td>
</tr>
<tr>
<td>2007</td>
<td>0.51 (0.01)</td>
<td>0.65 (0.06)</td>
<td>0.27 (0.14)</td>
<td>0.73 (0.07)</td>
</tr>
<tr>
<td>2008</td>
<td>0.50 (0.02)</td>
<td>0.64 (0.10)</td>
<td>0.29 (0.18)</td>
<td>0.74 (0.06)</td>
</tr>
</tbody>
</table>

Figure 4.3: Receiver-operator curves for 10-fold cross-validation procedure for the years 2006–08. The dashed line indicates an AUC value of 0.5 for an indiscriminate model. An AUC of +1 indicates perfect predictive abilities.
External validation

The naïve occupancy rates for the 67 habitat patches in tussock grasslands and 64 habitat patches in pasture grasslands monitored in 2010 were 0.55 and 0.44, respectively, with an overall mean naïve occupancy rate of 0.49. Using the logistic regression function estimated by the top-ranked model the average occupancy probability for habitat patches in tussock grasslands was 0.50 (SE = 0.20) and for habitat patches in pasture grasslands was 0.24 (SE = 0.15) with an overall mean occupancy probability of 0.38 (SE = 0.21). Using an optimised threshold of 0.43 derived from the 2006 data-set, a TSS of 0.49 was estimated for the model using the total 2010 data-set. The AUC of the overall model was estimated as 0.76 when using the total 2010 data-set. The TSS and AUC measures indicate that the model is...
a good predictor of grand skink occupancy when combining data from both matrix types (Hosmer and Lemeshow 1989, Allouche et al. 2006).

Assessing the predictive ability of the top-ranked model separately for both matrix types resulted in higher TSS and AUC values for habitat patches in tussock grasslands. The model predictions for presences were more accurate for habitat patches in tussock grasslands (sensitivity = 0.76) compared to habitat patches in pasture grasslands (sensitivity = 0.43). For both habitat patches in tussock and pasture grasslands, the specificity measure were higher than the sensitivity measures (Table 4.7)

<table>
<thead>
<tr>
<th></th>
<th>correct classification rate</th>
<th>sensitivity</th>
<th>specificity</th>
<th>TSS</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pasture 2010</td>
<td>0.70</td>
<td>0.43</td>
<td>0.92</td>
<td>0.36</td>
<td>0.71</td>
</tr>
<tr>
<td>Tussock 2010</td>
<td>0.76</td>
<td>0.76</td>
<td>0.83</td>
<td>0.59</td>
<td>0.84</td>
</tr>
<tr>
<td>total</td>
<td>0.75</td>
<td>0.62</td>
<td>0.87</td>
<td>0.49</td>
<td>0.76</td>
</tr>
</tbody>
</table>

**DISCUSSION**

**Habitat patch characteristics**

Habitat-patch characteristics had a strong influence on all metapopulation parameters (occupancy, colonisation, extinction and detection probabilities) estimated by the top-ranked model. However, the strength and direction of the influence of habitat patch characteristics (size, structure, vegetation cover and matrix type) differed between metapopulation parameters. The size of the habitat patch had the most influence on metapopulation parameters. Many empirical and
theoretical studies have found this relationship (Hill et al. 1996, Hanski 1998). By definition, local sub-populations of a metapopulation are small and prone to extinction. Larger habitat patches can accommodate populations of greater size, and provide more resources such as food and refugia which reduces a population probability of extinction due to stochastic processes. In this study, larger habitat patches had higher occupancy and colonisation probabilities, and lower extinction probabilities. The size of the habitat patch influences colonisation probabilities by increasing the chance of an animal encountering a habitat patch while moving through the landscape. Furthermore, in this study, the size of the habitat patch was positively correlated with the height of the outcrop (Gebauer, unpublished data). Higher outcrops could be assumed to be more visible to migrating individuals, especially in tussock grasslands. In her study on the homing abilities of grand skinks, Stanley (1998) found that grand skinks were more likely to return to their home-outcrop if it was visible from the release location (and within 70 m). Therefore grand skinks may be more likely to colonise a habitat patch which is visible from their residential habitat patch. Moreover, detection probabilities were higher in larger habitat patches which are likely to accommodate a larger number of animals. With increasing abundances of grand skinks the likelihood of detection also increases.

Matrix type was as important for the parameters of the grand skink metapopulation as habitat-patch size. Habitat patches in native tussock grassland had higher occupancy and colonisation probabilities and lower extinction probabilities than habitat patches in modified pasture grasslands, similar to the findings of Seddon et al. (2011). Higher colonisation probabilities indicate higher rates of successful movements of grand skinks between habitat patches in tussock grasslands, and confirms the findings of Berry et al. (2005), who showed that populations of grand skinks in habitat patches in pasture were genetically more isolated than grand skinks in habitat patches in tussock grasslands. Movements between habitat patches can expose grand skinks to risk of predation. Norbury (2001) demonstrated that high densities of introduced rabbits in pasture grasslands support larger populations of introduced mammalian predators that take lizards as secondary prey. Higher
perceived predation risk, rather than actual predation during movements could also reduce colonisation probabilities in grand skinks. In contrast to tall tussock grasses, close-cropped pasture grasslands do not provide shelter during movements of grand skinks between habitat patches. Indeed, studies using radio-transmitters on grand skinks recorded more movements between habitat patches in tussock grasslands than in pasture grasslands (Chapter 2). Therefore the disposition of grand skinks to move to new habitat patches in pasture grasslands may be reduced and may lead to lower colonisation probabilities. Furthermore, matrix type was more important for colonisation probabilities than was distance between habitat patches, indicating that low pasture grasses had a larger effect on colonisation probabilities than did distance to the nearest neighbour habitat patch.

Habitat-patches surrounded by pasture grasslands had higher extinction probabilities than did habitat patches embedded in tussock grassland. Outcrops in structurally more diverse tussock grasslands might provide a better invertebrate food source for grand skinks, thus leading to reduced extinction rates compared to those of outcrops in pasture grasslands. However, Tocher et al. (2003) found higher invertebrate abundances but similar species composition in pasture habitats compared to tussock habitats, which suggests that differences in food resources supplied by the matrix are not a major influence extinction probabilities. A more likely explanation is a higher level of predation of grand skinks in pasture habitats because of increased predator numbers caused by relatively high rabbit abundances (Norbury 2001). Additionally, a possible rescue effect by regular movements of grand skinks between habitat patches is reduced in pasture habitat. Together increased predation risk and a decreased disposition to move across pasture grasslands lead to higher extinction probabilities for grand skink populations in habitat patches in pasture grasslands.

Overall, the final model predicted higher occupancy probabilities of habitat patches in tussock grasslands compared to those in pasture grasslands which was also found for generic (not habitat patch specific) rates by Whitaker (1996) and Seddon et al. (2011). The higher occupancy of habitat patches in tussock grasslands is due to a
combination of higher colonisation and lower extinction probabilities. The detection probabilities of grand skinks were higher in habitat patches surrounded by tussock grasslands than pasture grasslands. These results contrast with the findings of Seddon et al. (2011) who found no differences between the detection probabilities of the two matrix types, but confirm the findings by Whitaker (1996). Whitaker (1996) reported higher densities of grand skinks in habitat patches surrounded by tussock grasslands rather than pasture grassland, and a higher proportion of single animals in habitat patches surrounded by pasture grassland. A higher density of grand skinks in habitat patches in tussock grasslands would make it more likely for observers to see at least one skink during surveys.

The structure of habitat patches had no great influence on occupancy and colonisation probabilities and therefore structure was not included in the models of occupancy and colonisation probabilities. However, structure influenced extinction and detection probabilities. Extinction probabilities were higher in habitat patches consisting of dispersed rock-tors compared to habitat patches with one discrete rock-tor. Although, dispersed rock-tors could potentially provide more cracks and crevices as refugia for grand skinks, thereby potentially reducing predation rates and providing space for greater abundances of grand skinks, rock-cracks might be too shallow to provide shelter especially in winter. Murphy (1994) reported differences in crevice dimension choices of adult, sub-adult and juvenile grand skinks, with adult skinks preferring much larger crevices than those selected by juvenile animals. Additionally, the tendency of the highly saxicolous grand skinks to stay on the rock-tors and not to move through grasslands (Chapter 2) would reduce interaction of animals on dispersed rock-tors, and therefore mating opportunities and reproduction, thus increasing extinction probabilities.

The variable ‘vegetation cover’ was retained only in the extinction probability model. More vegetation in a habitat patch decreased the extinction probabilities in a specific habitat patch. The vegetation cover on an outcrop plays an important part in providing food for grand skinks, directly in the form of fruit and indirectly by attracting and housing invertebrates especially as outcrops support plant species
which is largely absent from the matrix. Grand skinks also use the plants as refugia from predators and for shade against overheating in hot temperatures.

The distance between two neighbouring habitat patches was not retained, neither for the occupancy or the colonisation probability model. Grand skink adults have been found to predominantly move between 0 and 50 m (Coddington and Cree 1994, Chapter 2), while juveniles and subadults have been recorded to move up to 400 m (Houghton 2000, Whitaker 1996). However, only a very small proportion of grand skinks disperse overall (Whitaker 1996). The average nearest neighbour distance at the study site was 46 m (SE=1.4m, range 10 – 133 m, unpubl. data), indicating that all habitat patches are reachable for grand skinks which might explain why nearest neighbour distance was not important for the models. However, this study showed that the type of matrix had a stronger influence on the isolation of the habitat patch than the Euclidean distance, indicating that the disposition of the grand skink to move through the grasslands is more important for the colonisation process than the ability of the skink to travel the distance.

I found temporal variation in extinction and detection probabilities while colonisation probabilities stayed constant over time. Seddon et al. (2011) also found detection probability to vary between years, however, contrary to my results their models suggested constant extinction probabilities but colonisation probabilities that varied between years. Their study encompassed five years (compared to 3 years for this study) which would potentially provide a more robust estimation of metapopulation parameters. However, they did not derive habitat patch-specific metapopulation parameters that take outcrop size, structure, vegetation cover and isolation into consideration. Occupancy probabilities in this study increased from 2006 to 2007 because of extinction probabilities being lower than colonisation probabilities. An increase in extinction probabilities for the period between 2007/08 to the same level as the colonisation probabilities resulted in similar occupancy in 2007 and 2008. This result and those of Seddon et al. (2011) indicate that there are likely to be fluctuations in colonisation and extinction probabilities in the grand skink populations over longer time frames, and long-term monitoring will be
required to determine the metapopulation trends. This study supports the findings of Seddon et al. (2011) that there is no overall decline in grand skink occupancy at this study site.

The average detection probabilities of 0.53 – 0.60 in this study are lower than in previous studies of grand skinks (Seddon et al. 2011). Although surveys were conducted in weather conditions chosen to ensure high skink activity it is likely that especially for heliotherm animals such as skinks detection probabilities will differ with small changes in weather conditions. This and the abilities of the observer to detect a skink lead to the differences of the detection probabilities between years and between studies, emphasizing the need to account for incomplete detection probabilities in the study design.

**Validation process**

The internal and external validation process showed that the best fit model had adequate predictive properties, but correct-classification-rates decreased over the three year study-period. The validation process also revealed that the model predicted occupancy of grand skinks in pasture grasslands less accurately than in tussock grasslands. Fielding and Bell (1997) emphasized that sometimes species do not occupy all the available habitat, and this will influence the ability of the model to discriminate between positive and negative locations. Because of possibly higher predation pressure in pasture grasslands it is likely that some suitable outcrops are not inhabited by grand skinks. If predation events on outcrops and resulting extinction of a grand skink population are random and cannot be attributed to a specific habitat patch characteristic, the resulting model will have a lower predictive ability. Results for predictive abilities from my external validation process were similar to the internal validation process. Because of the restricted range of grand skinks, the study sites for the external validation process were still relatively close to the original study sites. Therefore, bias potentially introduced by spatial autocorrelation could be similar to that which internal evaluation procedures are
subject to. However, the external validation data were collected several years after the original data-set, introducing temporal independence. To my knowledge there are no evaluation measures available in the literature that take into consideration the incomplete detectability accounted for in the models presented here. Evaluation measures for dichotomous data are based on comparing correctly and incorrectly predicted cases; however as a consequence of acknowledging incomplete detectability in the modelling process, it can no longer be assumed that all absences observed are true absences. Because of the incomplete detectability of the species, the model will predict a number of observed absences as presences which common evaluation measures will penalise as wrong predictions. Owing to the study design with four surveys per monitoring period only 3 – 6 % of observed absences would be classified as presences by the model. Furthermore, all presences would be classified correctly by a ‘perfect’ model because of the underlying assumption of correct identification of the species. Because evaluation measures do not account for incomplete detectability, specificity values would be wrong by 3 – 6 % in my study. Future studies that incorporate incomplete detectability and seek to evaluate their models will also need to address this problem.

One limitation of this study is the relatively short time period of three years which only allowed for an estimation of two colonisation and extinction probabilities. To reach a more robust estimation of variability of extinction and colonisation probabilities longer time-frames should be taken into consideration. Furthermore, trivial turnover events caused by grand skinks wandering on and off an outcrop, and not forming a subpopulation with independent demographics as requested by metapopulation theory can result in an overestimation of the colonisation and extinction probabilities. However, several reasons minimise the potential of overestimation of parameters because of trivial turnover events: a) grand skinks show high site fidelity, spending most of their daily life on their home outcrop and only occasionally cross grasslands to move to a different outcrop (Chapter 2); b) significant populations can occur on even the small-sized outcrops resulting in non-trivial extinction and colonisation events; and c) the probability of recording a grand
skink’s movement on and off an outcrop are very small because of rarity of those events.

This study emphasized that metapopulation dynamics are not necessarily driven by habitat patch size and isolation alone but also by other attributes of the habitat patch that influence the ecology of the study species, and the surrounding matrix. For example, in this study, matrix type was a better measure of habitat patch isolation than distance. The difference between various studies on the relative importance of habitat patch and matrix are likely due to differences in the ecology of the species being studied. Because of this large variation between species it is imperative to use existing knowledge of the study species to decide which variables play important roles in the metapopulation dynamics according to the ecology of the study species. I decided to choose easy-to-measure variables so the data can be collected relatively quickly and with low cost, addressing important ecological factors influencing the metapopulation dynamics of grand skinks. The results of this study will enable the classification of habitat patch suitability for grand skinks and guide planning for translocations and the creation and management of skink conservation areas. I also pointed out shortcomings of classic evaluation measures for models incorporating detection probabilities which should be addressed in future research.
CHAPTER FIVE

Spatially explicit metapopulation models

Schist-rock outcrops in tussock grasslands (foreground) and pasture grasslands (background) at the Redbank study site
INTRODUCTION

In conservation biology modelling population dynamics is important to gain insight into the influence of management actions, land use change, predicted climate change or species invasions on population variation and persistence (Dunning et al. 1995, Vitousek et al. 1997). Increasing habitat fragmentation through anthropogenic destruction and modification of natural habitats has increased the need for spatially realistic models which take into consideration the spatial distribution of habitat patches in the landscape (Dunning et al. 1995, Driscoll 2007). In fragmented landscapes, populations in discrete habitat patches may be connected by migration. The degree of migration between habitat patches can be used to place a population along a gradient from low migration rates in classic metapopulations, to high migration rates in patchy populations (Harrison 1991, Hanski and Gilpin 1997, Driscoll 2007).

In classic metapopulations, each sub-population has some probability of extinction, while empty habitat patches can become colonised, making spatial dimensions an essential component of the modelling process since modelling only localised population processes would be insufficient and potentially misleading (Hanski and Thomas 1994). Metapopulation models based on occupancy data are simplistic in the sense that habitat patches are recorded as either occupied or unoccupied, whereas deterministic population models track the survival and dispersal of individuals in each sub-population (Dunning et al. 1995, Akcakaya and Atwood 1997). However, a large amount of data and computing power is needed to run simulations of individual-based models. Occupancy data, on the other hand, can be collected relatively quickly and at low cost. Although some details of population size and composition in individual patches will be lost, occupancy data can be used to model large-scale processes of species distribution, such as range shifts, expansions and contractions, in addition to large-scale population dynamics (Bulman et al. 2007, Driscoll 2007). For example, incidence function models developed by Hanski (1994) require a minimum of only one presence-absence survey to estimate the parameters necessary for the metapopulation model. Because
the recording of false absences in surveys can have large impacts on the estimation of metapopulation parameters, more than one survey is recommended (Hames et al. 2001, Moilanen 2002, MacKenzie et al. 2003). In contrast to the first metapopulation models developed by Levins (1969) which assumed all habitat patches are of equal size and quality, and with equal colonisation probability, incidence function models integrate habitat patch sizes and their spatial distributions. Comparing incidence function models with two other metapopulation modelling approaches, the logistic regression model and a demographic model, Kindvall (2000) showed that all three approaches yield good predictions of turnover rates and temporal changes in the regional occupancy of the bush cricket (*Metrioptera bicolour*), but less accurate predictions regarding the length of occupancy of individual habitat patches. However, incidence function models assume steady state metapopulations (Hanski and Gilpin 1997), whereas models estimating colonisation and extinction rates with logistic regression analysis can be used to describe metapopulation dynamics that are not in equilibrium.

The refinement of metapopulation models led to investigations of the influence of habitat patch characteristics, such as isolation and habitat quality, on metapopulation parameters (Kindvall 1996, Schooley and Branch 2009). Habitat patches of different quality can lead to source-sink dynamics within the metapopulation (Jaquiery et al. 2008) where high quality habitat patches provide migrants to low quality habitat patches and therefore influence colonisation probability and, via the rescue effect, extinction probabilities. Furthermore, attention has been given to the heterogeneity of the matrix surrounding the habitat patches and its influence on colonisation and extinction parameters (Berggren et al. 2001, Ricketts 2001, Fischer and Lindenmayer 2007).

A classic metapopulation structure is observed in the threatened New Zealand grand skink (*Oligosoma grande*) which inhabits schist-rock outcrops that are surrounded by indigenous tussock and exotic pasture grasslands (Whitaker 1996). Grand skinks are a long-lived species and very sedentary. The grasslands surrounding the schist outcrops are used only by a small proportion of animals for migration between
outcrops (Coddington and Cree 1997, Houghton 2000). The modification of the native tussock grasslands into exotic pasture grasslands and the introduction of mammalian predators have been identified as their major threats (Whitaker 1996, Tocher 2006). It is estimated that grand skinks today occupy only 8% of their assumed historical range (Whitaker and Loh 1995). Monitoring and management of the population has been conducted for more than two decades and intensive predator control has been shown to allow grand skink population recovery (Reardon et al. 2012). Localised population estimates show that grand skink numbers at sites in disturbed habitats decline rapidly compared to sites with predator control and native tussock grasslands (Reardon et al. 2012). However, grand skink populations continue to exist in pasture habitat converted 30 years ago (Whitaker 1996). The concept that species can initially survive large scale habitat change but experience delayed extinctions, termed extinction debt, has been introduced by Tilman et al. (1994). This study demonstrates how a spatially explicit metapopulation model using habitat patch specific colonisation and extinction probabilities can increase the knowledge about the population dynamics and support management decision making by investigating the influence of land use change and predator control programs on metapopulation dynamics of grand skinks. The influence on metapopulation dynamics of the divergence of colonisation and extinction probabilities from estimated values will be investigated, and the influence of the maximum dispersal distance of grand skinks on metapopulation dynamics is explored. In addition, how the metapopulation model can be used to guide the selection of appropriate translocation sites will be shown.

**METHODS**

The model landscape

Simulations of the metapopulation dynamics of grand skinks were run utilising the locations and characteristics of habitat patches at the Redbank study site, whose natural features were described in detail in Chapter 4. Following the definition by
Whitaker (1996) habitat patches were defined as schist-rock outcrops or a group of schist-rock outcrops separated by a minimum of 10 m of matrix grassland from any other schist-rock outcrop. The model uses a discrete landscape consisting of 89.2 ha pasture grasslands with 115 habitat patches in the north-west and 188.6 ha tussock grasslands with 174 habitat patches in the south-east (Fig. 5.1).

**Figure 5.1:** Model landscape with location of habitat patches used for simulating metapopulation dynamics of grand skinks. The landscape is divided into a pasture grassland site (A) and a tussock grassland site (B). Open circles depict unoccupied and filled circles occupied habitat patches identified in four surveys in 2006.
Construction of the simulation model and assigning of parameter values

The basic model

Using the software R version 2.12.0 (R Development Core Team 2010) a spatially explicit metapopulation simulation model was developed which utilizes the spatial distribution of habitat patches at the study site, and habitat patch-specific colonisation and extinction rates.

The model simulates the persistence or extinction of grand skink populations in each occupied habitat patch, and the colonisation of unoccupied habitat patches over time, taking into consideration the location and characteristics of each habitat patch. The model utilizes the occupancy status of year \( t \) (initial occupancy \( t = 0 \)) to determine the occupancy status of the following year \( t+1 \). The decision tree that the simulations follow to identify the occupancy status of the habitat patches during a time step is visualised in Fig. 5.2. For occupied habitat patches, the patch-specific extinction probability is used to determine if the population in a given habitat patch goes extinct or survives. For habitat patches which are unoccupied the model modifies the patch-specific colonisation probability according to a defined maximum movement distance for grand skinks (threshold distance) and the number and distance of occupied habitat patches within this threshold distance. If there are no occupied habitat patches within the threshold distance, the habitat patch will not be colonised and its occupancy state for the following time step will remain ‘unoccupied’. If there are occupied habitat patches within the threshold distance the model weights the colonisation probability according to the distance and number of the occupied habitat patches using the weighting parameter \( \omega \). Multiplying the habitat patch specific colonisation probability \( \gamma \) with \( \omega \) will create the modified, patch-specific colonisation rate \( \gamma' \). The occupancy status of a habitat patch is then determined by comparing a random number drawn from a uniform distribution between 0 and 1, to the extinction probability or the modified colonisation probability. Both probabilities are a number between 0 and 1. A probability larger
than the random number would change the occupancy status and a probability smaller than the random number would keep the occupancy status the constant for the next time step, therefore allowing rock-tors with large colonisation or extinction probability values to have a higher probability of occupancy status change.

Figure 5.2: Algorithm that the simulation model uses to define the occupancy status of each habitat patch. The algorithm is repeated during each time step.
**Habitat-patch specific colonisation and extinction probabilities**

Habitat patch-specific colonisation and extinction probabilities were estimated in Chapter 4 using logistic regression functions and taking into consideration the probability of detecting a grand skink during one survey. The most parsimonious model in Chapter 4 estimated colonisation probabilities as being dependent on the size of the habitat patch and the type of matrix surrounding the habitat patch (Table 5.1). Extinction probabilities were influenced by size, structure and vegetation cover of the habitat patch and the surrounding matrix type (Table 5.1). Furthermore, the model estimated constant colonisation probabilities over the 3-year study period but different extinction probabilities between the first and second year, and the second and third year (Table 5.1). The logistic regression coefficients estimated in Chapter 4 were used to calculate habitat patch-specific colonisation ($\gamma$) and extinction probabilities ($\varepsilon_{\text{low}}$ (2006/07) and $\varepsilon_{\text{high}}$ (2007/08)) for the simulation model (Table 5.1). Because over the three year period only two extinction probabilities can be estimated, the actual extent of the variation in extinction probability is not known. Therefore the simulation models using the known extinction probabilities investigate metapopulation dynamics that have long-term average extinction probabilities equivalent to the estimated values.

**Table 5.1: Logistic regression coefficients to estimate habitat patch specific colonisation and extinction probabilities for grand skink metapopulations**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coefficient estimate</th>
<th>Standard error</th>
<th>Value range</th>
<th>Tussock</th>
<th>Pasture</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Colonisation probability</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept</td>
<td>-5.187</td>
<td>-0.878</td>
<td>$\gamma = 0.21–0.56$</td>
<td>$\gamma = 0.05–0.21$</td>
<td></td>
</tr>
<tr>
<td>Size</td>
<td>0.782</td>
<td>-0.234</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matrix type</td>
<td>1.533</td>
<td>-0.363</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Extinction probability</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Intercept (2006/2007)</td>
<td>-0.880</td>
<td>-1.239</td>
<td>$\varepsilon_{\text{low}} = 0.02–0.23$</td>
<td>$\varepsilon_{\text{low}} = 0.03–0.34$</td>
<td></td>
</tr>
<tr>
<td>Intercept (2007/2008)</td>
<td>0.210</td>
<td>-1.279</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Size</td>
<td>-0.394</td>
<td>-0.310</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Structure</td>
<td>0.904</td>
<td>-0.498</td>
<td>$\varepsilon_{\text{high}} = 0.04–0.48$</td>
<td>$\varepsilon_{\text{high}} = 0.07–0.61$</td>
<td></td>
</tr>
<tr>
<td>Vegetation cover</td>
<td>-0.645</td>
<td>-0.478</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Matrix type</td>
<td>-0.540</td>
<td>-0.448</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The threshold distance

To define a maximum distance that grand skinks could move through the matrix to reach an unoccupied habitat patch, movement distances from previous studies were taken into consideration. Overall, only a small proportion of grand skinks migrate between habitat patches (Whitaker 1996, Coddington and Cree 1997, Houghton 2000) with the largest reported distance moved by a grand skink being 678 m by a juvenile (Houghton 2000). The majority of recorded movements occurred at 100 – 200 m for juvenile grand skink and 0 – 50 m for adult grand skinks (Coddington and Cree 1997, Houghton 2000, Chapter 2). The presence-absence data used in Chapter 4 revealed that within the 3-year time period no colonisation event of an unoccupied habitat patch was observed when the distance to the nearest occupied neighbour was more than 165 m (Appendix 3), which falls well within the reported distances of the previous studies. Therefore a distance of 165 m was used as a threshold dispersal distance for grand skinks for most simulation scenarios in this study, and the effect of using different maximum distance on metapopulation dynamics was investigated.

The weighting parameter $\omega$

The probability of colonisation is not constant but decreases with increasing distance to the next occupied habitat patch (Hanski 1998, Appendix 3), therefore $\omega$ was calculated as:

$$\omega = 1 - \exp (-S x \alpha)$$

with $\alpha$ being a tuning parameter influencing how much weight the distance between an occupied habitat patch and an unoccupied habitat patch has on the colonisation probability of the unoccupied patch (Fig. 5.3). $S$ is the sum of the inverse of the distances between occupied patches and the unoccupied habitat patch. As a result, occupied habitat patches large distances away from the unoccupied patch will still have an effect on its colonisation probability. This effect, however, is smaller than that of occupied habitat patches closer to the unoccupied patch. Note that only the
number of occupied habitat patches within the threshold distance is taken into consideration.

Because habitat patches were defined as rock-outcrops or groups of rock-outcrops that are separated by more than 10 m of grassland, a tuning parameter of $\alpha = 30$ was chosen. With this tuning parameter a single occupied habitat patch at 10 m from an unoccupied habitat patch ($S = 0.1$) results in a weighting parameter $\omega = 0.95$ and no major change in the estimated patch specific colonisation probability, while distances larger than 10 m result in an exponential decline of the colonisation probability. Several habitat patches within 10 m of the unoccupied habitat patch will thus result in a slightly better colonisation probability compared to a single habitat patch within 10 m.

Figure 5.3: Influence of the tuning parameter $\alpha$ on the weighting parameter $\omega$ which is used to modify the colonisation probability of unoccupied habitat patches. $S$ is the sum of the inverse of the distances between the unoccupied and occupied habitat patches.
Running the metapopulation simulation

All simulation models in this chapter were run using the real spatial distribution and characteristics of the habitat patches at the Redbank study site (Fig. 5.1), specifying in each case if the landscape of the site A (matrix = pasture grassland), of the site B (matrix = tussock grassland) or of the whole study site is used. While the measures for the habitat patch-specific characteristics size, vegetation cover and structure, and the location of the habitat patch stay constant for each habitat patch, the matrix type (pasture or tussock) can change according to the simulation specifications. As the initial occupancy state of the habitat patches for each simulation model, except for the translocation scenarios, the presence-absence data from the 2006 surveys was used (Fig. 5.1). As described above, the habitat-specific colonisation ($\gamma$) and extinction probabilities ($\epsilon_{low}$, $\epsilon_{high}$) were calculated using the highest ranked model from Chapter 4 (Table 5.1). Both, extinction and colonisation probabilities are dependent on habitat-patch characteristics, which stay constant, and on the matrix type surrounding the habitat patch, which changes according to the simulation scenario. Therefore colonisation and extinction rates for a habitat patch can differ between simulation scenarios but will stay constant for all runs within the same simulation scenario. Repeated runs of the simulation model enabled the calculation of a predicted mean (SE) occupancy rate after 100 years and an assessment of the variability of the predicted outcomes using the standard deviation.

Threshold distance variation scenario

Varying the range threshold distances allows investigation of the maximum distance that grand skinks are able or willing to move across grasslands, and how this distance influences metapopulation dynamics. The simulation model was run with 21 different threshold distances between 10 m and 400 m at 10 m intervals leaving all other parameters constant. For each threshold distance the model was run 100 times, each over 100 annual time-steps, and the mean number of occupied habitat patches after 100 years was recorded.
Influence of variation in colonisation and extinction probabilities

Colonisation and extinction probabilities were estimated using a relatively short period of three years which provides only two periods for possible extinction or colonisation events because colonisation and extinction events are identified by differences in the occupancy status of a habitat patch between two years. By varying colonisation and extinction probabilities I investigated the impact of deviations from the estimated values which can be caused by estimation error or change in management strategies (e.g. predator control). The habitat patch-specific colonisation and extinction probabilities were varied by adding or subtracting a constant value (0.05, 0.10, 0.15 and 0.2). For each combination of varied colonisation and extinction probabilities, the average number of occupied habitat patches was recorded from 100 runs of the simulation model for 100 years.

Habitat modification scenarios

The simulation model was used to investigate the metapopulation persistence with different scenarios of habitat modification:

a) using the habitat in its current status;

b) converting current tussock habitat (site B) into pasture habitat (= the whole site is pasture grassland);

c) converting pasture habitat (site A) into tussock habitat (= the whole site is tussock grassland).

Scenarios b) and c) explore metapopulation persistence if management actions change the proportion of matrix types. To simulate the transformation of tussock grassland into pasture grassland or the other way around, the habitat patch-specific colonisation and extinction probabilities were calculated using the value for the grasslands type they were converted into (Pasture = 1, Tussock = 2) as the matrix
type. The simulation model was run 100 times with the converted colonisation and extinction times and average occupancy rates recorded for each time step.

**Translocation scenarios**

The simulation model also offers the opportunity to investigate the suitability of translocation sites for the establishment of a metapopulation and the site characteristics that may result in the greatest increase in occupancy over time. The landscape of the study site was used to demonstrate how the simulation model could be used by conservation managers to aid decision making for translocations. At the start of the simulation all habitat patches in the study site were defined as unoccupied, except the one habitat patch designated as a release site for a founding population of translocated grand skinks, with the whole landscape of the study site defined as tussock grassland. The occupancy models indicated that large habitat patches had the highest occupancy probability and, additionally, low extinction probabilities (Table 5.1; Chapter 4). Large habitat patches can also accommodate a larger founding population which increases the probability of population establishment and growth (Griffith et al. 1989, Seddon et al. 2007, Armstrong and Seddon 2008). Simulations were run 100 times each, using each large habitat patch as a release site in turn. Each simulation was run for 100 years and the number of occupied habitat patches in the landscape was recorded at each time step. Utilizing the simulation model output, I investigated which habitat patch characteristic (nearest neighbour distance, structure, vegetation cover) contributed to the number of occupied habitat patches in the landscape at 5, 10, 25, 50 and 100 years after the translocation, using linear regression models. I used to p-values less than 0.05 to identify significant relationships between the x-variable (nearest neighbour distance, structure or vegetation cover) and the y-variable (number of occupied habitat patches 5, 10, 25, 50 and 100 years after the translocation, respectively) determined by comparing the values of the F-statistics of the linear regression model including the x-variable and a model without the x-variable (null-hypothesis).
RESULTS

The metapopulation simulation

The spatial distributions of occupied and unoccupied habitat at year 1, 50 and 100 of one exemplary simulation run each, utilising the pasture grassland site A and the tussock grassland site B separately, are shown in Fig. 5.4 and Fig. 5.5, respectively, and utilising the complete study site, are shown in Fig. 5.6. The density of occupied habitat patches increases towards the northern end of both sites. High extinction probability in the pasture grasslands caused the metapopulation to decline to near-extinction in the example simulation. The simulation model predicted an increase of the overall occupancy rate in the study site from initially 0.42 to a mean overall occupancy rate of 0.59 (SE = 0.003) using the lower extinction probability, and a decrease to 0.36 (SE = 0.003) using the higher extinction probability (Fig. 5.7). Simulating the metapopulation dynamics separately in the tussock grassland site and the pasture grassland site revealed that occupancy in the tussock grassland site increased from initially 0.52 to 0.75 (SE = 0.003) with low extinction probabilities and stayed constant at 0.53 (SE = 0.004) with high extinction probabilities. The occupancy in the pasture site however, stays constant at 0.29 (SE = 0.005) with the low extinction probabilities and strongly decreases with higher extinction probabilities, from 0.27 to 0.04 (SE = 0.004) after 100 years. The very low standard deviations of 0.03 – 0.05 indicate only small variations in the overall predictive outcomes.
Figure 5.4: One simulation run of the metapopulation dynamics in the pasture grasslands (site A) over 100 years. Shading in the maps depicts density of occupied habitat patches (dark – high, light – low). Black and white circles are occupied and unoccupied habitat patches, respectively. Arrows indicate year 1, 50 and 100.
Figure 5.5: One simulation of the metapopulation dynamics in the tussock grasslands (site B) over 100 years. Shading in the maps depicts density of occupied habitat patches (dark – high, light – low). Black and white circles are occupied and unoccupied habitat patches, respectively. Arrows indicate year 1, 50 and 100.
Figure 5.6: One simulation of the metapopulation dynamics in the tussock and pasture grasslands combined over 100 years. Shading in the maps depicts density of occupied habitat patches (dark – high, light – low). Black and white circles are occupied and unoccupied habitat patches, respectively. Arrows indicate year 1, 50 and 100.
Figure 5.7: Occupancy rates for habitat patches predicted separately for the pasture and tussock grassland sites and for the overall study site combining the pasture and tussock grassland sites. Metapopulation simulation models were run 100 times for 100 years each with low extinction probabilities (grey lines) and high extinction probabilities (black lines).
Variation of threshold distances

For landscapes with tussock grasslands the estimated occupancy rate after 100 years reached an asymptote with threshold dispersal distances greater than 160 m. Simulations for pasture grasslands with the lower extinction probabilities reached an asymptote for occupancy rates with thresholds greater than 230 m, whereas simulations with high extinction probabilities did not reach an obvious asymptote for occupancy rates. The asymptotic value for the occupancy rates was dependent on the extinction probabilities and the matrix type, with higher occupancy values reached for lower extinction probabilities in tussock grasslands compared to pasture grasslands. Very low occupancy rates, below 0.1, were reached for thresholds up to 70 m for tussock grasslands, while pasture grasslands still had low occupancy rates up to thresholds of 100 m and 250 m for low and high extinction probabilities, respectively (Fig. 5.8).

Colonisation and extinction probabilities

Investigating the influence of variation in colonisation and extinction probabilities indicates that metapopulations in tussock grasslands are able to persist even with relatively large divergence from the estimated colonisation and extinction probabilities, whereas metapopulations in pasture grasslands are predicted to go extinct with only relatively small increases in extinction probabilities and/or decreases in colonisation probabilities (Figs. 5.9 and 5.10; for better visual perception Figs. 5.11 and 5.12 show the same data separated for each grassland type).
Figure 5.8: Influence of a range of threshold distances on the occupancy rate at year 100 of metapopulation simulations repeated 100 times. White boxes show results for simulations using low extinction probabilities, grey boxes for high extinction probabilities. The range of recorded maximum movement distances of grand skinks in tussock grasslands is marked.
**Figure 5.9:** Influence of the variation of the low extinction probabilities and colonisation probabilities on the occupancy rate of habitat patches in the pasture and tussock grassland sites at 100 years in the metapopulation simulation.
Figure 5.10: Influence of the variation of the low extinction probabilities and colonisation probabilities on the occupancy rate of habitat patches in the pasture and tussock grassland sites at 100 years in the metapopulation simulation.
Figure 5.11: Influence of the variation of the low extinction probabilities and colonisation probabilities on the occupancy rate of habitat patches in the pasture and tussock grassland sites at 100 years in the metapopulation simulation. The filling of the boxes depicts the proportion of occupied habitat patches in the study site.
Figure 5.12: Influence of the variation of the high extinction probabilities and colonisation probabilities on the occupancy rate of habitat patches in the pasture and tussock grassland sites at 100 years in the metapopulation simulation. The filling of the boxes depicts the proportion of occupied habitat patches in the study site.
Habitat modification scenarios

Converting current pasture grasslands into tussock grassland is predicted to increase the overall occupancy rate for the study site from 0.59 (SE = 0.003) and 0.36 (SE = 0.003; Fig. 5.13a) to 0.76 (SE = 0.003) and 0.54 (SE = 0.003; Fig. 5.13b) for low and high extinction probabilities respectively. Converting the tussock grasslands (site B) into pasture grasslands will result in a reduction of occupancy to 0.29 (SE = 0.003) and 0.04 (SE = 0.002; Fig. 5.13c) for low and high extinction probabilities, respectively.

Translocation scenarios

The translocation simulations showed that different habitat patches would develop different occupancy rates in the short to mid-term (several years), but will result in very similar occupancy rates in the long-term (50 – 100 years, Figs. 5.14 and 5.15). Regression analysis revealed that of the habitat patches that were chosen to serve as translocation sites because of their large size (n = 76), habitat patches with the shortest distance to the nearest habitat patch achieved higher occupancy rates irrespective of the extinction probability (low (Fig. 5.16) or high (Fig. 5.17, Table 5.2). The strength of the influence decreased with increasing time after the translocation. Furthermore the influence was similar in years 5 and 10 after translocation for simulations with high and low extinction probabilities. However, in the simulations with low extinction probabilities the influence of the distance of the nearest habitat patch on the achieved occupancy rate decreased to insignificant levels in years 50 and 100 after translocation, whereas in models with high extinction probabilities the strength of the relationship decreased but stayed significant for the whole 100 years of simulation (Table 5.2). For vegetation cover of habitat patches, a non-significant trend of increased occupancy rates for habitat patches with higher vegetation cover emerged (Figs. 5.16 and 5.17). The structure of the translocation site had no influence on the number of occupied habitat patches.
Figure 5.13: Average occupancy rates of grand skinks at the study site predicted by the metapopulation simulation model. Presented are the average occupancy rates from 100 simulations at each time step using a low extinction probability (grey lines) and a high extinction probability (black lines). (a) matrix type “pasture” and “tussock” as in current field conditions, (b) pasture grasslands (site A) converted to tussock grasslands and (c) tussock grasslands (site B) converted to pasture grasslands.
Table 5.2: Results of the regression analyses of the achieved occupancy rate against the nearest neighbour distance, structure and vegetation cover for the selected habitat patch. The translocations were simulated 100 times with high and with low habitat patch-specific extinction probabilities.

<table>
<thead>
<tr>
<th>Year</th>
<th>low extinction probabilities</th>
<th>high extinction probabilities</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Nearest neighbour distance</td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>$F_{(74)}=7.582$ p=0.007</td>
<td>$F_{(74)}=8.117$ p=0.006</td>
</tr>
<tr>
<td>10</td>
<td>$F_{(74)}=6.151$ p=0.015</td>
<td>$F_{(74)}=6.194$ p=0.015</td>
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<tr>
<td>25</td>
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<td>$F_{(74)}=7.938$ p=0.006</td>
</tr>
<tr>
<td>50</td>
<td>$F_{(74)}=3.485$ p=0.066</td>
<td>$F_{(74)}=7.618$ p=0.007</td>
</tr>
<tr>
<td>100</td>
<td>$F_{(74)}=2.965$ p=0.089</td>
<td>$F_{(74)}=6.809$ p=0.011</td>
</tr>
<tr>
<td></td>
<td>Structure</td>
<td></td>
</tr>
<tr>
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<td>$F_{(74)}=0.279$ p=0.599</td>
</tr>
<tr>
<td>10</td>
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<td>$F_{(74)}=0.031$ p=0.861</td>
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<td>$F_{(74)}=0.005$ p=0.944</td>
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<td>$F_{(74)}=0.057$ p=0.812</td>
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<tr>
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<td>$F_{(74)}=1.258$ p=0.266</td>
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<td></td>
<td>Vegetation cover</td>
<td></td>
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<td>$F_{(74)}=2.400$ p=0.126</td>
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<tr>
<td>100</td>
<td>$F_{(74)}=1.810$ p=0.183</td>
<td>$F_{(74)}=2.577$ p=0.113</td>
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Figure 5.14: The influence of translocation site choice on the occupancy rate of the landscape over time when simulating the metapopulation using the low extinction probability. Circles depict habitat patches and the size of circles indicates the occupancy rate of the landscape that can be achieved when choosing this habitat patch as translocation site. The histograms show the number of habitat patches which would achieve the occupancy rate when chosen as a translocation site.
Chapter five: Spatially explicit metapopulation model

Figure 5.15: The influence of translocation site choice on the occupancy rate of the landscape over time when simulating the metapopulation using the high extinction probability. Circles depict habitat patches and the size of circles indicates the occupancy rate that can be achieved when choosing this habitat patch as translocation site. The histograms show the number of habitat patches which would achieve the occupancy rate of the landscape when chosen as translocation site.
Figure 5.16: Influence of translocation site characteristics on the predicted total number of occupied habitat patches after 5, 10 and 25 years using a low extinction probability in the simulation model settings.
Figure 5.17: Influence of translocation site characteristics on the predicted total number of occupied habitat patches after 5, 10 and 25 years using the high extinction probability in the simulation model settings.
DISCUSSION

Simulating the metapopulation dynamics of grand skinks enabled prediction of the persistence of the metapopulation over long time periods (100 years) under different management scenarios. The grand skink population in the pasture grasslands was predicted to persist only with a long-term average extinction probability that is either lower than, or equivalent to the lower of the two estimated extinction probabilities ($\varepsilon_{\text{low}}$ and $\varepsilon_{\text{high}}$). Even slight increases in extinction probabilities or decreases in colonisation probabilities can result in predicted extinctions of the metapopulations. In contrast, predictions for populations in tussock grassland show stable conditions even with higher extinction probabilities than those of current estimates. With the currently available data, the full scale of variation of extinction probabilities between years over long time frames cannot be estimated. However, as the analysis showed, populations in tussock grasslands will persist over a wide range of average extinction and colonisation probabilities, while populations in pasture grasslands are threatened by extinction with only slight deviation from the current estimated low extinction probability. The pasture grassland populations display a slow decline to extinction, in accordance with extinction debt theory (Bulman et al. 2007, Malanson 2008). In this specific grand skink metapopulation, the adjacent tussock grassland population might act as source population for the pasture grassland population and could slow the extinction process.

Although the presented graphs of the simulation model results display a stabilising of the overall occupancy level of the population over time, it should be noted that on the habitat patch level turnover events still occur. The frequency of those turnover events depends on the colonisation and extinction probabilities and on the isolation of the habitat patch. Therefore, small habitat patches (high extinction probabilities and low colonisation probabilities) will experience a higher turnover frequency, while large habitat patches (high colonisation probabilities and low extinction probabilities) will go extinct or become (re-)colonised less frequently. Furthermore, more isolated habitat patches will also experience low frequencies of state changes because of their low colonisation probabilities. The stability of the
occupancy level is observable in the conservation area at Macraes where the grand skink metapopulation occurs in relatively stable occupancy levels despite ongoing colonisation and extinction events for over two decades now.

A number of limitations have to be taken into consideration when using these simulation models. My model is likely to overestimate the persistence of the metapopulation because environmental stochasticity has not been included. Especially metapopulations with very small occupancy rates would be influenced very strongly by stochastic events influencing colonisation and extinction probability (Pimm et al. 1988, Hanski 1991). Therefore the populations in pasture habitat could potentially go extinct much earlier than predicted. Variation in extinction probabilities over time has been shown in Chapter 4, however, because only two different extinction probabilities were estimated in this study the scale and temporal variation of extinction probability fluctuations is still unknown. Extinction probabilities are assumed to depend to some extent on the predator numbers in the landscape which in turn are driven by rabbit and rodent population size (Norbury and McGlinchy 1996, Norbury 2001). Fluctuations in prey populations due to environmental conditions, for example heavy rains during breeding seasons (Robson 1993), could therefore influence the metapopulation dynamics of grand skinks. Pasture grasslands are assumed to have a larger population of rabbits compared to tussock grasslands, however during periodic mast seeding, tussock grasslands can experience unusually large amounts of rodent populations which could also lead to increased predator numbers in tussock grasslands. The masts are correlated with high temperatures the summer before seedfall, which are linked to La Niña conditions (Schauber et al. 2002). Therefore an increase in frequency of El Niño-Southern Oscillation dynamics due to global climate change could increase the frequency of high predator abundance and thereby negatively impact the grand skink metapopulation dynamics.

Another limitation of the model is its geographic coverage, with habitat patches available outside the study side not being considered in the weighting of the colonisation probability of habitat patches close to the edge of the study site. This
factor could lead to an underestimation of colonisation probabilities and therefore occupancy rates especially in the periphery of the study site. Similarly, at the border between tussock and pasture grasslands, the current model will tend to underestimate and overestimate colonisation probabilities for habitat patches in pasture and tussock grassland, respectively. The weighting of the colonisation probabilities does not consider the matrix type surrounding the habitat patch that provides the migrating grand skink. An unoccupied habitat patch in tussock grasslands close to the border to pasture grasslands will be modelled with the same colonisation probability whether the occupied habitat patch is surrounded by pasture or by tussock grasslands as long as the distance to the unoccupied habitat patch is the same. For further investigations into this edge effect, the model would have to be fitted with an algorithm detecting the matrix type along the pathway a grand skink would have to travel to reach the unoccupied habitat patch. The exact behaviour of grand skinks moving between habitat patches and within different grassland types is unknown and will require further investigation.

Nevertheless, the metapopulation model as it is presented here provides insight into the differences between metapopulation dynamics of grand skinks in tussock grasslands and pasture grasslands. To improve metapopulation dynamics and occupancy rates especially in threatened pasture grassland populations, conservation managers should aim to increase colonisation probabilities of habitat patches or decrease extinction probabilities. Theoretically, colonisation probabilities can be increased by shorter distances between habitat patches, converting pasture grasslands into tussock grasslands and increasing the number of grand skinks moving between habitat patches. Reducing the distance between habitat patches is unrealistic since grand skinks occupy large, complex rock-outcrops which can not simply be moved or replicated. Converting pasture grasslands into tussock grasslands will be difficult on private land which is used as cattle and sheep farms. However, creating islands of tussock grasslands encompassing small numbers of habitat patches within large areas of pasture grasslands might increase the persistence of grand skink populations on a larger scale. Further studies are needed
to investigate possible island size, number of habitat patches included in the islands and distances to other islands.

The most tangible possibility to increase colonisation probabilities is provided by the influence of the threshold distance on occupancy outcomes. The simulation model stressed that the grand skink metapopulation dynamics are driven by the dispersal of juvenile grand skinks since movements of adult grand skinks were not far enough to create colonisation dynamics for persisting metapopulations. Increasing the survival rate and therefore the number of juvenile animals dispersing in order to increase colonisation probabilities could be achieved with predator control. Simultaneously, predator control could reduce extinction probabilities of habitat patches, stabilising metapopulation dynamics even further. Predator suppression with large-scale trapping programmes and predator exclusion by mammal-proof fences have already been shown to increase survival rates of grand skinks dramatically, allowing for fast population growth (Reardon et al. 2012). Predator control is also possible on private farmland with the consensus of the owners. The metapopulation simulation for tussock grassland populations suggest that a reduction in extinction probabilities could result in the occupation of all available habitat patches by grand skinks, potentially creating a patchy population rather than a classic metapopulation (Driscoll 2007).

Modelling the conversion of the study site into all-pasture grassland landscape or all-tussock grassland landscape emphasized the likely impacts on the grand skink metapopulation. While conversion into tussock grasslands resulted in an expected increase in occupancy, conversion into pasture grasslands resulted in the extinction of the grand skink population in the long-term.

Because of the large reduction in the range of grand skink populations, translocating grand skinks into areas which cannot be reached through natural dispersal from their current locations because of natural or anthropogenic obstacles, is a possible management action to increase the range and population size (Whitmore et al. 2011). Choosing an appropriate translocation site is essential for establishing a new
population of grand skinks and the results of this study can be used by conservation managers to guide decision making on appropriate translocation sites. The location and the three habitat patch characteristics of size, vegetation cover and structure of any candidate release site can easily be entered into the existing model to simulate the effectiveness of various habitat patches as translocation sites. The simulations revealed that habitat patches with nearest neighbours within 60 m and a high degree of vegetation cover should be used as translocation sites. The small nearest-neighbour distance is especially important in metapopulations where high extinction probabilities are expected, for example, because of high predator numbers. The connectivity of habitat patches to surrounding habitat has also been identified in other studies as an important factor supporting population establishment and expansion (Berggren et al. 2001).

Unlike many other metapopulation studies, in the case of the grand skink metapopulation, neither the number nor the quality of the habitat patches was changed directly with the modification of the landscape. Furthermore it is unlikely that the grand skink population experienced a significant reduction in animal numbers through the actual process of converting of tussock grasslands to pasture grasslands such as where habitat destruction causes habitat fragmentation (Kuussaari et al. 2009). However, converting the matrix between the habitat patches led to changes in overall metapopulation dynamics and reduced the quality of the habitat patches indirectly. Following the extinction debt theory (Tilman et al. 1994) the population of grand skinks would slowly decline to extinction in pasture grasslands over several skink generations. This highlights that metapopulations research should not only concentrate on the amount of habitat lost as a cause of metapopulation extinctions. In the case of the grand skink, habitat itself is not lost, however the land-use mediated change in the matrix has resulted in increased isolation of habitat patches and potentially increased predator pressure, likely leading to an extinction debt. Similarly, Vögli et al. (2010) found matrix attributes to be major contributors in explaining occurrence and density of metapopulation forming steppe-birds.
The simulation model presented here provides an insight into the metapopulation dynamics of grand skinks. Important information for conservation managers, such as the sensitivity of pasture grassland populations to changes in colonisation and extinction rates, the importance of the spatial location of translocation sites, and the importance of juvenile dispersal for grand skink metapopulation persistence, have been highlighted. Further research is needed to incorporate stochasticity and the influence on colonisation and extinction probabilities of any boundary between pasture and tussock grasslands. Finally, ongoing monitoring could improve the accuracy of the colonisation and extinction rates used in this model as well as provide new information on impacts of predator control programs or accuracy of predicted trends made by the simulation models.
CHAPTER SIX

General discussion

Predator-proof fence protecting 18 ha of native tussock grassland with schist-rock outcrops inhabited by grand skinks at Macraes Flat, New Zealand
Effects of Land use change on grand skinks at the Individual level and the (meta-) population level

Land-use change resulting in habitat fragmentation and increasing isolation of habitat fragments is a major threat to biodiversity worldwide (Travis 2003, Foley 2005). The aim of conservation scientists, managers and practitioners is to protect species from its impact or to mitigate damage already done. To put in place successful measures for species conservation, understanding the species-specific requirements is essential (Saunders et al. 1991, Fahrig 2007, Kadoya 2009). Metapopulation theory has been used widely to investigate population dynamics of species occurring in habitat fragments surrounded by an uninhabitable matrix (Hanski 1994, Baguette and Dyck 2007). Until recently the matrix has been treated as a homogenous landscape and landscape connectivity was derived from habitat patch characteristics rather than matrix attributes or animal behaviour (Tischendorf and Fahrig 2000, Fahrig 2007, Kadoya 2009).

This research investigated the impact of land-use change in the matrix on metapopulation dynamics of the threatened grand skink. Therefore, some results are specific to grand skinks in the studied area, others have more general applications. Because understanding the individual-level responses to land-use change is essential to understand population-level effects which in turn are essential for effective conservation strategies (Rodewald and Shustack 2008), the effects of land use change were investigated on the individual-level (Chapter 2 and 3) and the population-level (Chapter 4 and 5) for grand skinks.

Land-use change resulted in differences in the behaviour (Chapter 2) and physiology (Chapter 3) of grand skinks. Firstly, grand skinks in tussock grasslands had larger home ranges and moved longer distances than grand skinks on outcrops in pasture grasslands. Additionally, the generally rare movements between outcrops occurred mostly in tussock grasslands (Chapter 2). The results indicate that the reluctance to cross the habitat patch-matrix boundary (boundary effect, Fahrig 2007) was increased by the conversion of tussock grassland into pasture grasslands.
It has been shown that an animal’s decision to cross the boundary into the matrix may depend on the animal’s disposition to move between habitat patches, the distance to the nearest habitat patch and the perceived risk level of crossing the matrix (Lima and Dill 1990, Fahrig 2007, Kadoya 2009). Therefore, the lack of shelter from avian predators in the short pasture grasslands may increase the boundary effect for grand skinks. The second, somewhat unexpected result was that grand skinks in pasture landscapes had a better body condition, especially in autumn, compared to grand skinks in tussock grasslands (Chapter 3). Lower grand skink densities on outcrops (Whitaker 1996), less movements (Chapter 2) and higher invertebrate abundances (Tocher 2003) may lead to these body condition differences.

To develop the spatially explicit metapopulation model, individual-level information on grand skink movements (Chapter 2) was used to make a distinction between habitat patches and the matrix (Hanski 1994). Although movements and home range size of grand skinks have been studied before (e.g., Murphy 1994, Coddington and Cree 1997, Marshall 2000), the extent of the use of the matrix grassland surrounding the rock-outcrops by grand skinks was largely unknown. Occasional sightings of grand skinks in grasslands between outcrops have been reported, suggesting that grand skinks might be foraging for food (Murphy 1994, Eifler and Eifler 1999a, Marshall 2000). The use of radio-telemetry enabled me to investigate daily movements of grand skinks independent of the differences in visibility of grand skinks on rock surfaces or in grasslands between rock-outcrops. My research showed that on a daily basis, grand skinks used neither tussock nor pasture grasslands surrounding the outcrops for foraging but were largely restricted to rock-surfaces and vegetation growing on the outcrops, while the rare occurrence of grand skinks in tussock and pasture grasslands was associated with movements between outcrops (Chapter 2). Therefore rock-outcrops defined as all rock structures separated by less than 10 m of grassland (Whitaker 1996) were suitable to serve as distinct habitat patches surrounded by uninhabitable landscape (matrix) as required for classic metapopulation theory (Hanski 1998).
Modelling extinction and colonisation probabilities and simulating metapopulation dynamics revealed that land-use change had a significant effect on grand skinks at the population-level. In metapopulations, movements of individuals between habitat patches play an essential role for the colonisation of empty habitat patches and the persistence of existing populations through the rescue effect (Hanski 1994). Analysis of grand skink presence-absence data revealed that the probability of colonisation of unoccupied outcrops in pasture grasslands was lower than in tussock grasslands (Chapter 4), resulting from the lack of movements between outcrops in pasture grasslands (Chapter 2). Although movements of grand skinks between outcrops are generally rare, even in native tussock grasslands (Berry et al. 2005), Chapter 2), this study found that further reduction of movements would decrease potential rescue effects and contribute to higher extinction probabilities in pasture grasslands (Chapter 4). However, the major factor leading to the high extinction probabilities in pasture grasslands would be the indirect landscape effect of increased predation of grand skinks by introduced mammalian predators in pasture grasslands (Dunning et al. 1992, Norbury 2001). Extreme population decline events on single outcrops after predator sightings have been recorded (Reardon et al. 2012) along with the predation of marked animals on outcrops (Gebauer, pers. obs. 2012). Allee effects in small populations can accelerate increases in extinction probabilities further. Lower probabilities of pregnancy of female grand skinks in pasture grasslands could result from lack of finding mates on outcrops with low abundances of grand skinks (Chapter 3). Therefore, higher extinction probabilities in pasture grasslands could be caused by a combination of through indirect landscape effects from the conversion of tussock grasslands into pasture grasslands (increased predation, (Norbury 2001), ceased rescue effects through reduced migration of animals (Chapter 2) and the Allee effect of small populations (Chapter 3).

In addition to the strong effects of matrix type, the size of the rock-outcrops influenced extinction probabilities negatively, an effect commonly found in metapopulation studies caused by the positive correlation of habitat patch size with population size (Hanski 1998, Schooley and Branch 2009, Hodgson et al. 2011). Furthermore, habitat patch quality (outcrop structure and vegetation cover)
influenced extinction probabilities. More compact outcrops and higher vegetation cover decreased the probability of extinction while clustered outcrops, split into several rock-tors separated by small areas of grassland (<10 m), and low vegetation cover on the outcrops increased extinction probabilities for grand skinks (Chapter 4).

The simulations of the metapopulation dynamics showed that with the estimated colonisation and extinction probabilities, grand skink populations in pasture landscapes are likely to become extinct, while populations in tussock grasslands are likely to remain or increase (Chapter 5). Although the conversion into pasture grasslands occurred over 30 years ago, grand skinks still inhabit outcrops in the pasture landscape but appear to experience what has been termed ‘relaxation time’ (Diamond 1972, Saunders et al. 1991) or ‘extinction debt’ (Tilman et al. 1994). Although, colonisation probabilities might have declined right after the conversion of tussock into pasture grasslands through changes in dispersal behaviour of grand skinks, the increase of extinction probabilities influenced by an increase in predator numbers would have shown delayed response. After the conversion of tussock grasslands into pasture grasslands, rabbit populations would require time to increase to their current levels, followed by increases in predator population which in turn may have led to a delayed increase in extinction probabilities of grand skinks. Furthermore, the extinction of grand skink population in pasture grasslands at the Redbank study site is likely to have been further slowed because of source-sink dynamics between tussock grasslands and adjacent pasture grasslands. Pulliam (1988) showed that large sink populations can be maintained for long time periods under the right conditions, a balance of migration rates from source to sink habitats, and the survival probability in sink habitats.

This research showed that habitat patches should not be treated as discrete units that exist isolated from the surrounding landscapes. Land-use change of the matrix grasslands affected grand skinks occurring in habitat patches directly (boundary response, Fahrig 2007) and indirectly (increased predator numbers, Norbury 2001, changes in food availability Tocher 2003). Many metapopulation studies
concentrate their analysis purely on habitat patch characteristics and treat the matrix as homogenous “non-habitat” with habitat patch isolation being based on occupancy of other patches and distance between patches (Hanski 1994, Tischendorf and Fahrig 2000, Donald and Evans 2006). There is no consensus in the literature about the relative importance of factors impacting on metapopulation persistence. For example, Hodgson et al. (2009) suggested that increased habitat area and quality are the factors most effectively increasing metapopulation dynamics, while Doerr et al. (2011, in response to Hodgson et al. (2009)) emphasize that practitioners should not overlook increasing structural connectivity and therefore should also concentrate on matrix properties. My research supports authors that emphasize an integration of species-specific connectivity measures into metapopulation modelling (Saunders et al. 1991, Kadoya 2009, Doerr et al. 2011). For the grand skink metapopulation, the land-use change of the matrix from indigenous tussock grasslands to exotic pasture grasslands resulted in reduced functional connectivity and increased extinction probabilities, most likely through a combination of increased predation pressure, Allee effects and reduced rescue effects.

Conservation of the grand skink

The results of this research have added to our knowledge about the behaviour and population dynamics of grand skinks which can be used to improve and support conservation management of the species. The analysis of the presence-absence data supported previous studies which revealed low detectability of grand skinks (Seddon et al. 2011, Chapter 4). This study showed that four surveys were necessary to achieve approximately 95% detection of occupied sites. Designing monitoring programs and sampling designs for further research should take the incomplete detectability into consideration to avoid false absences and biased results (e.g. multiple surveys and choosing appropriate weather conditions).

The metapopulation models emphasized that with current colonisation and extinction probabilities, grand skink metapopulations in pasture landscapes are
heading towards extinction (Chapter 4 and 5). Both parameters (colonisation and extinction probabilities) were largely influenced by the matrix surrounding the habitat patches (rock-outcrops) with reduced colonisation probabilities in pasture grasslands (Chapter 4) caused by the reluctance of grand skinks to traverse the short pasture grasslands (Chapter 2) and increased extinction probabilities through increased predation pressure. Additionally, lower pregnancy probabilities, possibly caused by low grand skink densities on outcrops, might influence extinction probabilities in pasture grasslands (Chapter 3). However, there are several factors which could increase metapopulation persistence of grand skinks even in pasture landscapes. Firstly, predator control can both reduce extinction probabilities and increase colonisation. Large-scale predator control and predator proof fences in tussock landscapes have resulted in large increases in grand skink population size (Reardon et al. 2012). However, large-scale predator control in pasture landscapes has not been attempted yet. Predator control would allow populations on outcrops to increase and provide more potential migrants for colonisation of unoccupied outcrops. Therefore, lower predation pressure might increase functional connectivity of outcrops which can lead to increases in the colonisation probabilities of grand skinks occurring on outcrops in pasture grasslands. Increased population densities on outcrops would also increase the pregnancy probability further, which leads to further reductions in the extinction probabilities. Secondly, colonisation probabilities would increase with increasing vegetation structure of the grasslands (e.g., restoration of tussock grasslands) between outcrops. However, restoration of tussock grasslands will be difficult to implement ecologically, and on private farmland.

Success in captive breeding operations and increasing numbers of grand skinks in predator proof fences and core predator trapping areas enable translocations of grand skinks into protected areas where grand skinks have become extinct. This study demonstrated how simulation models can be used to assess the suitability of future translocation sites. The model predicted that the fastest increase in occupied rock-outcrops resulted on sites with a high density of preferably large rock-
outcrops. Additionally, rock-outcrops with relatively high vegetation cover showed a tendency for being more successful translocation sites.

**Recommendations for future research**

- *Predator behaviour and abundance*

  Introduced mammalian predators have caused large declines in New Zealand’s endemic fauna (Daugherty et al. 1993). However, detailed information on predator abundance and behaviour in all types of grassland ecosystems is rare (but see Norbury and McGlinchy 1996, Norbury 2001). Detailed information on small-scale habitat use by predators in tussock and pasture grasslands could improve designs of trapping programs and habitat restoration for grand skinks.

- *Feasibility and impact of rabbit control*

  Rabbit populations have been found to be the bottom-up control of predator populations in pasture grasslands in New Zealand, and additionally they are an agricultural pest. Feasibility studies could investigate if cooperative rabbit control programs (e.g., poisoning and rabbit fences) between Department of Conservation and farmers might be an option to reduce predator numbers in pasture grasslands.

- *Impact of vegetation structure on grand skink dispersal*

  This study looked at two extremes of grassland habitats, highly structured indigenous tussock grasslands and grazed exotic pasture grasslands. However, grand skinks might accept reduction of structure in grasslands to a certain level before ceasing movement between rock-outcrops. Investigations on the level of structure complexity that needs to be maintained in grasslands to retain grand skink movements between outcrops could inform habitat restoration programs.
• **Grand skink body condition**

This study revealed differences in body condition between grand skinks occurring on outcrops in pasture and tussock grasslands. Several hypotheses were brought forward to explain the findings. Studies of the differences in invertebrate species and their abundance between the two grassland types, the impact of intra- and inter-specific competition (e.g., sympatric McCann’s skinks (*Oligosoma maccani*) and Otago skinks (*Oligosoma otagense*)) and differences in movement behaviour are needed to tease apart the contribution of each of the factors in explaining the body condition differences of grand skinks.

• **Effects of climate change**

Climate change could impact on grand skinks in several ways. Milder winters would allow the emergence of grand skinks during times of low food availability and possibly lead to decreased body condition in spring, which in turn can negatively impact reproduction and survival. Furthermore, increased frequency of La Niña events might increase the occurrence of mast seeding in tussock grasslands, which in turn increase rodent populations leading to increased predator numbers.

• **Dispersal of juvenile grand skinks**

Dispersal of juvenile grand skinks is a driving force of the metapopulation dynamics since adult movements are not great enough for colonisation processes that sustain the metapopulation dynamics. However, information on the timing and extent of juvenile dispersal movements of grand skinks is not available. If dispersal of grand skink juveniles is seasonal, could increased vegetation structure during the dispersal season improve movements between outcrops in pasture grasslands? For example, taking stock off pastures before grand skink dispersal events could allow pasture grasses to increase in height, potentially improving between-outcrop movements.
REFERENCES


REFERENCES


Bates, D. and M. Maechler. 2010. lme4: Linear mixed-effects models using S4 classes. R software package.


REFERENCES


REFERENCES


REFERENCES


REFERENCES


Moore, J., J. Hoare, C. Daugherty, and N. Nelson. 2007. Waiting reveals waning weight: Monitoring over 54 years shows a decline in body condition of a long-
lived reptile (tuatara, *Sphenodon punctatus*). Biological Conservation *135*:181–188.


Murphy, T. J. 1994. Activity rhythms, microhabitat selection, home range and social communication in Grand skinks (*Leiolopisma grande*) at Macraes Flat, Central Otago, New Zealand. Otago Conservancy, Department of Conservation, Dunedin, NZ.


REFERENCES


Waye, H. L. and R. T. Mason. 2008. A combination of body condition measurements is more informative than conventional condition indices:
Temporal variation in body condition and corticosterone in brown tree snakes (*Boiga irregularis*). General and Comparative Endocrinology **155**:607–612.


REFERENCES


APPENDICES
APPENDIX 1: VHF Radio telemetry pilot- and beacon-study in grand skink populations

Introduction

It is essential for wildlife researchers to know the location of animals in the environment to estimate habitat and resource use, home range sizes and movements of animals. Because animals cannot always be followed and locations visually recorded by observers in the field, radiotelemetry has been widely used to calculate approximate animal locations by estimating the bearings of the animal’s transmitter signal from several known locations (triangulation). Numerous studies have emphasized that the bearings are only estimates and the triangulated location is not error-free (Heezen and Tester 1967, White and Garrott 1986, Saltz 1994). Using imprecise telemetry data to assess habitat use can lead to the wrong conclusions as resource use cannot be classified reliably (White and Garrott 1986, Montgomery et al. 2011). The relative influence of the telemetry error on the accuracy of determining habitat patch use becomes less with increased patch sizes while smaller patch sizes increase the probability of misclassification (Kauhala and Tiilikainen 2002, Montgomery et al. 2010, Montgomery et al. 2011). The accuracy and precision of locations can be affected by signals bouncing of reflective surfaces, weather, topography, animal movements, technology, user error, and canopy cover (Lee et al. 1985, Harris et al. 1990, Montgomery et al. 2010). The accuracy of the location estimate is the distance between the true location and the estimated location (Withey et al. 2001). Precision of telemetry data is often measured as the standard deviation of the difference between the true bearing and the estimated bearing (Lee et al. 1985) or an error polygon or error ellipse defined by the intersections of the bearings (Saltz 1994). How to use the information about the error associated with each location should be carefully considered since removing locations from the analysis with unacceptable error might lead to bias towards locations which have smaller errors because of habitat characteristics or their association with animal
behaviours that reduce telemetry error. Methods have been developed to incorporate location errors in statistical analysis, for example, resource selection modelling (Montgomery et al. 2010, Montgomery et al. 2011). The radiotelemetry error can be quantified in beacon studies where the transmitter is placed in a known location and its position is estimated emulating field data collection (Harris et al. 1990).

Home range size and movements of the endangered New Zealand grand skink have previously been estimated by marking grand skinks with non-toxic paint marks or toe-clipping, and recording re-sight or re-capture locations (Murphy 1994, Eifler and Eifler 1999a, Marshall 2000). The studies relied on re-sightings and re-captures of grand skinks on rock-outcrops because grand skinks are nearly impossible to find in high tussock grasslands and dense vegetation. Therefore the recorded locations are biased to grand skink on rock-outcrops and, even further, to visible grand skinks which are not in dense vegetation or rock crevices. Occasionally, grand skinks have been found to move between rock-outcrops and anecdotal evidence refers to sightings of grand skinks in grasslands surrounding the outcrops (Whitaker 1996, Eifler and Eifler 1999a). To investigate the extent of the use of the grasslands by grand skinks a study on habitat use, home range size and movements of grand skinks using radio-telemetry was planned. In order to develop an efficient monitoring scheme which results in robust location estimates a trial study and a beacon study were conducted. A general aim of the trial study was to estimate the time needed to collect location points of skinks fitted with transmitters in the field as well as to familiarise the observer with the behaviour of the grand skink and the environment on the study site. During the beacon study the transmitters were deployed at known locations in the field to investigate the precision and accuracy of the triangulated location estimates but excluding factors such as animal movement and weather conditions which might influence observer error. During the trial study grand skinks were fitted with radio-transmitters and locations were collected under field conditions.

Several specific questions were identified that were important to develop a rigorous and efficient sampling design which would result in location estimates of the quality
needed to answer the research questions. The first question was: what is the precision and accuracy of the triangulated location estimates? Which leads to the second question: How does the estimated precision and accuracy during the beacon study compare to location estimate precision and accuracy of location estimates in the trial study? The third question was: Are precision and accuracy of the location estimates influenced by the animal’s environment such as vegetation and obstacles? Furthermore, do the home ranges that were estimated using true locations differ in size, shape and position from home ranges estimated with locations determined by triangulation? Finally, with limitations on the transmitter weight (<1 g) which should not exceed 5% of the grand skinks body weight (up to 27 g) to avoid significant influence on the skink’s movement abilities, limitations on battery life would dictate the length of the study. This raised the question of how many locations were needed to obtain robust home range estimates for grand skinks.

**Methods**

**Study site and species**

The grand skink is one of New Zealand’s largest and most threatened lizard species, reaching a snout-vent-length of 113 mm and weights up to 27 g (Cree 1994). Grand skinks are very long-lived reaching 19 years in the wild (N. Whitmore, Department of Conservation, pers. comm., 2012) and mature at 3 – 4 years (Cree 1994). They are highly saxicolous, occurring on rock-outcrops which are scattered throughout grasslands in the central South Island, New Zealand. Introduced mammalian predators and habitat destruction have been identified as their biggest threat (Whitaker and Loh 1995). This study was conducted south of Macraes Flat (45°28′ S, 170°28′ E) where populations of grand skinks occur on rock-outcrops in tussock grasslands protected by the Department of Conservation and in pasture grasslands.
Beacon study

In April 2009, a beacon study was undertaken to assess the accuracy of triangulating transmitters positioned in the field. The transmitters were placed in different locations on and around a rock-outcrop at the study site emulating possible grand skink locations. The position of the transmitter was consigned to one of four categories: 1) on the surface of the rock-outcrop, 2) in vegetation on or around the outcrop, 3) behind an obstacle (rock) from the observer’s perspective and 4) inside a crevice in the outcrop. The observer did not know the location of the transmitter during the triangulation and all bearings were taken on the same day to exclude influences of weather variables such as strong winds which can influence the ability of the observer to hear the transmitter signal strength.

Points were triangulated by estimating the bearing of the direction of the strongest signal with the help of a handheld compass from three stations. The location coordinates of the stations was determined using a handheld GPS. The stations were located 20 – 30 m from the outcrop which was the distance assumed large enough so the observer did not disturb the grand skinks while taking the bearings. The three bearings taken for each observation were used to estimate the transmitter location by triangulation calculated with the computer software SNAP. Additionally, the software was used to perform a least square adjustment of the estimated coordinates resulting in corrected location coordinates (Easting, Northing) and a horizontal error ellipse for each point. Distances between the triangulated points and the GPS points (Lin.Err.) were calculated and used to assess the accuracy (mean Lin.Err.).

Trial study

Between 29. March – 03. May 2009, five adult grand skinks were fitted with radio-transmitters to investigate an optimal monitoring regime. The grand skink locations were estimated by triangulation following the same protocol as described in the beacon study. After taking the three bearings the observer attempted to sight the
grand skinks with the help of binoculars from the last triangulation station. If the skink was sighted its position was marked on a map. The GPS coordinates of all mapped positions were taken at the end of the study to not disturb the animals during the observation period.

Similar to the beacon study, all locations which could be confirmed visually were used to analyse the accuracy of the triangulation points by calculating the mean of Lin.Err., and by assessing the radius of the horizontal error ellipse (Hor.Err). After finding no influence of the transmitter’s locations on accuracy in the beacon study, coordinates with very large Hor.Err (>10 m) were excluded from the analysis. The triangulated coordinates were used to estimate the home range sizes with fixed kernel estimation procedures using the computer software Ranges 8. The number of locations needed to estimate relative robust home range sizes was determined by establishing the approximate number of locations needed to reach an asymptote when plotting the number of locations versus estimated home range size.

Home range estimates were also determined from a) true locations and b) their triangulated counterparts for the beacon study and the trial study to visually assess differences in shape, size and position between the two groups.

Results

Beacon study

The location of the transmitter estimated by triangulation was on average 6.5 m (SE = 0.62 m) off the true location (Fig. A1.1) and had a mean Hor.Err of 3.3 m (SE = 0.6 m, Fig. A1.2). Only one triangulated location (3.6 %) out of 28 locations measured was within 2 m of the true location. Visual assessment shows a directional bias towards the south-west for most estimated locations (Fig. A1.1). However, neither the distance between true and estimated transmitter location nor the radius of the horizontal error of the estimated location differed between the four
different location types (distance: $F_{(24)} = 0.99$, $p = 0.41$, horizontal error: $F_{(24)} = 0.39$, $p = 0.76$). The Hor.Err did not correlate with Lin.Err and the maximum acceptable value was set at 10 m for analyses in the trial study.

**Figure A1.1.** Relative position of the estimated location (symbols) to the true location of the transmitter (0,0). Inset: Distribution of the distance between estimated and true location of transmitter during the beacon study. Bin size=1 m
Figure A1.2: Distribution of the large radius of the horizontal error ellipse of locations triangulated during the beacon study. Bin size = 1 m

Trial study

Each grand skink was located on average 61 times (SE = 5.4) using triangulation methods with 33.9 % (SE = 3.1) of the locations visually confirmed with the help of binoculars. The Hor.Err estimates for 270 locations were within 10 m (mean = 1.9 m, SE = 0.1 m), but 36 triangulations resulted in very large error estimates which were excluded from the following analysis (Fig. A1.3). For 85 locations with horizontal errors smaller than 10 m, visual conformation of the true grand skink location was possible. Locations were triangulated with a mean Lin.Err.
of 7.3 m (SE = 1.1 m, Fig. A1.4). 17 triangulated locations (20%) were within 2 m of the true location. Similar to the beacon study, a directional bias in the estimated location relative to the true position towards the south-west is evident (Fig. A1.5).

The home range size varied largely between the individual grand skinks (Fig. A1.6). The mean home range size was estimated as 367 m$^2$ (SE = 488 m$^2$) using all triangulated positions which had a Hor.Err. less than 10 m. The incremental analysis resulted in an average of 20.6 locations needed to reach an asymptotic home range estimate (Fig. A1.7). Two skinks developed a second asymptote after 47 and 32 observations (Fig. A1.7 b, e). Home range sizes were over and underestimated to varying degrees (Fig. A1.8). Additionally the overlap with the home ranges estimated from true locations varied. Differences in shape, position and size of the home range estimates are evident (Fig. A1.9).

![Figure A1.3: Distribution of the large radius of the horizontal error ellipse of the locations estimated by triangulation during the trial study. Bin size: main graph = 100 m, inset =1 m](image-url)
Figure A1.4. Linear distance between GPS locations and the true location estimated by triangulation. Bin size: main graph= 10 m, inset = 1 m.

Figure A1.5. Relative position of the estimated location of grand skinks to the visually confirmed location (0,0).
Figure A1.6. Fixed kernel home range estimates for five grand skinks. Contours are 95%, 75% and 50% kernel estimates. Small grey circles are individual locations estimated using triangulation procedures.
Figure A1.7. Percentage of maximum home range estimates for increasing numbers of locations using fixed kernel estimation procedures derived for five grand skinks.
Figure A1.8: Differences of 95% kernel home range size (m$^2$) estimated with GPS (true) locations and locations estimated by triangulation.
Appendices

a) Beacon study

b) Skink 1 (Trial study)

c) Skink 2 (Trial study)

d) Skink 3 (Trial study)

e) Skink 4 (Trial Study)

f) Skink 5 (Trial study)

Figure A1.9: Comparison of 95% kernel home range estimates using true locations (black outline) and the same locations estimated by triangulation (grey outline)
Discussion

The trial and beacon study were undertaken to investigate if triangulation could be used to obtain accurate positions of grand skinks on rock-outcrops. Although it has been shown that locations estimated by triangulation can be influenced by the position of the transmitter in the field through bouncing or reflection of the signal or obstacles between transmitter and receiver, this was not an issue in this study as the beacon study revealed.

However, the trial and the beacon study showed that triangulation of the grand skinks location would not provide location estimates accurate enough to investigate small-scale habitat use by grand skinks. The rock-outcrops where grand skinks occur on vary largely in size and structure (Whitaker 1996, Gebauer, pers obs.). To identify if grand skinks utilise the grasslands/vegetation around the outcrop only a small error between true and estimated location is acceptable. Only 20% of the locations in the trial study were below an error distance of 2 m. As the aim of the main study was to investigate the extent to which grand skinks use the grasslands around the rock-outcrops, the accuracy of the locations was of large importance. A major concern in every study that seeks to investigate the behaviour of animals in their natural environments is that disturbance introduced by the observer leads to changes in the behaviour of the focal animal. The trial study showed that more than one third of the locations could be confirmed visually from large distances. Therefore, the observer should start the search for the focal grand skink approximately 20 – 30 m away from the outcrop, using binoculars and the estimated direction of the strongest transmitter signal. The observer can then slowly approach the outcrop until the grand skink is located. After spotting the animal, its location can then be marked on a map of the outcrop, and GPS points can be collected after the transmitter has been taken of the grand skink at the end of the study. This way, the disturbance to the animals by observers would be kept to a minimum and very accurate locations can be collected. Visual conformation of the locations has the advantage that on-rock and off-rock (in grasslands) locations can be identified in the
field. Very accurate location estimates can then be used for investigations into small scaled habitat use and movements by grand skinks. It has to be noted that those locations will also have an error associated with them. One part of the error will be associated with identifying the location from the map on the rock-outcrop and a second part is associated with the accuracy of the GPS position. Close attention to mapping the locations as well as highly accurate GPS will reduce the error to a level considered to be well within the requirements for this thesis.

For the home range analysis, incremental analysis showed that at least 20 locations for each individual grand skink should be collected to obtain robust home range estimates. The transmitters used for the trial study had a battery life of approximately 28 days, and at least one location per day needs to be collected. This study confirmed the often repeated caution that triangulated locations are only location estimates and it should be ensured that the accuracy of the location estimates is appropriate to answer the research question.
APPENDIX 2: Comparison of body condition indices

Introduction

Body condition indices have been used to describe the health of an animal. The condition index is then related to demographic and ecological traits. A number of review articles are available that describe the use, underlying assumptions and development of body condition indices (Jakob et al. 1996, Green 2001, Stevenson and Woods 2006). Simple body condition indices include ratios between mass length measurements which have been criticised for scaling the two dimensional length incorrectly to the three dimensional mass component (Green 2001). Simple ratio indices were further developed by including power or log transformations (Jakob et al. 1996). Stevenson and Wood (2006) reviewed literature on body condition indices and found that scientists were more likely to use body condition indices which were used by their peers. This traditional use of body condition indices resulted in residuals of linear regressions being used most commonly in terrestrial ecological studies in recent years (e.g., mammals: Murray 2002, birds: Blums et al. 2005, reptiles: Warner and Shine 2007).

A number of papers have criticised the use of residuals because statistical and biological assumptions are likely to be violated (Green 2001, Freckleton 2002, Peig and Green 2010). On the other hand, several authors defend the use of residuals of ordinary least square (OLS) regression as condition indices (eg. Schulte-Hostedde et al. 2005). In his review, Green (2001) listed numerous assumptions which residuals of OLS regression are likely to violate. For example, OLS regression underestimates the slope of the regression line which leads to biased residuals for large values in length (Legendre 1998, Peig and Green 2009). Careful consideration should also be given to the linear relationship of the mass and length variable as violation of this assumption will lead to further bias. Wilkelsi and Trillmich (1997) showed that the assumed linear relationship between mass and size measurements of many body condition indices is clearly violated in some reptiles. A second group
of assumptions relates to the correct relationship of the body condition index and the structural size of the individual (Green 2001). The last group of assumptions relates to underlying assumptions of the regression analysis. Ordinary least square regressions assume no error in x (length measurement), whereas standard major axis (SMA) regression allows for errors in x (length) and y (mass) for the estimation of the coefficients. As this thesis requires finding the best method for determining the body condition index for grand skinks, I will not discuss the reasons why the methods potentially violate key assumptions, instead I refer to the reviews of Green (2001), Peig and Green (2010) and Schulte-Hostedde et al. (2005) for further details.

Peig and Green (2009) introduced a new body condition index which is based on statistically and biologically relevant arguments and demonstrated that for several species the scaled mass index M was a better, more robust approximation of body condition than the residuals index (e.g., for meadow voles (*Microtus pennsylvanicus*), European starlings (*Sturnus vulgaris*), water snakes (*Nerodia sipeon*). Unlike condition an index based on residuals, the scaled mass index M accounts for effects of growth and scaling, and is therefore comparable between animals of different age groups and populations (Peig and Green 2009). Here I compare residual indices of OLS and SMA regressions with the scaled mass index M using a large dataset of grand skink (*Oligosoma grande*) measurements to 1) demonstrate to what extent different body condition indices can lead to varying results when used in statistical analyses and 2) how there body condition indices vary between size classes of grand skinks.

**Methods**

Data on grand skink measurements \( n = 4574 \) were extracted out of a long-term database accumulated by the New Zealand Department of Conservation. For detailed descriptions of the data set see Chapter 3. Body condition indices were calculated using three different approaches: residuals of OLS regression \((CI_{OLS})\),
residuals of SMA regression ($C_{\text{SMA}}$) and the scaled mass index ($C_{\text{M}}$). The scaled mass index ($C_{\text{M}}$) was calculated as recommended by Peig and Green (2009), using the slope of the SMA regression of log (mass) against log (SVL) ($b = 3.15$) and the arithmetic mean of SVL ($L_0 = 73.0$) of the total dataset ($n = 4754$).

For monitoring purposes, grand skinks are generally classified into four size classes by conservation managers: size class 1 (neonates, $SVL \leq 50$ mm), 2 (1 – 2 years old, $SVL = 51 – 68$ mm), 3 (2 – 3 years old, $SVL = 69 – 84$ mm) and 3 (3+ years old, $SVL \geq 85$ mm, Whitaker 1996). To assess how the three body condition indices account for growth, mean body condition indices for each size class were compared.

To investigate how the different body condition indices might influence model selection results, I created 49 different models and ranked them according to the corrected Akaike Information Criterion (AICc, Burnham and Anderson 2002). Fixed factors for the global model were sex, habitat, season and year, and the interaction terms season:sex, habitat:sex, habitat:season, year:season. Random factors included were year, skink ID, catcher, rock ID (for details and justification of variable choice refer to Chapter 3).

All statistical analyses were performed with R version 2.12.0 (R Development Core Team 2010).

**Results**

I found a strong linear relationship between log (SVL) and log (mass) ($R^2 = 0.98$, Fig. A2.1). However, the slope estimated by the OLS regression was significantly lower than the slope estimated by SMA regression (Table A2.1), although the difference between the slopes was very small (Fig. A2.1). Tukey HSD post-hoc comparisons of the three body condition indices between size classes revealed major differences amongst the results for the three methods. $C_{\text{OSL}}$ showed a significant difference in body condition among size classes 2 and 4, whereas $C_{\text{SMA}}$ and $C_{\text{M}}$ indicated that size class 1 was significantly different from size classes 2 to
4 (all $p < 0.05$, Fig. A2.2). Additional, $\text{CI}_{\text{OSL}}$ indicated an increasing trend of body condition from age class 2 to 4.

The model selection process for each of the three different body condition indices investigating temporal, seasonal, sex and habitat differences in body condition resulted each in one model with $\Delta \text{AIC} < 2$. However, different models were ranked first with each body condition index. Using $\text{CI}_{\text{OSL}}$ and $\text{CI}_{\text{SMA}}$ as the body condition index resulted that the highest ranked model included the sex:season interaction. The highest ranked model for $\text{CI}_M$ also included the sex:season interaction and additionally the habitat:season interaction term (Table A2.2).

**Table A2.1**: Regression coefficients for standard major axis (SMA) and ordinary least square (OLS) regression on log-transformed mass against snout-vent-length of grand skinks.

<table>
<thead>
<tr>
<th>Model</th>
<th>Estimate</th>
<th>lower confidence interval</th>
<th>upper confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>OSL</td>
<td>intercept</td>
<td>-11.27</td>
<td>-11.32</td>
</tr>
<tr>
<td></td>
<td>slope</td>
<td>3.11</td>
<td>3.09</td>
</tr>
<tr>
<td>SMA</td>
<td>intercept</td>
<td>-11.43</td>
<td>-11.49</td>
</tr>
<tr>
<td></td>
<td>slope</td>
<td>3.14</td>
<td>3.13</td>
</tr>
</tbody>
</table>
Figure A2.1: Linear regression line estimated for log-transformed snout-vent length versus mass for *Oligosoma grande* (n = 4754 data points). The dark line corresponds to an ordinary least square regression and the dashed line to the standard major axis regression.

Figure A2.2: Mean body condition indices for grand skinks (*Oligosoma grande*) of different size class estimated by three different statistical methods: residuals of ordinary least square regression (CI_{OSL}), residuals of standard major axis regression (CI_{SMA}) and the scaled mass index (CI_{M}). Bars depict standard errors. Different letters within the graph refer to significant differences at 5% level based on Tukeys HSD post-hoc tests.
Table A2.2: Influence of the body condition index on the outcome of the model selection procedure. Reported are the highest rank models from model sets of 49 models, each set using one of the three body condition indices CI\textsubscript{OSL}, CI\textsubscript{SMA} and CI\textsubscript{M}.

<table>
<thead>
<tr>
<th>Body condition index</th>
<th>Highest ranked model</th>
<th>model weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>CI\textsubscript{OSL}</td>
<td>season + sex class</td>
<td>0.72</td>
</tr>
<tr>
<td>CI\textsubscript{SMA}</td>
<td>season + sex class</td>
<td>0.72</td>
</tr>
<tr>
<td>CI\textsubscript{M}</td>
<td>season:sex class + habitat:season</td>
<td>0.95</td>
</tr>
</tbody>
</table>

CI\textsubscript{OSL} – residuals from an ordinary least square regression of log (snout vent length) against log (mass)
CI\textsubscript{SMA} – residuals from a standard major axis regression of log (snout vent length) against log (mass)
CI\textsubscript{M} – scaled mass index (Peig and Green 2009)

Discussion

This study revealed differences between body condition indices estimated with three statistical methods (OSL regression, SMA regression, and the scaled mass index M), and their relationship to the size classes of grand skinks when used in model selection procedures. The OSL regression underestimated the slope of the linear regression of log (mass) and log (SVL) as found by Peig and Green (2010), but the difference was only very small. However, the distribution of the means of the body condition indices across size classes varied significantly in this study. The resulting CI\textsubscript{OSL} showed an increasing trend in body condition for the size classes 2 to 4 indicating a bias towards larger animals, therefore probably not accounting sufficiently for the effect of differences in growth rates (Peig and Green 2009, 2010). This increase in values was not apparent in the CI\textsubscript{SMA} and CI\textsubscript{M} indices. Therefore, the estimated steeper slope of the SMA regression, accounting for errors in x (SVL) and y (mass), resulted in a more appropriate estimation of the SVL to mass relationship. The distribution of the mean values for the CI\textsubscript{SMA} and CI\textsubscript{M} indices across size classes was very similar. Both body condition indices revealed relative high body condition in the grand skinks of age class 1. There are a number of factors that could lead to this result, including: 1) disproportional large measurement errors for very small individuals which could not be accounted for in SMA regression, 2) a real difference in body condition between newborn (size class 1) individuals and older grand skinks (size classes 2–4), and 3) newborns could
have different physiological or structural features (e.g. big heavy heads, a different body shape) that might be influencing their body condition index.

The relationship of body condition and size classes looks very similar for CI_{SMA} and CI_{M}. However, when using both condition indices to investigate the relationship of grand skink body condition over time, between seasons, sexes and habitats, different models were selected as the most parsimonious in the model selection procedure. The CI_{SMA} behaved more similarly to the CI_{OSL} in the model selection process than when compared to CI_{M}. Habitat effects that differed across seasons were not estimated by the highest ranked models for CI_{SMA} and CI_{OSL} but for the highest ranked model using CI_{M}. For this study, I can not test the assumptions of mass being an accurate index for energy reserves specifically in grand skinks and no historic data is available on this topic. However, Peig and Green (2009) convincingly demonstrated that using residuals as body condition indices violates various statistical and biological assumptions, and results should be interpreted with caution if they are not repeatable with the scaled mass index M. The assumption of there being a linear relationship between log (mass) and log (SVL) was fulfilled for the grand skink data set, and for three of the four size classes the scaled mass index M did account correctly for growths. Therefore I chose the scaled mass index M as body condition index to analyse the influence of time, seasons, sexes and grassland type on grand skinks in this thesis.

Further research should investigate the reliability of body condition indices and the factors influencing them. This example shows that different body condition indices may provide varying results and scientists should critically evaluate which body condition index is the most robust for their data, and if their data violates any underlying statistical assumptions.
APPENDIX 3: Spatial dependencies of the colonisation probability

The highest ranked logistic regression model for colonisation probabilities in Chapter 4 accounted for habitat patch characteristics and matrix type but did not take into consideration the spatial distribution of the habitat patches within the matrix or the occupancy status of surrounding habitat patches. It is possible that the colonisation probability of a habitat patch depends on the distance that grand skinks would have to travel through the matrix grasslands between an occupied habitat patch to an unoccupied patch, and the occurrence of grand skinks in habitat patches within that distance. However, using the connectivity measure ‘nearest neighbour distance’ was eliminated in the model selection process. Prugh (2009) found that nearest neighbour distance can be a poor predictor for a species’ occupancy, and suggested using distance to the next occupied habitat patch as a powerful and practical connectivity measure instead. Using the presence-absence data from Chapter 4, a model set was developed to investigate the influence of the distance to the nearest occupied neighbour (NNdist) on the colonisation probability of habitat patches, ranking the models by using the second-order bias corrected AIC values (AICc, Burnham and Anderson 2002). This analysis is possible because detection probability estimates in Chapter 4 indicated that the occurrence of grand skinks in the habitat patch was identified with a probability of 0.94–0.97 (Chapter 4) and therefore provided a 94–97% accurate picture of occurrence of grand skinks in the study area. The model set includes three models. Model A is the most parsimonious model developed in Chapter 4, model B, the most parsimonious model including additionally NNdist in the model for the colonisation probabilities, and model C, the most parsimonious model including an interaction term between NNdist and matrix type (Table A3.1). The interaction term was included because of findings that grand skinks are less likely to cross pasture grasslands than tussock grasslands, which could result in a larger decline of colonisation probabilities with increasing distance to the nearest occupied habitat patch in pasture grassland. Out of the three models, Model B had the lowest AICc value and is therefore the most parsimonious model.
in the candidate model-set (model weight = 0.71). It was followed by Model C with a $\Delta$AICc = 2.38 which received some support (model weight 0.22). The models B (Fig. A3.1) and C (Fig. A3.2) estimated colonisation probabilities as decreasing with increasing NNdist. Model C, which received less support than model B additionally estimates the colonisation probabilities in pasture grasslands to decline faster with increasing NNdist compared to colonisation probabilities in tussock grasslands.

Table A3.1: Results of modelling presence-absence data of grand skinks. The basic models for occupancy probability ($\psi$), colonisation probability ($\gamma$), extinction probability ($\varepsilon$) and detection probability ($p$) in Model A include following variables: $\psi$ – habitat patch size, matrix type; $\gamma$ – habitat patch size, matrix type; $\varepsilon$ – habitat patch size, structure, vegetation cover, matrix type; $p$ – habitat patch size, structure, matrix type. Model B and C include additionally variable ‘distance to the nearest occupied neighbour’ (NNdist).

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>Deviance</th>
<th>AICc</th>
<th>$\Delta$AICc</th>
<th>weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>B</td>
<td>20</td>
<td>2897.81</td>
<td>2940.94</td>
<td>0.00</td>
<td>0.71</td>
</tr>
<tr>
<td>C</td>
<td>22</td>
<td>2895.52</td>
<td>2943.32</td>
<td>2.38</td>
<td>0.22</td>
</tr>
<tr>
<td>A</td>
<td>18</td>
<td>2907.01</td>
<td>2945.54</td>
<td>4.60</td>
<td>0.07</td>
</tr>
</tbody>
</table>

$k$ – number of parameters
Figure A3.1: Predicted patch-specific colonisation probabilities including habitat type, rock-tor size and the distance to the nearest occupied rock-tor in the model.

Figure A3.2: Predicted patch-specific colonisation probabilities including habitat type, rock-tor size, the distance to the nearest occupied habitat patch (NNdist) and the interaction term matrix type:NNdist in the model.