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Behavioural and Ecological Factors Affecting the Trappability of Two Skink Species in Nelson

Petrina Duncan

A thesis submitted for the degree of Master of Science of the University of Otago, Dunedin New Zealand

24 September 1999
The spotted skink, *Oligosoma lineocellatum*, found amongst loose rocks on a sub-alpine scree slope in the Marlborough region, March 1998.

February 1777:

"...we found no reptile here, except two or three sorts of small harmless lizards."

*Cook (1784)*
ABSTRACT

The syntopic skink species *Oligosoma infrapunctatum* and *O. lineoecellatum* appear to have different trappability estimates at Lake Station, Nelson. Long-term mark-recapture data has shown that *O. lineoecellatum* has a consistently lower trappability than *O. infrapunctatum*. In the present study several factors were investigated at Lake Station and in captivity to determine their effects on skink trappability. These factors included: (1) effect of bait type on captures, (2) occurrence of trap escapes, (3) activity patterns of skinks and (4) thermal sensitivity of sprint-running ability. The ecology of *O. infrapunctatum* and *O. lineoecellatum* was also compared, based on results from this study and others.

Two different bait types, pear and live invertebrates, were used in pitfall traps to determine their effectiveness for capturing skinks over two four-day periods at Lake Station. Bait type had a strong effect on capture success, with pear bait being superior to invertebrate bait in attracting both species to traps. Bait was not considered to be a factor influencing the trappability difference because both species were captured in high numbers using pear bait. The occurrence of escapes from traps was investigated in the field and in captivity. Skinks were left in traps for 9 h (in captivity) or 24 h (in the field) and monitored regularly. Although few escapes occurred for either species in the field and none occurred in captivity, *O. lineoecellatum* had a slightly higher escape rate than *O. infrapunctatum* and was significantly more often consumed by nocturnal predators. Higher predation rates on *O. lineoecellatum* may contribute to a low trappability estimate. At the field site, activity patterns of both populations were determined by monitoring skink captures at intervals throughout each day. Both species exhibited unimodal diel activity patterns. Skinks were taken into captivity to assess individual activity regimes using video surveillance. *O. lineoecellatum* spent significantly less time active than *O. infrapunctatum* and also emerged later and retreated earlier in the day. *O. lineoecellatum* may have a lower trappability because of its limited activity time. The effect of ambient temperature on sprint speed was tested in captivity. Skinks repeatedly ran along a track, following brief exposure to different ambient temperatures. *O. lineoecellatum* sprinted significantly faster than *O. infrapunctatum* across a wide range (6-32°C) of body temperatures. *O. lineoecellatum* appears to be well adapted physiologically to extreme temperatures. During this study it was also noted that *O. lineoecellatum* appeared to be more agile, wary and alert than *O. infrapunctatum*.

Results suggest that *O. lineoecellatum* is less trappable than *O. infrapunctatum* because it (1) spends less time active (especially during wet weather), (2) experiences higher rates of predation and may escape more often while in traps and (3) shows heightened wariness which may contribute to trap-shyness. In general, most of the behavioural and ecological differences between *O. infrapunctatum* and *O. lineoecellatum* may be attributed to adaptations for survival in the different habitat types which they are associated with.
ACKNOWLEDGEMENTS

This thesis represents not only my own extensive efforts over the last one and a half years, but also the efforts of numerous others. I would firstly like to thank my two excellent supervisors, Dr Peter Webb and Dr Phil Bishop. Pete: your support, help and humour during the first year of this research was invaluable and much appreciated. Phil: thanks for taking me on after Pete left, your editing skills and enthusiasm ensured that I finished well and with a smile. Secondly, I must thank three key figures at Landcare Research – Bruce Thomas, Dr Murray Efford and Nick Spencer – who allowed me to collaborate with their work and provided essential technical assistance in Nelson and Dunedin. Thirdly, many thanks to Bernard Goetz for allowing me to carry out captive skink work at his research facilities and for providing ongoing technical support and valuable ideas. Fourthly, I thank Dr Caryn Thompson and Dr Richard Barker for their extensive statistical help and for showing a genuine interest in my project.

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# TABLE OF CONTENTS

Title Page  
Frontispiece  
Abstract  
Acknowledgements  
Table of Contents  
List of Tables  
List of Figures  
List of Abbreviations  

## CHAPTER 1  GENERAL INTRODUCTION

1.1 Herpetofauna of New Zealand  
1.2 Sympatric and syntopic lizards  
1.3 The importance of ecological studies  
1.4 Trappability as an issue in population studies  
1.5 Trappability of skinks at Lake Station  
1.6 Focus of the present study  
1.6.1 Bait preferences  
1.6.2 Escape abilities  
1.6.3 Activity regimes  
1.6.4 Thermal sensitivity  
1.7 Aims and objectives  

## CHAPTER 2  DESCRIPTIONS OF SPECIES STUDIED AND STUDY SITES

2.1 Skink species studied  
2.2 Field study site  
2.3 Captivity study site
CHAPTER 3  INTERACTIONS BETWEEN LIZARDS AND TRAPS: BAiT ATTRACTIVENESS AND ESCAPE ABILITIES

3.1 Introduction
   3.1.1 Bait preferences in population studies 19
   3.1.2 Escape abilities of trapped skinks 22

3.2 Methods
   3.2.1 Bait attractiveness in the field 24
   3.2.2 Escapes from traps in the field 27
   3.2.3 Trap escapes and behaviour under captive conditions 28

3.3 Results
   3.3.1 Bait attractiveness in the field 30
   3.3.2 Escapes from traps in the field 38
   3.3.3 Trap escapes and behaviour under captive conditions 40

3.4 Discussion
   3.4.1 Capture success and bait type 40
   3.4.2 Possible factors influencing capture probabilities 41
   3.4.3 Usefulness of bait investigations 44
   3.4.4 Occurrence of trap escapes 44
   3.4.5 Occurrence of predation in traps 46
   3.4.6 Usefulness of escape investigations 47
   3.4.7 Conclusion 48

CHAPTER 4  TEMPORAL RESOURCE PARTITIONING, ACTIVITY PATTERNS AND LOCOMOTOR RESPONSES TO TEMPERATURE IN LIZARDS

4.1 Introduction
   4.1.1 Resource partitioning in sympatric lizard populations 49
   4.1.2 Factors affecting lizard activity 50
   4.1.3 Methodology for studying lizard activity 52
   4.1.4 Partitioning of time by O. infrapunctatum and O. lineocellatum 53
4.2 Methods

4.2.1 Population activity patterns in the field
4.2.2 Individual activity regimes under captive conditions
4.2.3 Thermal sensitivity of locomotor activity in captive skinks

4.3 Results

4.3.1 Population activity patterns in the field
4.3.2 Individual activity regimes under captive conditions
4.3.3 Thermal sensitivity of locomotor activity in captive skinks

4.4 Discussion

4.4.1 Unimodal activity regimes in lizards
4.4.2 Species differences in diel activity patterns
4.4.3 Factors limiting activity of *O. lineoocellatum* and *O. infrapunctatum*
4.4.4 Conclusion

CHAPTER 5 GENERAL DISCUSSION

5.1 Ecological differences between *O. infrapunctatum* and *O. lineoocellatum*

5.1.1 Spatial resource partitioning
5.1.2 Trophic resource partitioning
5.1.3 Temporal resource partitioning
5.1.4 Foraging modes
5.1.5 Physiological characteristics
5.1.6 Responses to climatic conditions
5.1.7 Agility and wariness

5.2 Factors affecting skink trappability

5.2.1 Attraction to bait
5.2.2 Effects of weather conditions
5.2.3 Time spent active
5.2.3 Predation and escapes from pitfall traps
5.2.5 Behavioural characteristics

5.3 Future prospects for *O. infrapunctatum* and *O. lineoocellatum*

5.4 Conclusions

References
## LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Abbreviated Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.1</td>
<td>Skink captures per subplot during bait experiment</td>
<td>30</td>
</tr>
<tr>
<td>3.2</td>
<td>Total skink captures per day during bait experiment</td>
<td>31</td>
</tr>
<tr>
<td>3.3</td>
<td>Model fitting summary for <em>O. lineoocellatum</em></td>
<td>35</td>
</tr>
<tr>
<td>3.4</td>
<td>Model fitting summary for <em>O. infrapunctatum</em></td>
<td>38</td>
</tr>
<tr>
<td>4.1</td>
<td>Skink captures per subplot during activity investigation</td>
<td>60</td>
</tr>
<tr>
<td>4.2</td>
<td>Lizard species that exhibit unimodal activity patterns</td>
<td>71</td>
</tr>
<tr>
<td>4.3</td>
<td>Sympatric lizards that exhibit temporal resource partitioning</td>
<td>75</td>
</tr>
</tbody>
</table>
# LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Abbreviated Title</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>2.1</td>
<td>(a) Distribution of <em>O. infrapunctatum</em> in New Zealand</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>(b) Distribution of <em>O. lineoocellatum</em> in New Zealand</td>
<td></td>
</tr>
<tr>
<td>2.2</td>
<td>Photo of <em>O. infrapunctatum</em> and <em>O. lineoocellatum</em> individuals</td>
<td>12</td>
</tr>
<tr>
<td>2.3</td>
<td>Geographical location map of study site and local area</td>
<td>13</td>
</tr>
<tr>
<td>2.4</td>
<td>(a) Photo of the Lake Station study site on a terrace scarp</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>(b) Close-up view terrace scarp and field site</td>
<td></td>
</tr>
<tr>
<td>2.5</td>
<td>Aerial photo of study site scarp showing position of subplots</td>
<td>16</td>
</tr>
<tr>
<td>2.6</td>
<td>(a) Photo of an open pitfall trap</td>
<td>17</td>
</tr>
<tr>
<td></td>
<td>(b) Photo of a closed pitfall trap</td>
<td></td>
</tr>
<tr>
<td>2.7</td>
<td>Photo of outdoor enclosure used for captive skink experiments</td>
<td>18</td>
</tr>
<tr>
<td>3.1</td>
<td>(a) Photo of pitfall traps inside captivity enclosure</td>
<td>29</td>
</tr>
<tr>
<td></td>
<td>(b) Close-up photo of <em>O. infrapunctatum</em> individual during escape experiment in captivity</td>
<td></td>
</tr>
<tr>
<td>3.2</td>
<td>Capture frequencies for <em>O. infrapunctatum</em> and <em>O. lineoocellatum</em> during the bait experiment</td>
<td>32</td>
</tr>
<tr>
<td>3.3</td>
<td>Captures per subplot with each bait type for</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td>(a) <em>O. infrapunctatum</em> and (b) <em>O. lineoocellatum</em></td>
<td></td>
</tr>
<tr>
<td>3.4</td>
<td>Mean skink captures per subplot per day for</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td>(a) Session One and (b) Session Two</td>
<td></td>
</tr>
<tr>
<td>Figure</td>
<td>Abbreviated Title</td>
<td>Page</td>
</tr>
<tr>
<td>--------</td>
<td>----------------------------------------------------------------------------------</td>
<td>------</td>
</tr>
<tr>
<td>3.5</td>
<td>Proportionate outcomes of skinks which went missing from traps in the field</td>
<td>39</td>
</tr>
<tr>
<td>4.1</td>
<td>Captive activity filming arena showing (a) entire area and (b) one side of arena in detail</td>
<td>58</td>
</tr>
<tr>
<td>4.2</td>
<td>Timing of skink captures in the field</td>
<td>61</td>
</tr>
<tr>
<td>4.3</td>
<td>Activity regimes of 16 O. infrapunctatum in captivity</td>
<td>63</td>
</tr>
<tr>
<td>4.4</td>
<td>Activity regimes of 16 O. lineoocellatum in captivity</td>
<td>64</td>
</tr>
<tr>
<td>4.5</td>
<td>Timing of activity for (a) O. infrapunctatum and (b) O. lineoocellatum in captivity</td>
<td>65</td>
</tr>
<tr>
<td>4.6</td>
<td>Mean time spent active per day by skinks in captivity</td>
<td>67</td>
</tr>
<tr>
<td>4.7</td>
<td>Relationship between sprint time and body temperature</td>
<td>69</td>
</tr>
</tbody>
</table>
## LIST OF ABBREVIATIONS

<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Full Form</th>
</tr>
</thead>
<tbody>
<tr>
<td>mm</td>
<td>millimetre</td>
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<tr>
<td>cm</td>
<td>centimetre</td>
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<tr>
<td>m</td>
<td>metre</td>
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<tr>
<td>km</td>
<td>kilometre</td>
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<tr>
<td>ha</td>
<td>hectare</td>
</tr>
<tr>
<td>asl</td>
<td>above sea level</td>
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<tr>
<td>sec</td>
<td>second</td>
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<tr>
<td>min</td>
<td>minute</td>
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<tr>
<td>h</td>
<td>hour</td>
</tr>
<tr>
<td>°C</td>
<td>degrees celcius</td>
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<tr>
<td>L</td>
<td>litre</td>
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<tr>
<td>g</td>
<td>gram</td>
</tr>
<tr>
<td>E</td>
<td>east</td>
</tr>
<tr>
<td>S</td>
<td>south</td>
</tr>
<tr>
<td>SE</td>
<td>standard error of the mean</td>
</tr>
<tr>
<td>SVL</td>
<td>snout-vent length</td>
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<tr>
<td>VTL</td>
<td>vent-tail length</td>
</tr>
<tr>
<td>T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>body temperature</td>
</tr>
<tr>
<td>NZST</td>
<td>New Zealand Standard Time</td>
</tr>
<tr>
<td>W/cm&lt;sup&gt;2&lt;/sup&gt;</td>
<td>Watts per square centimetre</td>
</tr>
<tr>
<td>RH</td>
<td>relative humidity</td>
</tr>
<tr>
<td>p</td>
<td>probability of achieving the given statistical value at a significance level of 95%</td>
</tr>
</tbody>
</table>
CHAPTER 1

GENERAL INTRODUCTION

1.1 HERPETOFAUNA OF NEW ZEALAND

New Zealand is a temperate archipelago located in the South Pacific Ocean. The many islands of New Zealand support a highly diverse assemblage of herpetofauna. At present there are about 65 endemic species of terrestrial amphibians and reptiles, comprised of frogs, lizards and tuatara (Daugherty et al. 1994; Towns and Daugherty 1994). Ancestors of the frogs (*Leiopelma*) and tuatara (*Sphenodon*) are believed to have existed on the super-continent Gondwanaland 160-200 million years ago (Gill and Whitaker 1996). It is now thought that lizards may have also reached New Zealand prior to its separation from Gondwanaland around 85 million years ago (Towns et al. 1985; Daugherty et al. 1994). Therefore all of the present day terrestrial herpetofauna is ancient and has been isolated for many millions of years.

The lizards are the most diverse group of New Zealand’s herpetofauna in terms of species numbers, despite being represented by just two families, Gekkonidae and Scincidae. At least 29 gecko and 30 skink species are known to currently exist (Daugherty et al. 1994; Towns and Daugherty 1994) and these numbers are likely to increase as more genetic and field research is carried out. New Zealand’s skinks are represented by two genera: *Cyclodina* (8 species) and *Oligosoma* (22 species). Prior to 1995 the genus *Oligosoma* was referred to as *Leiolopisma*, but was changed because its species were found to be well differentiated morphologically and genetically from *Leiolopisma* species (Patterson and Daugherty 1995). Over millions of years the skink fauna has undergone extensive speciation and has spread throughout all areas of New Zealand. Skinks now occupy many different habitat types from the ocean
shore to the alpine zone (Daugherty et al. 1994). Two unique features are exhibited by the skink assemblage in New Zealand (Towns and Daugherty 1994). Firstly, the diversity of sympatric skink species is high for an area with a cool temperate climate. Secondly, assemblages of sympatric skink species are often comprised of a large number of congeneric species. On the mainland of New Zealand, the best examples of areas with high diversity of sympatric skink species are in the subalpine tussock grasslands of the South Island (Towns et al. 1985; Towns and Daugherty 1994). In certain locations, such as Macraes Flat in Eastern Otago, up to six *Oligosoma* species are found at the same locality. An even higher skink species diversity is found on many of New Zealand's offshore islands (Towns and Daugherty 1994). For example, on Great Barrier Island (27 761 ha) eight species of skinks (*Cyclodina* and *Oligosoma*) have been found in sympatry (Newman and Towns 1985), while on the smaller Middle Island (13 ha) seven different skink species (*Cyclodina* and *Oligosoma*) occur together (Towns 1991).

1.2 SYMPATRIC AND SYNTOPIC LIZARDS

At a number of locations in New Zealand, two or more lizard species occur in syntopy. At these sites they share not only the same geographic area (sympatry) but also occupy the same habitat. For example, *O. lineoocellatum* and *O. waimatense* can both be found under rocks on subalpine scree slopes in inland Marlborough (pers. obs.). Also, *O. grande* and *O. otagense* both occupy schist rock outcrops in gullies at Macraes Flat (Towns 1985; Coddington and Cree 1997). In previous lizard studies there has been little or no acknowledgement of the term 'syntopic'. This term, however, clearly defines the relationship between sympatric species by including an additional spatial dimension of habitat. Syntopic species are particularly interesting as their ability to co-occur depends upon partitioning of resources (e.g. food, habitat, time) within their shared habitat. Studies of New Zealand skinks have shown that sympatric species often differ in their microhabitat preferences (Gill 1976; Towns 1985; Towns et al. 1985; Patterson 1992; East et al. 1995; Freeman 1997; Efford et al., in prep [b]), diet (Freeman 1997; Spencer et al.
Chapter One: General Introduction

1998; M. Efford, unpubl. results) and to some extent in their timing of activity (Towns et al. 1985; Coddington and Cree 1997; Freeman 1997). Syntopic lizard species may also show significant differences in their life history traits (Spencer et al. 1998) in terms of survival, size and age at maturity, timing of breeding and reproductive output.

1.3 THE IMPORTANCE OF ECOLOGICAL STUDIES

New Zealand’s endemic herpetofauna has suffered extensive range contractions and extinctions in the last thousand years, following the arrival of humans (Bell et al. 1985; Towns and Daugherty 1994). At least 40% of all lizard species in New Zealand are considered to be endangered, rare or threatened using standard IUCN criteria (Daugherty et al. 1994). Of these 24 species, 13 are now confined to small offshore islands (Towns and Daugherty 1994). The primary cause of range contractions is likely to have been predation by introduced mammals, in particular rats (*Rattus exulans*, *R. norvegicus*, *R. rattus*), mice (*Mus musculus*), cats (*Felis catus*) and mustelids such as ferrets (*Mustela furo*) and stoats (*M. erminea*). Large nocturnal lizards are probably most vulnerable to mammalian predators, which may explain the absence of these lizards on the mainland where they historically existed (Towns et al. 1985). Present day lizard populations are still under pressure from predators and habitat modification. However, recent research combined with conservation measures and legislative changes are beginning to increase the likelihood of survival for many species. For particularly vulnerable and rare lizards (e.g. *Cyclodina whitakeri*, *Oligosoma grande*, *O. homalonotum*, *O. otagense*), long term population monitoring and research is carried out and recovery plans are revised every few years. Additional population studies around New Zealand, particularly those focusing on habitat use and response to habitat modification, also contribute greatly to our understanding about the ecology of many lizard species.

A number of studies in New Zealand have been carried out at locations which have diverse lizard assemblages (Towns 1985; Patterson 1992; East et al. 1995; Towns and
Elliot 1996). Diverse groups of sympatric lizard species are important to conserve because these are one of the unique features of the New Zealand herpetofauna. These species are also very interesting to study from an ecological perspective because of their ability to co-exist in the same geographic location. However, different species at one study site may show differing responses to the methodology used in field studies. For example, many population studies of cryptic ground-dwelling lizards rely on captures in pitfall traps to estimate animal abundance. This methodology assumes equal trappability among all lizard species. In reality, this assumption is probably violated more often than not.

1.4 TRAPPABILITY AS AN ISSUE IN POPULATION STUDIES

Trappability can be defined as the probability of capturing an individual on a particular day or during a trapping session from a study population. The term is commonly used in studies of small mammals (e.g. Bubela et al. 1998; Alterio et al. 1999) where live-trapping is used for population censusing or control. Authors of herpetological studies involving trapping or catching of study animals tend to use the term catchability (e.g. Peterson 1987; Henle 1989; Seburn 1993; Koper and Brooks 1998). In the present study the probability of capture will be referred to as trappability, regardless of whether animals were trapped or caught by hand.

In any study that involves capturing, marking and releasing animals for future capture, it is essential that marked and unmarked animals have an equal probability of being captured. This is an integral assumption of the mark-recapture technique for estimation of population size and other parameters (Pollock et al. 1990). However, this assumption is often violated in natural populations (Burnham and Overton 1979). Pollock et al. (1990) described two responses which may be exhibited by a population to produce unequal trappability: (1) heterogeneity of capture probability among individuals and (2) learned trap responses which may result in trap-happy or trap-shy animals. It was suggested that both of these responses may be present in a population (Pollock et al. 1990). Many authors of
population studies have reported evidence of unequal trappability among individuals (e.g. Peterson 1987; Seburn 1993; Bubela et al. 1998; Koper and Brooks 1998; Alterio et al. 1999).

Studying more than a single species at one site may become problematic if trappability varies within and/or between species. Although there are a number of mark-recapture models that can be used for population estimates when heterogeneity and/or trap response exists in a population (see Pollock et al. 1990), these models have not always been implemented in previous studies. In many cases mark-recapture models are not used at all. Instead population densities are estimated simply by using capture frequencies or capture rates (e.g. East et al. 1995) without regard to trappability differences among species. Trying to determine population size, density and other parameters, either by mark-recapture statistics or other methods, is likely to lead to inaccurate and incomparable results if trappability differences exist among individuals and/or species. Finding a trappability difference may lead to the discovery of significant behavioural and ecological variation within and/or among species (Langtimm et al. 1996; Efford et al., in prep [a]).

1.5 TRAPPABILITY OF SYNTOPIC SKINKS AT LAKE STATION

Lake Station farm is a large agricultural area of land situated in the upper Buller River valley in Nelson, New Zealand. The farm is located 12 km northwest of St Arnaud and is adjacent to Nelson Lakes National Park. Three species of Oligosoma skinks occur in syntopy on a scrub-covered terrace scarp at Lake Station: O. infrapunctatum, O. lineoocellatum and O. nigriplantare polychroma. The three species have different distributions within New Zealand (Gill and Whitaker 1996). O. infrapunctatum populations are confined to localised sites dotted around the mid to lower North Island and upper part of the South Island. O. lineoocellatum is restricted to the eastern side of the North Island and is widespread in the eastern upper half of the South Island. O. n. polychroma is widely dispersed south of the central North
Island and throughout the South Island. The species also occur on a number of different offshore islands (Gill and Whitaker 1996). All three species occur together in syntopy at only two sites: Stephens Island in the Cook Strait and Lake Station in Nelson. Thus the site at Lake Station is important in terms of species diversity and skink ecology.

The ecology of syntopic *O. infrapunctatum, O. lineoocellatum* and *O. n. polychroma* populations at Lake Station has been the focus of a long-term mark-recapture study, carried out by scientists from Landcare Research. Aspects of the skinks' ecology investigated so far include diet, life history traits, microhabitat associations, competition and population dynamics (Efford et al. 1997, in prep [a,b]; Spencer et al. 1998). Of particular interest is the finding that the two most commonly captured species at Lake Station, *O. infrapunctatum* and *O. lineoocellatum*, differ in their trappability (Efford et al., in prep [a]). Capture histories of 479 *O. infrapunctatum* and 216 *O. lineoocellatum* from eight four-day trapping sessions (April 1995-October 1996) were used in a mark-recapture analysis. Results showed that skink trappability was determined by an effect of time with the additive effect of species (Efford et al., in prep [a]). Estimates of recapture probabilities were 0.702 ± 0.034 per four days (mean ± SE) for *O. infrapunctatum* and 0.494 ± 0.060 for *O. lineoocellatum*. These results showed that *O. infrapunctatum* was far more trappable than *O. lineoocellatum* at Lake Station. Efford et al. (in prep [a]) could not explain the observed species difference in trappability, but suggested that behavioural variation between the species could have an effect on captures. Specifically, it was proposed that the time spent active, attraction to fruit bait and exploration habits could differ between *O. infrapunctatum* and *O. lineoocellatum*, thus contributing to the trappability difference (Efford et al., in prep [a]).
1.6 FOCUS OF THE PRESENT STUDY

The present study was undertaken to determine what factors may cause the difference in trappability exhibited between *O. infrapunctatum* and *O. lineoocellatum* at Lake Station. Many factors may be operating to affect the species' trappability, of which only a limited number could be included in the scope of this study. Factors investigated were skink interactions with traps and skink activity. Trap interaction work focused on bait preferences and escape abilities of each species (Chapter Three). Skink activity was examined by determining daily activity times and thermal sensitivity of locomotor activity (Chapter Four).

1.6.1 Bait preferences

The bait type used in the past to attract skinks into pitfall traps at Lake Station was canned pear. Many other sympatric and/or syntopic skinks studied exhibit species differences in fruit consumption and preferences (Twigg et al. 1996; Vrcibradic and Rocha 1996; Freeman 1997; D. Towns, pers. comm.). Therefore, preferences for fruit bait might differ between *O. infrapunctatum* and *O. lineoocellatum*, with the latter being less attracted to pear bait and therefore less trappable. In the present study, fieldwork at Lake Station was designed to investigate the capture responses of both skink species using fruit and invertebrate bait types (Chapter Three).

1.6.2 Escape abilities

During the Landcare Research study, the type of pitfall traps used to catch skinks at Lake Station were empty 4 L tins. It was assumed that lizards were not able to escape from these traps. However, it was not known whether or not escapes actually occurred. Other authors in New Zealand have suggested that skinks and geckos probably do escape from pitfall traps (Walls 1983; Towns and Elliot 1996), especially during warm weather when skinks are very active. If *O. lineoocellatum*...
has the ability to escape more frequently from traps, this would lead to a lower trappability estimate than that for *O. infrapunctatum*. Fieldwork at Lake Station and captive skink work at Nelson were designed to investigate if and when trap escapes occurred and also to compare escape abilities between the two species (Chapter Three).

### 1.6.3 Activity regimes

Few details are known about the daily activity regimes of most diurnal New Zealand lizards. A limited number of studies have found significant differences in the diel activity patterns of ground-dwelling sympatric and/or syntopic skinks in New Zealand (Freeman 1997) and other countries (Milton and Hughes 1986; Bergallo and Rocha 1994; Melville and Swain 1997a). The results of these studies suggest that differences in diel activity may also exist between *O. infrapunctatum* and *O. lineoocellatum*. Differences in activity regimes, especially time spent active, could have significant effects on skink trappability. *O. infrapunctatum* may spend more time active than *O. lineoocellatum*, therefore encountering traps more frequently, leading to a higher trappability estimate. Activity was investigated in the field at Lake Station and in captivity at Nelson to determine population and individual activity regimes and to compare these characteristics between the species (Chapter Four).

### 1.6.4 Thermal sensitivity

Environmental temperature is one of the most important factors influencing the activity of ectotherms such as lizards (Grant 1990; Hertz 1992). The sensitivity of skinks to the thermal environment can differ between syntopic species (Coddington and Cree 1997; Melville and Swain 1997a). Therefore the skink species at Lake Station, *O. infrapunctatum* and *O. lineoocellatum*, may show different responses to temperature with respect to their locomotion. If the locomotor abilities of *O.
infracunctatum are less restrained by temperature, this species may spend more time active than O. lineoocellatum, especially during cooler periods of the day. This in turn could lead to more trap encounters and a higher trappability estimate. In the present study, the thermal sensitivity of each species was determined and compared using sprint-speed as a measure of locomotor ability (Chapter Four). This work was carried out under captive conditions in Nelson.

1.7 Aims and objectives

In summary, the present study looked in detail at aspects of the behaviour and ecology of syntopic skinks, O. infrapunctatum and O. lineoocellatum, in a scrub/pasture habitat and in captivity. The overall objectives of the study were:

1. To determine what factors may affect the trappability of both species,
2. To expand on the current knowledge of the ecology and behaviour of O. infrapunctatum and O. lineoocellatum.

Within these broad objectives, there were a number of more specific aims pertaining to field and captive experiments. These were:

1. To compare the effectiveness of two different trap baits, with an emphasis on increasing captures of the less trappable O. lineoocellatum,
2. To compare the abilities of the two species to escape from pitfall traps,
3. To determine and compare the daily activity times of individuals and populations of each species,
4. To compare the thermal sensitivity of sprint-running ability in the two species.

Studies of sympatric and/or syntopic lizards are greatly needed in New Zealand to provide more information on the ecology of these rare reptiles, which in turn will help in their conservation management. The work carried out in this study aimed to provide new and interesting insights into the comparative behaviour of endemic skinks.
CHAPTER 2
DESCRIPTIONS OF SPECIES INVESTIGATED
AND STUDY SITES

2.1 SKINK SPECIES STUDIED

Two endemic New Zealand skink species (Lacertilia: Scincidae) of the genus *Oligosoma* were involved in this study. The speckled skink, *Oligosoma infrapunctatum* Boulenger, has a widespread but very localised distribution in New Zealand (Fig. 2.1a). In the North Island *O. infrapunctatum* has been found in the Bay of Plenty, Waikato, central and Wairarapa regions (Gill and Whitaker 1996). Isolated populations are also present on Stephens Island in the Cook Strait and in the Nelson and the northern Westland areas of the South Island. Habitats where *O. infrapunctatum* are found include mature and regenerating forest, scrub, vineland and to some extent grasslands and grazed pastures (East et al. 1995; Gill and Whitaker 1996; Efford et al., in prep [b]). *O. infrapunctatum* is usually found at low to mid-altitude sites, to a maximum elevation of about 600 m asl. Individuals of this diurnal species can measure up to 106 mm SVL (snout-vent length). Dorsal colouration is brown with speckles and a rough stripe down each side (Fig. 2.2). The ventral surface is orange, pale pink, grey or yellow with small black speckles. *O. infrapunctatum* is active all year but is infrequently seen during colder months (B. Thomas, pers. comm.). Mating occurs in late September through to November. Gestation lasts 12-14 weeks and live young (usually three to four individuals) are born between late January and March (Meads 1970).

The spotted skink, *Oligosoma lineoocellatum* Duméril & Duménil, has a restricted distribution in the North Island, present only in eastern areas from Hawke's Bay to Wellington (Gill and Whitaker 1996). This diurnal species is widespread on
islands in the Cook Strait and in eastern areas of the South Island, from Nelson and the Marlborough Sounds to south Canterbury (Fig. 2.1b). *O. lineocellatum* occurs in syntopy with *O. infrapunctatum* at two localities: on Stephens Island in the Cook Strait and at Lake Station in the upper Buller River valley, 100 km south of Nelson city. Spotted skinks are found in open, grassy and rocky sites, scrub and vineland areas, ranging from sea level to the alpine zone (Gill and Whitaker 1996). Maximum SVL recorded for this diurnal species is 111 mm. Individuals are coloured light brown, olive green or bright green with pale green spots on the dorsum (Fig. 2.2). The ventral surface is orange, pink, yellow or grey. Like *O. infrapunctatum*, the spotted skink is also active all year round but more so in the warmer seasons (B. Thomas, pers. comm.). Mating occurs in September and October, gestation lasts 12 weeks and three to six live young are born in January or February (Meads 1971).

FIGURE 2.1  Maps showing the distribution of (a) *Oligosoma infrapunctatum* and (b) *O. lineocellatum* in New Zealand. Data obtained from the Department of Conservation Amphibian and Reptile Distribution Scheme, July 1998.
Chapter Two: Species and Study Site Descriptions

FIGURE 2.2 *Oligosoma infrapunctatum* (in foreground) and *O. lineoocellatum*. Both individuals pictured are adults. The species are similar morphologically although head shape differs slightly. Colouration and patterning vary within each species. (Photo by B. Thomas)

2.2 FIELD STUDY SITE

All field work was carried out in February and March of 1998 at Lake Station in the upper Buller River valley, within the Nelson province of the South Island (Fig. 2.3). Lake Station is a large area of farmed land, situated 12 km northwest of St Arnaud and adjacent to Nelson Lakes National Park.

The study site is a terrace scarp at Lake Station (Fig. 2.4a, b) located near the Homestead Creek bridge on the main St Arnaud-Buller road (41° 45'S 172° 44'E). The site lies between 530 m and 580 m asl and is within the Rotoroa Ecological District. Substrate on the scarp is Moutere Gravel (Pliocene) capped by Tophouse glacial till and outwash gravel (middle Quaternary). In all but the last of the Pleistocene glaciations the site was covered by the Rotoiti glacier (Challis et al. 1994). Populations of three reptile species occur in syntopy on the scarp: *Oligosoma infrapunctatum*, *O. lineoocellatum* and *O. nigriplantare polychroma*. 
FIGURE 2.3 Geographical location maps of the study site. Smaller map shows general location of the upper Buller River valley in the South Island of New Zealand. Larger map shows location of the study site on the St Arnaud-Buller Road and major geographical features of the surrounding area.
Climate information for St Arnaud (at 634 m asl) shows an average rainfall of 1562 mm (evenly distributed throughout the year), mean daily air temperatures range from 14.8°C in February (summer) to 3.1°C in July (winter) and ground frosts occur on average 127 days per year (New Zealand Meteorological Service 1985).

Skinks were trapped on the northeast face of the terrace scarp (Fig. 2.4a) in gullies, on ridges and on hill faces (Fig. 2.4b). The dominant vegetation type in gullies and on hill faces was bracken fern (*Pteridium esculentum*), with patches of blackberry (*Rubus fruticosus*) and tutu (*Coriaria arborea*). Short and tall grasses dominated the ridges and were found to a lesser extent in all other areas. Large boulders and loose rock piles were present in patches on hill faces and in gullies.

Landcare Research scientists divided the study area into 13 subplots in 1995-1996 (Fig. 2.5). Each subplot consisted of a 25 m x 25 m square grid containing 25 pitfall traps spaced at 5 m intervals along five rows. These established subplots and pitfall traps were used in the present study to maintain consistency with older capture data. Subplots were separated from each other by at least 20 m. Each pitfall trap was 165 mm in depth and 155 mm in diameter (Fig. 2.6a). Traps had a square lid made of roofing iron (Fig. 2.6b) with the corners folded down at right angles. This enabled the lid to sit propped up slightly above the open top of the trap to allow skink access and prevent rain from entering traps. When not in use, pitfall traps were filled with dry vegetation and sticks to enable skinks to enter and exit traps at any time.
Chapter Two: Species and Study Site Descriptions

FIGURE 2.4 The study site at Lake Station in the upper Buller River valley, Nelson. 
(a) Northeast face of the long terrace scarp, on which the study area is situated. 
(b) Closer view showing the ridges, gullies, hill faces and vegetation at the site.
FIGURE 2.5 Aerial view of the terrace scarp at Lake Station where the skink study site was situated. The position of thirteen subplots is shown in red (each 25 m by 25 m), ten of which were used in the present study. Homestead Creek runs along the lower part of the picture. (Photo by B. Thomas)
FIGURE 2.6 Pitfall traps used for capturing skinks at the study site. (a) A trap with the lid removed, containing two skinks. (Photo by M. Efford) (b) A lidded trap showing unique trap number.
2.3 CAPTIVE STUDY SITE

During October and November of 1998, skinks of both species (*O. infrapunctatum* and *O. lineoocellatum*) were captured and removed from the Lake Station field site on three separate occasions. All skinks were taken to the Reptile Research Centre in Nelson, approximately 100 km northeast of Lake Station. At the Centre the skinks were housed and studied until their subsequent return to the field site up to two weeks later. An outdoor enclosure measuring 2 m by 2 m and 2.5 m in height (Fig. 2.7) was used to house all captive skinks. When not involved in experiments, skinks were kept individually in 2 L square containers (Fig. 2.7) with a supply of food, water and leaf litter. Captive skink work (including activity and trap escape filming) was carried out within the outdoor enclosure. Work investigating thermal effects on skink activity was carried out inside a laboratory, situated 10 m from the outdoor enclosure described above.

**FIGURE 2.7** Outdoor enclosure where skinks were housed and filmed during captivity work. Small square containers visible inside enclosure were used for housing individual skinks.
CHAPTER 3

INTERACTIONS BETWEEN LIZARDS AND TRAPS:
BAIT ATTRACTIVENESS AND ESCAPE ABILITIES

3.1 INTRODUCTION

3.1.1 Bait preferences in population studies

Although New Zealand’s skinks and geckos are predominantly carnivorous, a number of species have been observed consuming soft, fleshy fruits and nectar in the wild (Whitaker 1987). At least nine species of *Oligosoma* skinks consume fruits and/or berries as part of their diets (see Whitaker 1987; Patterson 1992; Efford et al. 1997; Freeman 1997; Spencer et al. 1998). Consequently, it is not surprising that fruit bait is often used as an attractant inside pitfall traps in lizard studies. The most common bait type used in recent studies is canned pear (Newman 1994; Towns and Elliot 1996; Freeman 1997; Efford et al., in prep [a]) and it is likely that the strong, sweet odour of pear is detected by foraging lizards which are subsequently caught.

Baiting of pitfall traps with fruit may present a source of variation in any study that involves sympatric or syntopic species. This variation is caused by food preferences, whereby the attraction to a bait type may differ between species. Attempting to gain reliable estimates of population densities from capture data could be problematic if the bait and/or food preferences of different species were not considered. For example, Towns and Elliot (1996) carried out five years of pitfall trapping to estimate population densities of five lizard species. The pitfall traps
were baited with pieces of canned pear. Although the cumulative data showed that the five species had different capture rates, it is possible that a preference for fruit in one or more species may have elevated or depressed the number of captures. The skink *Oligosoma nigriplantare polychroma* was found to have the highest capture rate across all seasons and years (Towns and Elliot 1996). However, this species is known to include substantial quantities of *Coprosma propinqua* fruit in its diet (Freeman 1997). Extensive areas of *C. propinqua* shrubs were present within the study area (Towns and Elliot 1996) and a preference for fruit by this species may have added an uncontrolled variable to the study by elevating the capture rates and the density estimates. Conversely, the two species found to have the lowest capture rates and densities, *Cyclodina whitakeri* and *Hoplodactylus maculatus*, may have actually been less attracted to fruit and thus unlikely to be trapped.

Surprisingly, no published studies have addressed the issue of bait preference in lizards prior to carrying out population studies. At least two unpublished experiments have been carried out in New Zealand to compare the effectiveness of different baits for capturing lizards (D. Towns, pers. comm., K. Nielson, pers. comm.). Although analysis of data has yet to be completed, strong preferences within and among species for different bait types have been suggested.

Although bait preferences of lizards have received little attention, the subject has been quite extensively researched using other animal groups. In particular, research has focused on the bait preferences of small mammals (Patric 1970; Rickart et al. 1991; Dilks et al. 1996; Woodman et al. 1996; Weihong et al. 1999), fish (Reebs et al. 1995) and invertebrates, particularly insects (Spurr 1995, 1996). Studies on these groups of animals give strong evidence that variation in bait preferences within and among species can have substantial effects on capture rates. For example, Patric (1970) evaluated the effectiveness of a range of baits in traps for capturing small mammals. Within and among each of the three main species captured, marked differences in bait preferences were exhibited. Only one of the many bait types tested gave a good indication of species composition at the study site (Patric 1970). Studies such as this provide good evidence that caution must be taken before
population densities and species compositions are inferred from capture rates in baited traps. Furthermore, this caution should be extended to lizard studies.

Trophic resource partitioning is thought to help in permitting potentially competing species to co-exist in one locality. Many authors have described differences between the dietary preferences of sympatric lizards (Huey and Pianka 1981; Porter 1987; James 1991; Patterson 1992; Bergallo and Rocha 1994; Twigg et al. 1996; Freeman 1997). More specifically, a number of studies have shown that sympatric lizard species can have different dietary preferences for fruit. For example, Freeman (1997) compared the diets of Oligosoma maccanni and O. n. polychroma using faecal pellet analysis. Fruit from C. propinququa made up 8% of items in O. n. polychroma pellets but did not feature at all in the diet of O. maccanni. Mabuya macrorhyncha and M. agilis also differ in their diet composition with fruits making up 8.1% of the total volume ingested by M. agilis compared to only 0.4% for M. macrorhyncha (Vrcibradic and Rocha 1996). Similarly, skinks of the genus Ctenotus exhibited marked differences in their preference for fruit (Twigg et al. 1996). For one of three sympatric species (C. grandis), seeds/berries were the third most important food type, whereas the two other skinks (C. helenae and C. pantherinus) showed little or no consumption of berries (Twigg et al. 1996). Considering the dietary differences illustrated in the previous examples, baiting pitfall traps with fruit may not be the best methodology when studying sympatric or syntopic species if their dietary preferences are unknown.

Diet analysis has been undertaken for the skinks at the Lake Station study site, Oligosoma infrapunctatum and O. lineocellatum, using scat contents. Both species consume a wide range of invertebrate taxa and also include fruit/berries in their diets (Efford et al. 1997; Spencer et al. 1998; M. Efford, unpubl. results). Despite considerable dietary overlap, major prey items differed between the two species in early and late summer, as did the variety of food types taken (M. Efford, unpubl. results). O. lineocellatum consumed a smaller variety and lesser amounts of prey than O. infrapunctatum. O. lineocellatum also took smaller amounts of fruit/berries than O. infrapunctatum. These results may have important implications for skink
trappability. Since *O. lineoocellatum* individuals consume only small quantities of fruit, they may be less attracted than *O. infrapunctatum* to the fruit bait (canned pear) used in pitfall traps at the Lake Station site. This in turn may correlate with fewer trap encounters and a lower trappability estimate for *O. lineoocellatum*, as found by Landcare Research (Efford et al., in prep [a]).

In an effort to increase the trap encounter rate and hence the trappability of *O. lineoocellatum* in the present study, an alternative bait type was trialed at the Lake Station site. Since both skink species are predominantly carnivorous (M. Efford, unpubl. results) the alternative bait used was live mealworms (*Tenebrio molitor* larvae). Furthermore, *O. lineoocellatum* includes more larvae in its diet than *O. infrapunctatum* and thus may be more attracted to traps containing larvae than those containing pear. This work allowed a comparison of the effectiveness of pear and invertebrate baits which has not been undertaken in any other published lizard studies in New Zealand. By using a mark-recapture approach for this work it was possible to model many factors affecting capture probabilities of skinks.

### 3.1.2 Escape abilities of trapped skinks

Sympatric lizards may exhibit species differences in their agility and subsequently their ability to escape from traps. Methodology in lizard studies involving pitfall captures assumes that all lizards are retained in traps. However, when traps are only checked once daily, as is common in many studies, escapes cannot be noted. Furthermore, if one of two sympatric species had greater agility, this could enable individuals to escape from traps more frequently than individuals of the less agile species. The occurrence of escapes from pitfall traps by geckos and skinks in New Zealand has been suggested previously by Walls (1983) on Stephens Island and by Towns and Elliot (1996) at Pukerua Bay. The authors of both studies suggested that trap escapes may be more likely when ambient temperatures are warm, at a time when lizards have greater mobility (Walls 1983; Towns and Elliot 1996).
Chapter Three: Interactions Between Lizards and Traps

Behaviourally the two syntopic skink species at Lake Station differ markedly in several respects. *O. infrapunctatum* is a fairly placid skink that will calm down quickly after a brief initial struggle when handled. In contrast, *O. lineoocellatum* is far more agile and will struggle and bite continuously whilst being held. Personal observations of skinks in pitfall traps have shown that *O. lineoocellatum* can leap almost to the top of traps and will do so repeatedly while captured, whereas *O. infrapunctatum* rarely shows escape attempts and appears not to be able to jump as high. Given that *O. lineoocellatum* is more agile and shows many escape attempts, it is likely that individuals of this species frequently escape from pitfall traps during trapping sessions. A high escape rate could contribute to the low trappability for *O. lineoocellatum* shown in Landcare’s study (Efford et al., in prep [a]). In the present study, an investigation into escape abilities was undertaken to assess the extent of escape occurrences and to make comparisons between the two species. Work was carried out with skinks in the field and in captivity. The fieldwork involved keeping captured skinks in pitfall traps for 24 hours and carrying out checks of traps at three hour intervals. The captive skink work involved filming skinks in pitfall traps for long continuous periods of the day to determine if and when escapes occurred.

In summary, the aims of this section of my research were to:

1. trial an invertebrate bait in pitfall traps in an effort to increase captures of the less trappable *O. lineoocellatum*,
2. compare between species the effectiveness of fruit bait and invertebrate bait for capturing skinks,
3. determine the outcomes of skinks held in pitfall traps in the field for 24 h periods,
4. compare trap escape abilities between the two skink species in an enclosure.

By exploring skink interactions with pitfall traps, it was hoped that more information regarding the causes of trappability differences between species would be revealed.
3.2 METHODS

3.2.1 Bait attractiveness in the field

Fieldwork to investigate the response of two skink species to different trap bait types was carried out in February 1998 at the Lake Station field site. Ten subplots each containing 25 pitfall traps (see Fig. 2.6) were used every day for eight trapping days. Subplots (described in Section 2.2) were separated by at least 20 m and were distributed widely across the field site (see Fig. 2.5). During the first four days all traps in five subplots were baited with a small piece (10 mm cube) of canned pear while all traps in the remaining five subplots were baited with live mealworms (Tenebrio molitor larvae). Bait types were randomly assigned to subplots. For the last four trapping days bait types were swapped at all subplots to allow for differences in weather effects between the two four-day trapping periods.

Canned pear pieces were cut into cubes approximately 10 mm$^3$ and placed directly onto the tin base of a pitfall trap. Pear bait in traps was replaced as necessary, usually once a day, because it either dried out or was consumed by skinks or ants. In each trap baited with mealworms, six larvae were used, each measuring 12-20 mm in length and 1-2 mm in width. To prevent skinks from consuming the bait, mealworms were placed inside a clear, plastic, topless container 38 mm in diameter and 60 mm in height. A pinch of mealworm food (stone ground flour mixed with baking bran) was added to each container to prevent worms from starving. Each mealworm container was stuck down to a white plastic lid (diameter 101 mm) using "Blu Tack" adhesive to prevent it from tipping over. This set-up was placed directly onto the base of the pitfall trap. Mealworms in traps were replaced when needed which tended to be once or twice during each four-day period. Some mealworms were eaten by skinks, many were consumed by ants, and others either overheated on hot days or drowned due to rain entering pitfall traps.
During the four days following initial baiting all traps were checked for skinks once every 24 h between 1-11 h after sunrise. Sunrise occurred at approximately 0700 h local time. When a trap lid was removed and the trap was found to contain one or more skinks each animal was individually processed. The trap number, time, species and capture type were noted. One of three capture types was allocated: new (never been caught before), session (a skink that had been caught previously but not during this experiment) or recapture (a skink that had been caught previously in this experiment).

New skinks were assigned a unique toe-code combination and toes were cut off accordingly using small scissors. Natural toe loss was integrated into the system where possible. In most cases two toes were removed from the first foot and one was removed from each of the other three feet. For new skinks, the following variables were recorded: the skink's belly colour, sex, reproductive state, SVL (snout-vent length), VTL (vent-tail length), the extent of tail regeneration (where present) and body weight. Sex was determined by applying pressure around the vent area to evert the two hemipenes, present only in males. If no hemipenes appeared during palpation, the skink was checked for typical female characteristics: two small red openings either side of, and below the anus (where the hemipenes are inserted during copulation). Gravid females were assumed to be only those with extremely enlarged abdomens. Tail regeneration was recorded as the length (mm) of new tail growth following partial or full tail loss (very common in both species). Body weight was measured to the nearest 0.5 g using a Pesola balance attached to a small plastic bag. For ‘session’ skinks (those previously toe-clipped in a different experiment), processing comprised simply of recording the existing toe-code combination, all other information having been previously recorded for these skinks by Landcare Research scientists. All skinks were given an identical marking on the dorsum using a gold xylene-free pen and then released near the trap where captured. Recaptured skinks (those with existing gold markings) had their toe-code recorded and were then released. Once all skinks in a pitfall trap were processed, bait was renewed as necessary and the lid was fitted back on top.
To record environmental variables a data logger (UNIDATA Starlogger, model 6004B) and three sensors (humidity/temperature transmitter, HUMITTER 50U/50Y from VAISALA and solar radiation sensor, NSSR-1) were placed within the field site for the duration of the fieldwork. When a trapping session was in progress the data logger was programmed to measure and record the date, time, air temperature (°C), relative humidity (% RH) and solar radiation (W/m²) 50 cm above ground level at five minute intervals throughout the day and night. Logged data were downloaded onto a laptop computer at the end of each trapping session. A general description of the prevailing weather was also made at all subplots visited during each day. A weather rating of Level 1 to Level 4 was assigned to each trapping day by calculating mean values for temperature, relative humidity and mean solar radiation during daylight hours. Fluctuation of these weather variables within a day was also taken into account. Weather Level 1 days were categorised by high humidity (normally as a result of showers), mild temperatures and low levels of solar radiation. Weather Level 4 days were categorised by low relative humidity, high mean temperatures and high levels of solar radiation.

To assess the effects of bait type and other variables on captures, data were analysed using the computer program MARK (White 1998). MARK is a mark-recapture program that provides parameter estimates from marked animals when they are re-encountered at a later time. Parameter estimates are computed via numerical maximum likelihood techniques. The number of estimable parameters is used to compute the quasi-likelihood Akaike Information Criterion value (AIC value). The AIC is then used to rank the various statistical models produced, with the 'best' model having the smallest AIC value (White 1998). Skink capture histories for the eight trapping days were determined and entered into MARK. A number of models were fitted to the data set for each species, with the assumption that both skink populations were closed since the trapping period was only eight days in duration. Models incorporated a number of factors such as subplot, time, weather conditions, bait type and the order of bait application. From the MARK analyses the best model was determined for each species by comparison of each model's AIC value and selection of the model with the lowest score.
3.2.2 Escapes from traps in the field

The ability of skinks to escape from pitfall traps was examined in the field by monitoring each captured animal in its trap over a 24 h period. Fieldwork was carried out in conjunction with the population activity investigation (see Section 4.2.2). Pitfall traps (Fig. 2.6) in two subplots (described in Section 2.2) were checked five times each day over a 4-day period during late February 1998, with another two subplots checked in a similar way in early March 1998. Each subplot contained 25 pitfall traps baited with a 10 mm$^3$ piece of canned pear. In total 100 pitfall traps were monitored for four days each. Trap checks were carried out at sunrise and at three, six, nine and twelve hours after sunrise.

Each skink captured in a pitfall trap was initially processed and then replaced in the same trap. Processing of skinks already possessing toe-code identification involved recording their location and species, then applying a mark to the dorsum with a gold marker pen. Markings changed daily to indicate the day of capture. Skinks captured for the first time during this fieldwork were allocated a unique toe-code combination and full processing was carried out (as described in Section 3.3.1). Skinks were released next to the trap after being held for 24 h.

When a trap known to contain a skink was found empty, time and trap number were noted, along with any other details which might explain why it was missing. These details included: position of trap lid (ajar or closed), description of skink remains (in or near the trap) and presence or absence of the pear bait. Data on missing skinks were divided into three outcome groups: 'escaped', 'eaten' and 'missing', the latter being a sum of 'escaped' and 'eaten' groups. Species differences within each outcome group were tested using a Chi-Square Test with the statistical program SAS (Release 6.12, SAS Institute Inc., NC, USA).
3.2.3 Trap escapes and behaviour under captive conditions

To assess the ability of captive skinks to escape from pitfall traps, daytime video surveillance of skinks in traps was carried out. Skinks were captured and removed from the Lake Station field site during October 1998 and were taken to the Nelson Reptile Research Centre. Here they were housed individually in small plastic containers (175 mm x 175 mm x 90 mm) within an outdoor enclosure (see Fig. 2.7) and studied until their return to the field site two weeks after capture. Within the outdoor enclosure, nine pitfall traps (depth 165 mm, diameter 155 mm) identical to those used in fieldwork were buried in the dry soil substrate, with the tops flush with the ground level (Fig. 3.1). Four sheets of frosted glass were propped up in a square around the traps to seal the area and ensure that any escapees did not roam far. A video camera with a wide-angle lens (Bischke TRI-Q-CCD, focal length 8.5-68.0 mm, maximum aperture F 1.4) was mounted from the enclosure's ceiling, 1 m above the traps. A 60 W heat lamp was also attached to the ceiling next to the camera to provide a heat source for skinks. Throughout the days of filming, a data logger (UNIDATA Starlogger, model 6004B) was positioned permanently in the outdoor enclosure, to record ambient temperature (°C) and solar radiation (W/cm²) at 15 min intervals.

On the first day of filming, skinks were assigned in random order to the nine pitfall traps (one skink per trap) at 1100 h (local time). Time-lapse video recording (using a Panasonic video recorder, model AG-6024, 24 h recording mode) began at this time and continued until 1900 h that evening, with one frame recorded every 10 seconds. The heat lamp above the traps was set by a timer to switch on at 1300 h and turn off at 1700 h. This allowed skinks to heat up considerably thereby maximising their activity and creating a thermal environment similar to the field site during summer. Skinks were removed from traps during the following morning. On the second day, three additional pitfall traps were added to the nine other traps in the enclosure. Twelve different skinks were then assigned randomly to the traps. Filming was carried out as detailed above for two more days until all
captive skinks had been filmed. A total of 16 *O. infrapunctatum* and 20 *O. lineocellatum* were filmed during this time.

(a)

(b)

FIGURE 3.1 The set up for filming of captive skinks during the escape experiment. (a) Nine pitfall traps (diameter 155 mm) buried in substrate within the outdoor enclosure and bordered by sheets of frosted glass. Temperature sensor on right was connected to a data logger. The video camera was situated directly above the traps. (b) Captive *O. infrapunctatum* skink with gold identification marking during the escape experiment.
3.3 RESULTS

3.3.1 Bait attractiveness in the field

Large numbers of both skink species were captured over the eight trapping days of the bait response experiment. For *Oligosoma infrapunctatum* 248 individuals were captured and a total of 453 captures occurred (Table 3.1), representing 68.1% of total skink captures (including multiple captures of the same animals). Fewer individuals of *O. lineoocellatum* were captured (n = 168) and fewer captures occurred (n = 212) (Table 3.2), representing the remaining 31.9% of the total skink captures. Among the ten subplots there were substantial differences within each species in the number of total captures and number of captured individuals (Table 3.1). *O. infrapunctatum* total captures were relatively high (n > 20) at eight out of ten subplots. Total captures of *O. lineoocellatum* were somewhat lower, with only three subplots yielding more than 20 captures (Table 3.1). There was also variation between the two species in the numbers of total captures and individuals at

<table>
<thead>
<tr>
<th>Subplot number</th>
<th>Total captures</th>
<th>Captured individuals</th>
<th>Total captures</th>
<th>Captured individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>25</td>
<td>14</td>
<td>46</td>
<td>35</td>
</tr>
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<td>2</td>
<td>42</td>
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<td>20</td>
<td>10</td>
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<td>9</td>
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<td>14</td>
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<td>10</td>
<td>37</td>
<td>29</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>11</td>
<td>133</td>
<td>72</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>12</td>
<td>28</td>
<td>18</td>
<td>14</td>
<td>11</td>
</tr>
<tr>
<td>13</td>
<td>41</td>
<td>27</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Total</td>
<td>453</td>
<td>248</td>
<td>212</td>
<td>168</td>
</tr>
</tbody>
</table>

*TABLE 3.1* Captures of *O. infrapunctatum* and *O. lineoocellatum* at each of the ten subplots over eight trapping days. Each subplot contained 25 pitfall traps baited with pear for four trapping days and live mealworms for the remaining four days.
each subplot. For *O. infrapunctatum* 29% of the total skink captures were recaptures while for *O. lineoocellatum* only 19% were recaptures. The total captures and individuals captured tended to be dominated by *O. infrapunctatum* at most subplots, with *O. lineoocellatum* captures only dominating at three subplots (Table 3.1).

Daily variation in total captures occurred in both species when data from all subplots were combined (Table 3.2). The number of *O. infrapunctatum* captures each day was consistently higher than *O. lineoocellatum* captures. Recaptures of *O. infrapunctatum* were also higher than the other species for all trapping days (Table 3.2).

**TABLE 3.2** Captures of *O. infrapunctatum* and *O. lineoocellatum* on each of the eight trapping days for all ten subplots combined. Number of recaptures are given in parentheses. Trapping days were split into two four-day sessions. Each subplot contained 25 pitfall traps baited with pear for one trapping session and live mealworms for the remaining session.

<table>
<thead>
<tr>
<th>Trapping day</th>
<th><em>O. infrapunctatum</em></th>
<th><em>O. lineoocellatum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>84</td>
<td>60</td>
</tr>
<tr>
<td>2</td>
<td>59 (27)</td>
<td>32 (7)</td>
</tr>
<tr>
<td>3</td>
<td>77 (32)</td>
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<td>44 (25)</td>
<td>28 (11)</td>
</tr>
<tr>
<td>5</td>
<td>93</td>
<td>20</td>
</tr>
<tr>
<td>6</td>
<td>16 (9)</td>
<td>3 (0)</td>
</tr>
<tr>
<td>7</td>
<td>12 (9)</td>
<td>3 (0)</td>
</tr>
<tr>
<td>8</td>
<td>68 (31)</td>
<td>22 (5)</td>
</tr>
</tbody>
</table>
The majority of *O. lineoocellatum* (81.5 %) were captured only once during the eight days of trapping (Fig. 3.2). Over half (56 %) of the *O. infrapunctatum* were also captured only once. Very few *O. lineoocellatum* were captured more than twice and no animals of this species were caught more than four times during the eight days of trapping (Fig. 3.2). Most *O. infrapunctatum* individuals had one to three captures, although a low percentage of animals had four or more captures.

FIGURE 3.2 Capture frequencies and associated capture percentages at each frequency for *O. infrapunctatum* and *O. lineoocellatum* over eight trapping days.
The bait type used at each subplot appeared to have a strong effect on the number of skink captures (subsequently tested using the program MARK). Over eight trapping days the mean number of *O. infrapunctatum* captures per day was higher with pear bait than with mealworm bait at eight of the ten subplots (Fig. 3.3a).

**FIGURE 3.3** Number of (a) *O. infrapunctatum* and (b) *O. lineoocellatum* captures per day (mean + 1 SE) in pitfall traps using two different bait types at each subplot. Subplots each contained 25 pitfall traps baited with pear for four days and mealworms for another four days.
Similarly *O. lineoocellatum* mean captures per day were much lower with mealworm bait than with pear bait at all but one of the subplots (Fig. 3.3b).

More captures of both species occurred in the first four-day trapping session (Fig 3.4a) than the second session (Fig 3.4b) for both bait types, averaging the captures across all

![Graph showing mean captures subplot -1 day -1 (+ 1 SE) for *O. infrapunctatum* and *O. lineoocellatum* baited with pear and mealworms.](image)

**FIGURE 3.4** Mean number of skink captures subplot -1 day -1 (+ 1 SE) at traps baited with pear and mealworms during (a) the first four trapping days (session one) and (b) the second four trapping days (session two). Traps at five subplots had pear bait; the remaining five subplots had mealworm bait. Bait types were reversed at all subplots for session two.
subplots. Pear bait was associated with more captures subplot$^{-1}$ day$^{-1}$ than mealworm bait during both the first (Fig. 3.4a) and second (Fig. 3.4b) trapping sessions.

After entering all the skink capture histories into the program MARK, different models were repeatedly fitted to the data. The best model for *O. lineoocellatum* (i.e. the one with the lowest AIC value) assumed that capture probability varied with both time and bait type at each subplot and that the effect of time was due primarily to variation in weather (Model 1 in Table 3.3). The model also assumed an effect of

<table>
<thead>
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<th>AIC</th>
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<th>Deviance</th>
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</thead>
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<tr>
<td>134.821</td>
<td>28</td>
<td>174.587</td>
</tr>
<tr>
<td>141.872</td>
<td>35</td>
<td>166.947</td>
</tr>
<tr>
<td>142.479</td>
<td>24</td>
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</tr>
<tr>
<td>144.352</td>
<td>25</td>
<td>190.367</td>
</tr>
<tr>
<td>151.656</td>
<td>32</td>
<td>183.047</td>
</tr>
<tr>
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<td>237.929</td>
</tr>
<tr>
<td>174.504</td>
<td>14</td>
<td>243.189</td>
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<tr>
<td>175.040</td>
<td>18</td>
<td>235.526</td>
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<tr>
<td>190.134</td>
<td>42</td>
<td>200.359</td>
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<td>211.165</td>
<td>34</td>
<td>238.349</td>
</tr>
<tr>
<td>286.167</td>
<td>138</td>
<td>75.332</td>
</tr>
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</table>
order on the time effect, i.e. the weather was ordered between the two four-day trapping sessions. Other models that included weather effects also had low AIC values (Models 3 and 4). The second best model (Model 2 in Table 3.3) assumed an effect of time on capture probability but this was not due to variation in weather. The time effect was not explained by weather and bait only (with no order effect), since Model 3 (Table 3.3) had a higher AIC value than Model 1 and did not include an order effect on the weather.

Models which did not include weather effects had higher AIC values (Model 2, Models 5-13). Models 8-10 incorporated a bait effect on the capture probabilities with no time or subplot effects. These three models also had higher AIC values, giving strong evidence that bait effects alone did not explain the capture rates for *O. lineoocellatum*. Time and subplot effects were therefore important. Models 12 and 13 had no bait effects and these had the largest AIC values of all the models, giving evidence that there was a bait effect.

The best model (Model 1) had a parameter that measured the effect of mealworm bait on capture rates, taking pear as the reference. The estimate of this parameter was -2.142 (SE = 0.283). The interpretation of this is that the natural logarithm of the odds of skink capture using mealworm bait is 2.142 less than the natural logarithm of the odds of capture using pear bait. This corresponds to an odds-ratio of 0.114, which indicates that the chance of *O. lineoocellatum* capture using pear was 8.8 times greater than when mealworms were used as bait. Therefore, it was much less likely that *O. lineoocellatum* would be caught with mealworm bait than with pear.

The effect of weather was important for explaining the capture probabilities of *O. lineoocellatum*. Each one-unit increase in the weather variable (on the 1-4 scale) resulted in an increase of 0.241 (SE = 0.123) in the log-odds of skink capture for subplots receiving pear bait first. At subplots which received mealworm bait first there was a 1.220 (SE = 0.234) increase in the log-odds of capture with each one-unit increase in the weather variable. This result gives evidence that the capture response to good weather at the five subplots receiving mealworm bait first was
Chapter Three: Interactions Between Lizards and Traps

stronger than the response at subplots with pear bait given first. This may be related to the fact that the weather was also ordered, since the worst weather for catching skinks occurred during the latter half (Session Two) of the trapping period.

The best model for *O. infrapunctatum* capture data (i.e. with the lowest AIC value) had common time variation at all subplots during both trapping sessions, and a bait effect (Model 1 in Table 3.4). This implies that the capture probabilities varied each day in parallel for subplots with the same bait type. Weather variables were included in Models 6-8 but were inadequate in explaining the time variation in capture probabilities. Models 8, 10, 12, 13 and 14 (Table 3.4) had no time effects and these had high AIC values, giving strong evidence that time was an important variable. Models 9, 12 and 13 did not include subplot effects and these models had larger AIC values compared to the models which included subplot effects. The worst model was Model 14 which had no bait effects or time effects but only a subplot effect. Subplot differences alone did not therefore explain the variation in *O. infrapunctatum* captures. Thus there is good evidence that both bait and time were important in determining capture rates.

One of the parameters of Model 1 (Table 3.4) measured the effect of the mealworm bait on capture rates, taking pear as the reference. The estimate of this parameter was -1.074 (SE = 0.174). This means that the natural logarithm of the odds of skink capture using mealworm bait was 1.074 less than the natural logarithm of the odds of capture using pear bait. This corresponds to an odds-ratio of 0.342. Therefore the likelihood of capturing *O. infrapunctatum* using pear bait was 2.9 times greater than when mealworm bait was used. Thus *O. infrapunctatum* much more likely to be captured using pear than mealworms. The result of the bait effect for *O. infrapunctatum* was similar to that found in *O. lineocellatum*, indicating that mealworms are an inferior bait to pear for capturing skinks at the study site.
### TABLE 3.4 Model fitting summary for *O. infrapunctatum* using the program MARK. Note that P and M represent pear bait and mealworm bait respectively. For each model a written description is given, along with the AIC value, the number of parameters and the deviance value. The asterisk symbol (*) has been used to represent an interaction effect. The cross symbol (+) represents an additive effect of a variable.

<table>
<thead>
<tr>
<th>AIC</th>
<th># Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
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<td>(a) Models with time varying capture probabilities</td>
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<td></td>
</tr>
<tr>
<td>1. (</td>
<td>p(g+2t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>2. (</td>
<td>p(g+2t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>3. (</td>
<td>p(g+2t) c=p N(g)</td>
<td>)</td>
</tr>
<tr>
<td>4. (</td>
<td>p(g+2t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>5. (</td>
<td>p(g+2t) c(p+k) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>6. (</td>
<td>p(g+2t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>7. (</td>
<td>p(g+2t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>8. (</td>
<td>p(g+2t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>(b) Other models</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9. (</td>
<td>p(2) c(2) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>10. (</td>
<td>p(g+t) c(p+g) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>11. (</td>
<td>p(g^2) c(g^2) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>12. (</td>
<td>p(2) c(2) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>13. (</td>
<td>p(2) c(2) N(g)</td>
<td>)</td>
</tr>
<tr>
<td>14. (</td>
<td>p(g) c(g) N(g)</td>
<td>)</td>
</tr>
</tbody>
</table>

### 3.3.2 Escapes from traps in the field

Five out of 105 *O. infrapunctatum* and 15 out of 99 *O. lineocellatum* disappeared from pitfall traps during the 24 h holding time. Skinks went missing from traps on two days during the first and second four-day trapping periods. Ample evidence was
collected at trap sites to suggest that the majority of these disappearances were due to nocturnal predation than to escaping. Trap lids were frequently found ajar and tails of skinks were found in many traps. It was assumed that a skink disappearance could be attributed to a successful escape if no evidence of predation was found.

From the statistical analysis there was no evidence of a significant difference between the two species in the proportion escaped (Chi-Square value = 1.522, \( p = 0.217 \)) although there was a significant difference in the proportion eaten (Chi-Square value = 4.481, \( p = 0.034 \)). There was also evidence of a species difference in the total number of missing skinks (the sum of 'escaped' and 'eaten' groups; Chi-Square value = 6.220, \( p = 0.013 \)). The actual proportions of total skinks which escaped, were eaten or went missing (in total) were small but the species differences were still clear (Fig. 3.5). Significantly higher proportions of *O. lineoocellatum* were eaten and went missing in total, and this species also had slightly higher (but not significantly) escape rates than *O. infrapunctatum*.

![Figure 3.5](image-url)
3.3.3 Trap escapes and behaviour under captive conditions

No individuals of either species escaped from pitfall traps in the filming enclosure. Active movements were infrequent for all animals. Very few attempts to escape were made by either species (i.e. jumping against the sides of traps towards the open top). Activity did not increase when the heat lamp switched on in the afternoons. No statistical analysis was carried out for this section of work, due to insufficient escape data and no apparent behavioural differences between individuals and the two species.

3.4 DISCUSSION

3.4.1 Capture success and bait type

The present study provides clear evidence that the type of bait used in pitfall traps markedly affects the likelihood of skink capture. Pear bait correlated with much higher numbers of captures than mealworm bait for both species. This trend was apparent at almost all of the ten subplots (Fig. 3.3) and during both trapping sessions (Fig. 3.4). The MARK analysis also confirmed that mealworms were an inferior bait type to pear. For *O. infrapunctatum* the chance of capture was 2.9 times greater with pear than mealworms, whereas for *O. lineoecellatum* it was 8.8 times greater. This result from the MARK analysis shows that not only was mealworm bait a poor attractant, but also that *O. lineoecellatum* was less likely than *O. infrapunctatum* to be caught in traps baited with mealworms. Since *O. lineoecellatum* includes more larvae than fruit in its diet compared to *O. infrapunctatum* (M. Efford, unpubl. results), it was unexpected that the former species was not particularly attracted to mealworms in traps.
The finding of a marked preference for one type of bait in the present study is consistent with results from studies of mammal and insect bait preferences. For example, Dilks et al. (1996) trialed a range of different bait types in tunnel traps and found that stoats (Mustela erminea) were caught more often using eggs as bait than with any of the other food-types. Spurr (1996) reported that wasps (Vespula vulgaris and V. germanica) were far more likely to be captured in traps baited with 30% sucrose solution than in traps containing other sweet substances. Although data from studies by D. Towns and K. Nielson are yet to be analysed, it appears that lizards are also capable of selecting preferred bait from a range of types. Similar to the present study where a preference for fruit bait was exhibited, chevron skinks (Oligosoma homalonotum) preferred fruit bait (banana) to other foods trialed in captivity and in the field (K. Nielson, pers. comm.). Catfood baits appear to be highly attractive to shoreline skinks (e.g. Oligosoma suteri) while peanut butter is highly attractive to a number of other skinks (Oligosoma and Cyclodina sp.) and geckos (Hoplodactylus sp.) (D. Towns, pers. comm.).

3.4.2 Possible factors influencing capture probabilities

In the MARK analyses the models which best explained the variation in capture probabilities for both species included time and bait effects (Table 3.3, 3.4). These results suggest that the bait type used in traps (pear or mealworms) and the effect of time (especially variability in climatic conditions for O. lineoocellatum) had a very strong effect on the trappability of skinks over eight days of trapping. For both species, the MARK models that were inadequate in explaining variation in capture probabilities included no time or bait effects. The effect of bait type on captures appeared to be similar at all subplots for both species, as models with parallel time effects among subplots had low AIC values. This result gives a good indication that each subplot was an effective replication unit in the bait experiment.

The MARK analyses also showed that interactions with climatic variables influenced the capture probabilities of O. lineoocellatum. The best model for this
species (Table 3.3) assumed that trappability varied with time primarily because of variation in weather (temperature, humidity and solar radiation) among trapping days. There was not such a strong response to weather for *O. infrapunctatum* trappability. These results provide evidence that *O. lineoocellatum* reacts differently to local climatic conditions than *O. infrapunctatum* does, which in turn affects the likelihood of *O. lineoocellatum* being captured. This was especially apparent during the second trapping period, when captures of *O. lineoocellatum* with pear bait were much lower than those of *O. infrapunctatum*, at a time when the weather was particularly unfavourable (wet with low levels of solar radiation). Differences between species in response to variable climatic conditions have been documented in other syntopic *Oligosoma* skinks in New Zealand (Coddington and Cree 1997).

An additional reason why *O. lineoocellatum* was infrequently caught with mealworm bait is that individuals were not attracted to the live invertebrates in traps. Chemical and visual receptors are the most important sensory systems used when lizards are foraging (Seburn 1993; Wapstra and Swain 1996). Since the mealworms did not give off a strong odour and were not visible inside traps, *O. lineoocellatum* individuals may not have been attracted to the available food source. In comparison, it appears that *O. infrapunctatum* were more attracted to mealworms, suggesting that this species either possesses slightly different sensory systems or that it falls into traps regardless of bait presence. A repeat of the bait experiment would be beneficial if a third bait category (i.e. no bait) was included in the design. In this way the preferences of both species to mealworms could be compared to the prevalence of accidentally falling into unbaited traps.

Another factor that may have influenced skink capture probabilities is their foraging mode. Lizards are often classified into one of two foraging categories: actively searching foragers or sit-and-wait predators (*sensu* Pianka 1966). This concept is discussed further in Chapter Four with regard to skink activity and also in Chapter Five. In relation to the bait experiment, *O. infrapunctatum* may have approached and entered traps more often than *O. lineoocellatum* when mealworm bait was used because the species relies on an actively searching mode of foraging.
Movements within a home range may be almost continuous during the day, thus leading to more trap encounters and captures. In contrast, *O. lineoocellatum* may utilise a sit-and-wait foraging mode more often. Infrequent movements for this species may lead to a smaller number of trap encounters and captures.

Foraging modes supposedly correlate with prey types consumed (Huey and Pianka 1981). The diet of sit-and-wait predators is likely to contain mostly mobile prey, whereas an active forager is likely to consume more sedentary prey and also plant food-types. Also, sit-and-wait animals are likely to eat smaller volumes of prey per day than active foragers because less prey are encountered (Huey and Pianka 1981). Diet data from Lake Station's skinks do not support the hypothesis that *O. lineoocellatum* is a sit-and-wait predator. This species consumed a wide range of prey taxa during summer, including sedentary prey such as larvae and fruits/berries (M. Efford, unpubl. results). These findings suggest that *O. lineoocellatum* is an actively foraging, opportunistic species. There is some evidence from dietary data that *O. infrapunctatum* may forage wider and for longer periods than *O. lineoocellatum*. The former species consumed larger volumes of food items from a wider range of taxa. In addition, a greater volume of fruits and berries were taken by *O. infrapunctatum*. Fruits commonly eaten by New Zealand lizards are mostly small (< 5 mm in diameter), odourless and coloured either white, pale blue, pale pink or are translucent (with some exceptions, e.g. *Leucopogon* is orange, *Coriaria* and blackberry *Rubus fruticosus* are almost black) (Whitaker 1987). In order to consume a substantial volume of fruit, a skink needs to be a widely searching forager rather than sedentary, otherwise most fruits would not be detected. Alternatively, it is possible that *O. infrapunctatum* consumes more fruits because fruiting plants are associated with its preferred microhabitat (Efford et al., in prep [b]). Fruiting plants are not strongly associated with the microhabitats where *O. lineoocellatum* is found at Lake Station.

Previous diet analysis has shown that *O. infrapunctatum* consumes more fruit than *O. lineoocellatum* during summer (M. Efford, unpubl. results). This preference for fruit could result in a heightened attraction to fruit bait in traps, resulting in higher
capture probabilities for O. infrapunctatum. However, in the bait experiment pear bait yielded high numbers of O. lineoocellatum captures at all subplots where this species was known to be locally abundant (Fig. 3.3b). This result indicates that a preference for fruit bait by O. infrapunctatum is unlikely to be a major factor affecting the capture numbers and trappability differences between the species.

3.4.3 Usefulness of bait investigations

The bait investigation undertaken in this study provides good evidence that bait type has a significant effect on the capture probability of skinks. It was also shown that syntopic species in the same genus exhibit different reactions to bait types and to variation in climatic conditions. All of these results strongly suggest that bait investigations are very useful and worthwhile in studies of syntopic lizards, especially if results are analysed using mark-recapture modelling. It is known that other skinks in New Zealand also show individual and species-specific bait preferences (K. Neilson, pers. comm.; D. Towns, pers. comm.). Therefore a pilot study to investigate bait preferences should always be carried out prior to a population study. This would enable researchers to use the best bait in pitfall traps to ensure that the maximum possible number of animals are captured from all lizard species present at the study site.

3.4.4 Occurrence of trap escapes

From the fieldwork conducted in the present study, it appears that O. infrapunctatum and O. lineoocellatum are unlikely to escape from pitfall traps. The captive work using video recording further emphasised this finding. Despite quite large differences in the agility of the two species (pers. obs.), this factor does not appear to affect escape rates. Since the fieldwork was carried out during warm summer months, when skinks were very active and agile, the results suggest that escapes are minimal in all seasons. The captive work shows that escapes are
unlikely during spring, even though substantial activity is exhibited by skinks during this period (B. Goetz, pers. comm.). The trap escape work in this study suggests that low trappability for *O. lineoocellatum* is not caused by an ability of this species to escape from traps. These results contrast with those from two studies of turtles in North America. Female painted turtles (*Chrysemys picta*) readily escaped from hoop net traps (80% in 24 h) during a trapping period (Frazer 1990). A similar escape ability for painted turtles was noted by Koper and Brooks (1998). Escape ability is considered to be a major factor affecting the trappability of painted turtles in population studies (Frazer 1990).

Although no significant species differences in escape occurrences were found, it is possible that the species differ in anti-predator behaviour within their natural habitats. To some extent *O. infrapunctatum* and *O. lineoocellatum* select different microhabitats at the Lake Station study area. *O. infrapunctatum* is more closely associated with shaded, closed-canopy sites with dense vegetation. In contrast *O. lineoocellatum* inhabits all areas of the study site, but is found less often in closed-canopy sites (Efford et al, in prep [b]). This species often occupies exposed habitats in other localities, whereas *O. infrapunctatum* is always found on the ground under dense vegetation. Therefore, the two species might differ in their responses to an approaching predator, since predation pressures would be different in open and closed habitats (Crowley 1985; Bulova 1994; Martin and Lopez 1995). Wariness, alertness and escape tactics may be heightened in *O. lineoocellatum* because of the high risk of aerial predation by birds in exposed habitats. *O. infrapunctatum* would not need to have such rapid escape responses or be as alert because it always occupies microhabitats that are protected from aerial predators. Heightened wariness in lizards occupying habitats with little or no cover is quite common (see Crowley 1985; Bulova 1994; Martin and Lopez 1995; Cooper 1997). Most studies have tested wariness by simulating a predator’s approach and then monitoring a lizard’s reactions. It would be interesting to conduct a similar experiment on skinks at Lake Station to determine whether habitat type influenced wariness and escape tactics. Species living in open habitats with sparse cover rely more on speed and running long distances than on refuges (Bulova 1994; Cooper 1997). From personal
Chapter Three: Interactions Between Lizards and Traps

observations, *O. lineoocellatum* seen in open habitats at Lake Station flees and disappears rapidly when disturbed. In contrast, *O. infrapunctatum* in sheltered habitats moves away from disturbance to vegetation cover but does not always disappear completely. These observations suggest that a species difference in escape tactics and wariness, relating to habitat structure, may exist.

In a previous study on the behaviours of *O. infrapunctatum* and *O. lineoocellatum*, East et al. (1995) noted that *O. infrapunctatum* in mature bush on Stephens Island employed tunnelling behaviour as an anti-predator tactic to avoid tuatara (*Sphenodon punctatus*). *O. infrapunctatum* occurring in vineland and scrub habitats on the same island did not show evidence of tunnelling, possibly because tuatara were absent from these habitats. Therefore the behaviour of *O. infrapunctatum* can relate directly to habitat structure. *O. lineoocellatum* also showed variation in its behaviour at different habitat types on the island. In vineland habitats, *O. lineoocellatum* was often seen basking on top of thickets, whereas individuals occupying open pasture habitats always stayed near shelter such as boulders, burrows and debris (East et al. 1995). These behavioural differences were possibly due to the high risk of aerial predation at open sites compared to the relative safety of dense vineland refuges. This study provides good evidence of habitat-specific anti-predator behaviour in *O. infrapunctatum* and *O. lineoocellatum*.

3.4.5 Occurrence of predation in traps

Unexpectedly a number of skinks were eaten by nocturnal predators while being held captive in pitfall traps. Similar findings have been described by several other researchers in New Zealand. Towns and Elliot (1996) lost a number of lizards to trap predation during their study. Judging from evidence left in traps, rodents such as mice (*Mus musculus*) and rats (*Rattus* sp.) and also mustelids (stoats, *Mustela erminea* and ferrets, *M. furo*) were suggested as possible predators (Towns and Elliot 1996). Newman (1994) also found evidence that rodents (mice) had killed lizards in traps within his study area. In the present study it is likely that ferrets were the
main predators of trapped skinks (B. Thomas, pers. comm.), based on the results of previous predator trapping at Lake Station and evidence left at trap sites.

The finding that significantly more *O. lineoocellatum* than *O. infrapunctatum* were eaten by predators may relate to the structure of skink microhabitats at Lake Station. *O. lineoocellatum* occupies all types of microhabitats including open and closed canopy sites (Efford et al., in prep [b]). In more exposed sites this species may be highly susceptible to being caught by mammalian predators such as rodents and mustelids. Dense vegetation in the closed canopy microhabitats preferred by *O. infrapunctatum* (Efford et al., in prep [b]) could prevent predation from occurring as often. A mammalian predator might be expected to concentrate its searching efforts in open areas where lizard prey is easier to catch. *O. lineoocellatum* is a diurnal species, therefore its anti-predator behaviour may not occur during the night when rodents and mustelids forage. The higher rate of predation on *O. lineoocellatum* may contribute to the finding of lower trappability for this species. Moreover, the relatively high number of *O. lineoocellatum* that went missing (15 out of 99 skinks) may also have implications for its trappability.

### 3.4.6 Usefulness of escape investigations

This work provided evidence that skinks can occasionally escape, and quite often be eaten by predators, whilst held in pitfall traps. Therefore it is possible that skinks could go missing from traps during other studies before being processed by fieldworkers. Although only a small proportion (0.05) of *O. infrapunctatum* went missing (total of escaped and eaten) from traps, three times as many *O. lineoocellatum* went missing (0.15). This proportion equates to 15 animals, a fairly substantial number of individuals from four days of trapping. These results indicate that it is worthwhile undertaking an escape investigation either during or after a lizard population study. The usefulness of such investigations is two-fold: not only can the rate of escapes be determined, but so too can the rate of predation. Assuming that evidence of predation is found in or near traps, the predators...
responsible for lizard deaths can often be established (Newman 1994; Towns and Elliot 1996). Parameters such as escape rate and predation rate could then be incorporated into emigration estimates for use in mark-recapture population models and analyses.

For future lizard studies where pitfall trapping is to be used, it is recommended that an escape investigation is undertaken. Additionally, night filming at traps should be trialed, to gain more information about the types of predators that approach traps. An alternative method to avoid nocturnal predation of trapped lizards is to check traps in the morning and evening, rather than just once a day, to limit the number of individuals left inside traps during the night.

3.4.7 Conclusion

In conclusion, a number of important findings were shown by the bait and escape investigations. Bait type had a marked effect on capture success, with pear bait being superior to mealworm bait in attracting both species to traps. Efforts to increase the trappability of *O. lineoocellatum* using an alternative live bait did not succeed, as *O. lineoocellatum* was even less likely to be trapped with mealworm bait than with pear bait. Species differences in capture probabilities may relate to interactions between skinks and the local climatic conditions and slight variations between the species in their foraging strategies. Apparent agility differences between species did not equate to significantly different escape abilities. Escapes were minimal for both species but predation rates on *O. lineoocellatum* in traps were quite substantial, possibly as a result of habitat structure. This work shows that bait and escape investigations are useful for generating valuable information about behavioural and ecological differences between syntopic lizard species. Implications of the bait and escape findings for trappability are discussed further in Chapter Five.
CHAPTER 4

TEMPORAL RESOURCE PARTITIONING, ACTIVITY PATTERNS
AND LOCOMOTOR RESPONSES TO TEMPERATURE IN LIZARDS

4.1 INTRODUCTION

4.1.1 Resource partitioning in sympatric lizard populations

When two or more lizard species occupy the same geographic locality, segregation is usually exhibited along at least one of four niche axes: habitat (spatial), diet (trophic), time of activity (temporal) or temperature (thermal) (Toft 1985; Hertz 1992; Bruna et al. 1996). Resource partitioning may help reduce competition between sympatric/syntopic species and increase feeding efficiency within a species, thereby increasing the carrying capacity (Simon and Middendorf 1976).

Many studies have focused on spatial and trophic resources (i.e. microhabitat and food availability) and how these are segregated by sympatric and/or syntopic lizard species. Spatial separation is commonly seen among many sympatric lizards (Pianka 1969; Webb 1985; Patterson 1992; Bruna et al. 1996; Grover 1996; Vrcibradic and Rocha 1996; Melville and Swain 1997b), and is considered to be the most important dimension for resource partitioning (Toft 1985). Trophic niche partitioning has also been documented in sympatric lizards (Lunney et al. 1989; James 1991; Patterson 1992; Bergallo and Rocha 1994; Twigg et al. 1996),
although the majority of trophic studies show little evidence for clear segregations between diets (Rose 1976).

Temporal segregation in activity among species is often considered the least important dimension within resource partitioning, since it is likely to be secondary to food or habitat partitioning (Toft 1985). Timing of activity is also difficult to assess because (1) species can vary their activity patterns daily and seasonally and (2) there are many environmental, physiological and behavioural factors to consider. Studies which have attempted to quantify the activity patterns of sympatric lizards show that temporal segregation among species is quite common (Webb 1985; Milton and Hughes 1986; Hertz 1992; Bergallo and Rocha 1994; Freeman 1997; Melville and Swain 1997a). Sympatric skinks *Niveoscincus microlepidotus* and *N. metallicus*, for example, show distinct differences in emergence and retreat times, diurnal behaviour, seasonal activity and total activity during summer (Melville and Swain 1997a). This chapter of the present study focuses primarily on temporal resource partitioning and activity in sympatric and syntopic lizards, with particular emphasis on ground-dwelling skinks.

### 4.1.2 Factors affecting lizard activity

The amount of time that diurnal lizards are active depends upon a wide range of environmental, physiological and behavioural factors. Of the environmental factors, weather (particularly ambient temperature) is probably the most important (Grant 1990; Hertz 1992; Rocha and Vrcibradic 1996; Towns and Elliot 1996; Coddington and Cree 1997), as ectothermic lizards tend to be restricted to a narrow window of thermal conditions for locomotor activity (Bennett 1980; Grant and Dunham 1988; Smith 1997). For example, two syntopic species of New Zealand skinks (*Oligosoma grande* and *O. otagense*) in eastern Otago appear to be far more active during sunny, warm and dry weather conditions than during...
overcast, cold and wet conditions (Coddington and Cree 1997). Other environmental factors which influence lizard activity include season (Grant 1990; Wapstra and Swain 1996), photoperiod (Foá et al. 1994), microhabitat structure (Moermond 1979; Milton and Hughes 1986), food availability (Hertz 1992), predation risk (Henle 1989; Hertz 1992) and habitat restrictions (e.g. structural instability, Towns 1975; availability of cover, Henle 1989).

More specific to the individual lizard are physiological factors such as body temperature (Waldschmidt et al. 1986; Firth and Belan 1998), sex (Wapstra and Swain 1996; Melville and Swain 1997a) and reproductive state (Fergusson and Algar 1986; Wapstra and Swain 1996) which may influence activity patterns. For example, activity of sleepy lizards (Tiliqua rugosa) was physiologically constrained by low body temperatures ($T_b$) during winter and spring and high $T_b$ in summer months (Firth and Belan 1998).

Mode of foraging is a behavioural trait, often specific to a lizard population or species, which is also thought to play a major role in activity (Pianka 1969). Foraging strategies are generally defined as ranging from 'sit-and-wait predator' (or rarely active) to 'actively searching forager' (or constantly active) (Pianka 1966; Toft 1985; Bergallo and Rocha 1994). Most species studied lie somewhere along the continuous spectrum between these two extremes (Moermond 1979; Pietruszka 1986; Taylor 1986; Lunney et al. 1989; Vrcibradic and Rocha 1996; Wapstra and Swain 1996). Other behavioural factors which may affect the period of time lizards spend active include behavioural thermoregulation (Crowley 1985), home range (Fergusson and Algar 1986) and social interactions, especially those relating to inter- and intraspecific competition and dominance/subordinance (Grant and Dunham 1988; Whittier and Martin 1992).

All of these factors (environmental, physiological and behavioural) can change and interact, resulting in activity patterns which vary within and between days, seasons and years (Toft 1985). For example, the feeding activity of Niveoscincus
ocellatus was affected by a multitude of different factors including microhabitat, season, environmental temperature, prey availability and foraging strategy (Wapstra and Swain 1996). Each factor appeared to interact with others (e.g. season with prey availability and temperature) to create the feeding activity patterns exhibited by skinks (Wapstra and Swain 1996).

4.1.3 Methodology for studying lizard activity

Methods for quantifying temporal resource partitioning and activity patterns of sympatric lizards tend to involve only field observations. Many activity studies have focused on the number of sightings or captures at intervals throughout the day. Different methods of quantifying and comparing activity include: totalling hourly detection rates each hour of the day (Milton and Hughes 1986), relating the proportion of animals basking per hour directly to numbers active (Hertz 1992), and totalling the number of captures in pitfall traps at regular intervals during the day, assuming that totals correlate with daily foraging activity (Freeman 1997).

An alternative method for investigating time partitioning by lizards is to monitor individuals in captivity. A variety of methods have been used to assess lizard activity in this way, including the following: totalling the proportion of lizards with their heads above the sand (i.e. active) at 2 h intervals (Waldschmidt et al. 1986), recording locomotor patterns using a tilting aktograph to produce daily activity traces (Porter 1987), and monitoring seasonal trends in surface activity using video surveillance in an outdoor enclosure (Goetz and Thomas 1994).
4.1.4 Partitioning of time by *O. infrapunctatum* and *O. lineoocellatum*

Before the present study was undertaken, little was known about the daily activity regimes of *O. infrapunctatum* and *O. lineoocellatum*. Although both species are commonly referred to as ‘diurnal’ in the literature (Gill and Whitaker 1996; Spencer et al. 1998), no studies have documented in detail how these species partition time. Given that the two species have very different distributions in New Zealand (see Fig. 2.1), and are presently only sympatric within two small geographic areas (the upper Buller River valley area and Stephens Island), it is possible that they show quite divergent daily activity patterns. Furthermore, differential partitioning of daily activity may allow the two species to coexist in areas of syntopy. At the Lake Station study site in the present study, where the two species occur syntopically, significant species differences in trappability have been documented by Landcare Research scientists (Efford et al., in prep [a]). This trappability difference may be due to the amount of diel time that each species spends active. It was predicted in this study that if the diel time spent active differs between *O. infrapunctatum* and *O. lineoocellatum* at the study site, the number of encounters with pitfall traps may also differ for each species. A higher trap encounter rate for one of the two species could contribute to a higher trappability estimate. Activity of *O. infrapunctatum* and *O. lineoocellatum* was therefore chosen as a factor to investigate in the present study.

The skink activity study was designed to encompass three specific areas: (1) the time-dependence of activity for the two populations in the field, (2) individual activity regimes in captivity and (3) thermal sensitivity of locomotor activity in captive skinks. Assessing the time-dependence of skink activity in the field provides an estimate of when individuals of the sampled population are actively foraging each day (see Freeman 1997). To observe how each individual behaves for every minute of the day, captive work with video surveillance is very useful (see Goetz and Thomas 1994). Therefore I combined fieldwork for assessing
population activity (using skink captures at intervals throughout the day as an indicator) with a captive study for quantifying daily activity regimes of individuals, using video surveillance equipment. The thermal sensitivity component of the activity work was undertaken to evaluate how the sprint-speed of each species is affected by variation in ambient temperature. Sprint speed is considered to be an organismal trait that integrates aspects of morphology, physiology and behaviour (Sorci and Clobert 1997). *O. infrapunctatum* is generally found at low altitudes, while *O. lineoocellatum* can be found anywhere from sea level to the alpine zone (Gill and Whitaker 1996). One population of *O. lineoocellatum* has been recorded at an elevation of 1300 m asl (R. Cuthbert, unpubl. data). Therefore it is possible that tolerance of extreme temperatures differ between species. For example, iguanid lizards (*Sceloporus undulatus*) living in a high-elevation locality in Colorado exhibited locomotor activity at lower body temperatures than populations from low-elevation New Mexico sites (Crowley 1985). The locomotor activity patterns of other sympatric skinks in New Zealand are known to differ between species in response to extreme climatic conditions, especially fluctuations in temperature (e.g. *O. otagense* and *O. grande*; Coddington and Cree 1997).

In summary, the aims of this part of my research were to determine, and make species comparisons of the following:

1. time-dependence of activity in field populations of sympatric *O. infrapunctatum* and *O. lineoocellatum*,
2. daily activity regimes of individual *O. infrapunctatum* and *O. lineoocellatum* under captive conditions,
3. thermal sensitivity of locomotor activity in captive *O. infrapunctatum* and *O. lineoocellatum*.

The results of examining these three aspects of activity would then be used to provide an overall description of how the two species may partition temporal
resources and how their activity may be affected by environmental, physiological and behavioural factors. Consequences of skink activity patterns for the trappability differences between *O. infrapunctatum* and *O. lineoocellatum* (Efford et al., in prep [a]) are discussed in Chapter Five.

4.2 METHODS

4.2.1 Population activity patterns in the field

Fieldwork to assess skink activity was carried out at Lake Station in the upper Buller River valley in the province of Nelson. The time-dependence aspect of skink activity was determined from the number of captures of skinks in baited pitfall traps at different times of the day. Activity was assessed at four of the ten subplots that were used in the bait experiment (see Fig. 2.5 for aerial view of subplots). Each subplot consisted of a 25 m x 25 m grid containing 25 pitfall traps at 5 m intervals. Pitfall traps were baited with small (10 mm) cubes of pear. Trapping was carried out at two subplots in February (summer) and two in March (autumn) 1998. Traps were checked at 0700 h NZST (New Zealand Standard Time) which was 5-10 min after sunrise (depending on date) and at 1000 h, 1300 h, 1600 h and 1900 h (3, 6, 9 and 12 hours after sunrise) over a four day period and were always checked in the same order.

When skinks were caught, the species, location of trap and time were recorded as well as the capture type (either a new animal bearing no toe-code, an animal caught for the first time in this trapping session with a previous toe-code, or a recaptured animal within the trapping period). For new skinks, unique toe-codes were allocated and full processing was carried out (as described in Section 3.2.1). For previously toe-clipped and recaptured animals only toe-codes were recorded. All skinks were marked with a gold xylene-free pen. Skinks were
replaced in traps where captured and left for a further 24 h to test their ability to escape (see Section 3.2.3). Pear bait was renewed in traps as needed. A data logger (UNIDATA Starlogger, model 6004B) recorded the ambient temperature, relative humidity and solar radiation at 5-min intervals at the field site throughout the activity fieldwork.

Capture data from five trap-check time periods was subdivided into 16 blocks to explain subplot and day variation in capture rates. Square root transformation was carried out on the data to satisfy the ANOVA assumption of normality. A balanced ANOVA was performed using the statistical program MINITAB (Release 8.2, Minitab Inc., PA, USA) to test for species differences in the number of skinks active at each time period. A Fisher’s Exact Test (2-tailed) was also carried out to test for species differences in activity times.

4.2.2 Individual activity regimes under captive conditions

The activity of skinks under captive conditions was assessed during October and November (spring) 1998. Skinks of both species (*O. infrapunctatum* and *O. lineoocellatum*) were captured at the Lake Station field site on three separate occasions during October and individually marked with gold xylene-free pen. All skinks were taken to the Nelson Reptile Research Centre, where they were housed and studied until their subsequent return to the field site, up to two weeks after capture. On the day following capture, each skink was measured in length, weighed and sexed.

Skinks were housed and filmed in an outdoor enclosure (see Fig. 2.7). This enclosure allowed skinks to experience natural daily light and thermal regimes similar to those of their original habitat. When not involved in experiments, skinks were individually housed in 2 L square containers with a supply of food, water and leaf litter. Within the enclosure an activity arena was constructed (Fig.
4.1a) consisting of two areas of equal size (400 mm x 810 mm), separated and bordered by sheets of frosted glass. Each of these areas contained a retreat site, open and shaded areas, water and food containers and a small piece of vegetation (Fig. 4.1b). A video camera (Bischke camera TRI-Q-CCD, focal length 8.5-68 mm, maximum aperture F 1.4) was mounted 1 m above the arena, and was fitted with a wide-angle lens to enable simultaneous viewing of both areas.

Skink activity was monitored using video surveillance over 24 h periods. A single skink was placed inside each of the two areas in the arena. If possible a skink of each species was filmed simultaneously. However, for logistic reasons, during the first three and last three days of filming only one species was filmed. Time-lapse video recording (using a Panasonic video recorder, AG-6024, 24 h recording mode) began at 2000 h (local time) and ended at 2000 h the following evening, with one frame recorded/10 sec. An infrared illuminator (model Bischke IR-20/12) was attached to the ceiling of the enclosure, 1 m above the arena, and aimed towards the filming areas. The lamp was attached to a timer, set to switch on at 1900 h and off at 0700 h, to enable viewing during the hours of darkness. Throughout the weeks of activity filming, a data logger (UNIDATA Starlogger, model 6004B) and two sensors recorded ambient temperature (°C) and solar radiation (W/cm²) at 15 min intervals in the outdoor enclosure.

The activity of 16 adult *O. infrapunctatum* skinks (1 male, 15 females) and 16 adult *O. lineoocellatum* skinks (6 males, 10 females) was recorded. Recorded activities exhibited by skinks were allocated codes. Codes described animal location (in the open, under the shaded area or under/on the hide) and whether it was active or inactive. Skink activity was recorded at 5-min intervals from the video footage by listing all of the actions that had taken place within that time interval. The effect of species on period of diurnal activity and the effect of sex was tested statistically in one-way ANOVAs using the program MINITAB (Release 8.2, Minitab Inc., PA, USA). The effect of ambient temperature on time spent active was tested in an ANCOVA General Linear Model.
FIGURE 4.1 Arena within outdoor enclosure where activity of captive skinks was filmed. (a) Both sides of filming arena, bordered by sheets of frosted glass. (b) One side of arena in detail showing soil substrate, orange brick hide, green shaded area, food and water sources and a skink (top right).
4.2.3 Thermal sensitivity of locomotor activity in captive skinks

To assess the effect of ambient temperature on activity, skinks of both species (O. infrapunctatum, \(n = 15\), O. lineoocellatum, \(n = 27\)) were taken from the Lake Station field site into captivity at the Nelson Reptile Research Centre during October and November 1998. On the day after capture, each skink was measured, weighed and sexed. Only adults and non-gravid females were used in the experiment, which involved briefly exposing each skink to either a cool, warm or hot ambient temperature and then testing to find its quickest sprint time along a track.

The body temperature of skinks was varied by placing them either in a small polystyrene insulated container (width 330 mm, breadth 270 mm, height 220 mm) containing an ice brick, or in a plastic enclosure (410 mm, 260 mm, 285 mm) without a lid situated under a heat lamp. Following 30 min acclimation to ambient temperature, skinks were removed and body temperature determined by inserting a temperature probe 5 mm into the cloaca. Each skink was then placed into a 1 m x 0.1 m open-top box which was used as a running track. The walls of the track were non-grip wooden board 190 mm high to prevent escapes. A stopwatch was used to record the time taken for each skink to run from one end of the track to the other. To initiate and sustain locomotion, skinks were repetitively nudged near the base of the tail using a pencil. All skinks performed four runs of the track within a total period of 3 min. The fastest of these sprint times was used for the statistical analysis. Body temperature data and sprint-time data were analysed using a General Linear Model (SAS, Release 6.12, SAS Institute Inc., NC, USA), with ‘species’ and ‘individual’ as factors and ‘body temperature’ as the covariate in the model.
4.3 RESULTS

4.3.1 Population activity patterns in the field

A total of 110 Oligosoma infrapunctatum and 100 O. lineoocellatum captures occurred at the four subplots across eight days of pitfall trapping. In total 81 individual O. infrapunctatum and 90 O. lineoocellatum were captured. For both species the number of captures and individuals varied between the four subplots (Table 4.1). At subplot 2 and subplot 7 more O. lineoocellatum were captured compared to subplots 3 and 9. The opposite was true for O. infrapunctatum, with most skinks being caught at subplots 3 and 9 (Table 4.1).

TABLE 4.1 Number of O. infrapunctatum and O. lineoocellatum individuals and captures at each subplot during eight days of pitfall trapping with five trap checks per day. Subplots each contained 25 baited pitfall traps.

<table>
<thead>
<tr>
<th>Species</th>
<th>O. infrapunctatum</th>
<th>O. lineoocellatum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subplot number</td>
<td>Captures</td>
<td>Individuals</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>6</td>
</tr>
<tr>
<td>3</td>
<td>47</td>
<td>37</td>
</tr>
<tr>
<td>7</td>
<td>10</td>
<td>9</td>
</tr>
<tr>
<td>9</td>
<td>45</td>
<td>29</td>
</tr>
<tr>
<td>Total</td>
<td>110</td>
<td>81</td>
</tr>
</tbody>
</table>

Combined data from all four subplots and all eight trapping days showed pronounced differences in the number of skink captures within each time period (Fig. 4.2). Almost all captures occurred 1-10 h after sunrise. Sunrise occurred at 0700 h local time during this field work. Both species showed unimodal activity patterns with peak activity (when the highest number of captures occurred) 4-7 h after sunrise. Similar numbers of captures were
recorded for both species 1-4 h after sunrise and 7-10 h after sunrise. Since skinks were almost exclusively captured during the first three time periods, only these periods were included in the ANOVA analysis. The other two time periods (10-13 h and 13-25 h after sunrise) were excluded since all values were zero except for a single *O. infrapunctatum* capture.

![Graph](image)

**FIGURE 4.2** Mean number of skink captures subplot⁻¹ 4 days⁻¹ (+ 1 SE) for *O. infrapunctatum* and *O. lineoocellatum*. Total number of captures for the two species were 110 and 100 respectively. During the study sunrise and sunset occurred between 0650-0700 h and 2000-2010 h NZST respectively.

There was no evidence of a difference in the time-dependence of activity between species (*F*₂,₆₀ = 0.32, *p* = 0.724; Fig. 4.2) or the level of activity *per se* (independent of time) between species (*F*₁,₆₀ = 0.07, *p* = 0.79). There was strong
evidence of activity differences between the three time periods independent of species ($F_{2,60} = 9.17, p < 0.001$).

4.3.2 Individual activity regimes under captive conditions

Time-lapse video recording was successful in monitoring skink activity in captivity without observer interference. Most skinks initially hid under the retreat area after being placed in the filming arena at dusk, but by the following morning most animals were active. Sunrise ranged from 0630 h (NZST) to 0600 h during the three weeks of captivity work.

There was considerable variation between diel activity regimes of each species. Most *O. infrapunctatum* individuals had emerged by 2 h after sunrise, were active for long continuous periods of the day, then retreated or became inactive 12-14 h after sunrise (Fig. 4.3). Five of the 16 *O. infrapunctatum* showed periods of inactivity during the day, lasting one to two hours. In contrast, *O. lineoocellatum* showed far more intraspecific variation in emergence and retreat times and activity patterns (Fig. 4.4), with most skinks showing initial activity 1-3 h after sunrise and ceasing activity 12-13 h after sunrise. Periods of inactivity (1-3 h in duration) during the day were exhibited by 7 out of 16 *O. lineoocellatum*. The longest total time spent active in one day for *O. lineoocellatum* was 11 h ($n = 5$, Fig 4.4), while the shortest total time active was 3 h ($n = 2$), compared to 14 h ($n = 2$) and 7 h ($n = 1$) for longest and shortest active times respectively for *O. infrapunctatum* (Fig. 4.3). The mean ambient temperature per day (daylight hours only) ranged from 15.4-17.9°C during the activity filming. The last four days of filming were the warmest (17.4-18.6°C). Mean ambient temperature during the hours of darkness ranged from 13.1-16.2°C over the entire filming period. No distinct trends in emergence or retreat times or
period of diel activity in response to weather were apparent in the activity regimes of either species.

FIGURE 4.3 Activity regimes of 16 *O. infrapunctatum* under captive conditions during spring. Rows indicate different individuals with unique I.D. numbers. Shaded areas show skink activity (i.e. at least one 5-min interval active during the hour). Areas with no shading indicate inactivity. Sunrise was at 0620 h on the first day of filming and 0600 h on the last day. Sunset changed from 1930 h to 1945 h from the start to end of the filming.
FIGURE 4.4 Activity regimes of 16 *O. lineocellatum* under captive conditions during spring. Rows indicate different individuals with unique I.D. numbers. Shaded areas show skink activity (i.e. at least one 5-min interval active during the hour). Areas with no shading indicate inactivity. Sunrise was at 0633 h on the first day of filming and 0605 h on the last day. Sunset changed from 1920 h to 1940 h between the start and end of the filming.
Both species showed unimodal diel activity patterns (Fig. 4.5). Between 1-13 h after sunrise more than 60% of all *O. infrapunctatum* individuals were active (Fig. 4.5a). In contrast, activity of more than 60% of *O. lineoocellatum* individuals was seen over a shorter period of 3-11 h after sunrise (Fig. 4.5b),

![Graph](image-url)

**FIGURE 4.5** Percentage of total (a) *O. infrapunctatum* and (b) *O. lineoocellatum* filmed that were active during one-hour time intervals throughout the day. Sample sizes were 16 adults for both species. Data from 13 days of filming for each species was combined. Sunrise was at 0633 h at the start of filming and at 0600 h by the end. Sunset was at 1920 h and 1945 h at the start and end of filming respectively.
further illustrating the shortened diel activity periods for this species. High percentages (> 80%) of *O. infrapunctatum* individuals were active from early morning (2 h after sunrise) through to early evening (12 h after sunrise), with peak activity (> 90% active) occurring 4-8 h after sunrise (Fig. 4.5a). *O. lineoocellatum* showed much lower percentages of individuals active throughout the day (Fig. 4.5b). Active behaviour was shown by more than 80% of individuals only during late morning (4-6 h after sunrise) and early to mid-afternoon (7-10 h after sunrise). Peak activity (> 90% active) occurred for a short period 7-8 h after sunrise. Only one *O. lineoocellatum* animal was active at first light and no activity was seen beyond 13 h after sunrise for any skinks of this species (Fig. 4.5b). In contrast, almost a third (> 30%) of *O. infrapunctatum* showed activity during the first hour after sunrise and activity continued until 14 h after sunrise for 44% of the animals, with one individual still active an hour after darkness began (Fig. 4.5a). Short periods of nocturnal activity were exhibited by four *O. infrapunctatum*, each active for a 15 min period between 2315 h and 0045 h. No nocturnal activity was shown by *O. lineoocellatum*.

As almost all the active behaviour exhibited by skinks occurred between 0700 h and 1900 h (1-13 h after sunrise), only video tape data from this period was analysed. For *O. lineoocellatum* there was no significant effect of sex on time spent active (F = 0.34, p = 0.571), suggesting that the differing activity patterns between individuals were independent of sex in this species. Only one of the 16 *O. infrapunctatum* filmed was male, therefore the differences between sexes were not analysed for this species. Further statistical testing showed that there was a highly significant difference between the species in the time spent active (one-way ANOVA, F = 13.16, p = 0.001). The mean number of 5-min intervals spent active per 12 hour day was 117.6 for *O. infrapunctatum* and 77.6 for *O. lineoocellatum* (Fig. 4.6), illustrating a clear difference in captive activity regimes between the two species.
Since the weather varied between days during the weeks of activity filming, ambient temperature variation inside the filming enclosure may have affected the activity patterns exhibited by skinks. To test the effects of mean, minimum and maximum daily temperatures on individual skink activity, three ANCOVA tests were performed. The temperature values were used as covariates and species used as a factor, and models included an interaction effect between species and the covariate. There was no significant effect of (a) mean daily temperature ($F = 0.01, p = 0.923$), (b) minimum daily temperature ($F = 0.08, p = 0.786$) or (c) maximum daily temperature ($F = 0.04, p = 0.842$) on the number of 5-min intervals that each species spent active. Furthermore there were no significant interaction effects between species and mean, minimum or maximum daily temperatures. Since the interaction effects were non-significant, the three ANCOVA tests were repeated without the inclusion of an interaction effect. Again, no significant effects of the temperature covariates on
skink activity times were found. These results indicate that fluctuations in environmental temperature did not play a major role in the intra- and interspecific variation in activity regimes. Therefore the species difference seen in Fig. 4.6, where *O. infrapunctatum* spent more time active than *O. lineoocellatum* is due to inherent activity differences between the two species, rather than an effect of fluctuating temperature.

4.3.3 Thermal sensitivity of locomotor activity in captive skinks

Exposing skinks to fixed ambient temperatures proved to be a successful method for adjusting their body temperatures. After 30 min almost all animals had body temperatures within 3°C of the ambient temperature to which they had been exposed. As expected, skinks ran faster at higher body temperatures, but the rate of decrease in the time it took to travel the length of the 1 m track was exponential rather than linear with increasing body temperature (Fig. 4.7). Sprint times were therefore log-transformed before performing GLM analysis.

Statistical analysis of sprint data showed four important points. First, there was a highly significant (*p* < 0.001) individual animal effect, as shown in Fig. 4.7 by the wide range in sprint times for each cluster of body temperatures. This variation was likely to be due to individual differences in morphology. Second, there was a highly significant (*p* < 0.001) effect of body temperature on sprint speed (Fig. 4.7). Third, there was a significant (*p* < 0.05) difference between species, indicating that *O. lineoocellatum* had faster sprint times than *O. infrapunctatum* across the range of body temperatures tested. Fourth, there was no evidence of an interaction effect of body temperature and species, suggesting that the sprint times of both species showed a similar relationship to increasing body temperature. Linear regression lines for correlations of SVL, total length and weight of skinks with time taken to sprint were non-significant for both species. This suggests that the speed of individuals did not increase or decrease with increasing/decreasing body size. It is
possible that the morphological measurements varied too much among individuals to explain the differences in sprint times at each body temperature (i.e. the significant 'individual animal' effect in the analysis).

**FIGURE 4.7** The relationship between sprint time and body temperature in *O. infrapunctatum* (open circles) and *O. lineoecellatum* (closed circles). Sprint time refers to the time taken (s) for a skink to move along a track 1 m in length. The dotted line represents the least-squares linear regression for *O. infrapunctatum* (*y* = 1.01 - 0.0196*x*, *r*² = 0.322, *F*₁,₄₂ = 19.4, *p* < 0.001). The least-squares linear regression for *O. lineoecellatum* is represented by the solid line (*y* = 0.774 - 0.0188*x*, *r*² = 0.535, *F*₁,₇₇ = 88.6, *p* < 0.001).
4.4 DISCUSSION

4.4.1 Unimodal activity regimes in lizards

The field and captivity work presented here provides the first evidence of unimodal diel activity patterns in *Oligosoma infrapunctatum* and *O. lineoocellatum* from a temperate South Island region. Unimodal activity regimes have also been documented in other New Zealand ground-dwelling skinks (Table 4.2). For example, *Oligosoma maccanni* and *O. nigriplantare polychroma* showed only one peak in their diel activity patterns in the field (Freeman 1997) and *Cyclodina aenea* and *C. ornata* showed continuous periods of activity from sunrise to late afternoon in captivity (Porter 1987). A number of lizard species in Australia, England, Italy, the USA and South America also show unimodal diel activity patterns (Table 4.2).

However, quite a large amount of variation exists between the unimodal activity patterns of populations in the field presented here (see Fig. 4.2) and those documented for other species. *O. infrapunctatum* and *O. lineoocellatum* showed very little foraging behaviour (i.e. few captures occurred) in the first four hours after sunrise (or before 1100 h) during summer. In contrast, *O. maccanni* showed a high level of activity (i.e. many animals foraging) early in the day, up to three hours after sunrise (Freeman 1997). Similarly, sleepy lizards (*Tiliqua rugosa*) showed most of their daily activity before 1100 h during summer (Firth and Belan 1998). Furthermore, Avery (1978) found that wall lizards (*Podarcis muralis*) began basking and foraging before 1000 h during warm weather.
### TABLE 4.2

List of some of the species studied (skinks and other lizard families) which show unimodal diel activity patterns. Unimodal refers to one clear peak in activity levels during the day. The general location of study sites, seasons when studies were conducted and author/s are also shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Season</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cyclodina aenea, C. ornata</td>
<td>Auckland, New Zealand</td>
<td>Summer, winter</td>
<td>Porter 1987</td>
</tr>
<tr>
<td>Oligosoma grande</td>
<td>Eastern Otago, New Zealand</td>
<td>Autumn</td>
<td>Murphy 1994</td>
</tr>
<tr>
<td>Oligosoma infrapunctatum, O. lineocellatum</td>
<td>Buller valley, New Zealand</td>
<td>Spring, summer</td>
<td>Present study</td>
</tr>
<tr>
<td>Oligosoma maccanni, O. nigripiantare polychroma</td>
<td>Canterbury, New Zealand</td>
<td>Summer</td>
<td>Freeman 1997</td>
</tr>
<tr>
<td>Leioplosma coventryi, Pseudemela spenceri, Sphenomorphus tympanum</td>
<td>New South Wales, Australia</td>
<td>Summer</td>
<td>Webb 1985</td>
</tr>
<tr>
<td>Tiliqua rugosa</td>
<td>Adelaide, Australia</td>
<td>Spring, summer</td>
<td>Firth and Belan 1998</td>
</tr>
<tr>
<td>Mabuya agilis, M. macrorhyncha</td>
<td>Southeastern Brazil</td>
<td>All seasons</td>
<td>Vrcibradic and Rocha 1996</td>
</tr>
<tr>
<td>Mabuya frenata</td>
<td>Southeastern Brazil</td>
<td>Winter</td>
<td>Vrcibradic and Rocha 1998</td>
</tr>
<tr>
<td>Scincella lateralis</td>
<td>Oklahoma, U. S. A.</td>
<td>Spring</td>
<td>Smith 1997</td>
</tr>
</tbody>
</table>

### Lacertidae

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Season</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Podarcis muralis</td>
<td>Tuscany, Italy</td>
<td>Spring</td>
<td>Avery 1978</td>
</tr>
<tr>
<td>Podarcis sicula</td>
<td>Pisa, Italy</td>
<td>Spring</td>
<td>Foà et al. 1994</td>
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### Iguanidae

<table>
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<tr>
<th>Species</th>
<th>Location</th>
<th>Season</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anolis cooki</td>
<td>Guanica, Puerto Rico</td>
<td>Winter</td>
<td>Hertz 1992</td>
</tr>
</tbody>
</table>

### Gymnophthalmidae

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<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Season</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neusticurus ecpleopus</td>
<td>Amazon region, Brazil/Ecuador</td>
<td>-</td>
<td>Vitt et al. 1998a</td>
</tr>
<tr>
<td>Priodontactylus eigenmanni</td>
<td>Southwestern Amazon, Brazil</td>
<td>Summer</td>
<td>Vitt et al. 1998b</td>
</tr>
</tbody>
</table>
Two other species of skinks, *Scincella lateralis* and *Mabuya frenata*, both show limited activity in the morning during spring (Smith 1997; Vrcibradic and Rocha 1998), similar to the skinks in the present study. However, both species greatly increase their morning foraging during hot summer months, changing their unimodal activity patterns to either bimodal (*S. lateralis*) or highly variable (*M. frenata*) (Smith 1997; Vrcibradic and Rocha 1998). Foraging behaviour during the early morning has also been reported in the skinks *Mabuya macrorhyncha* and *M. agilis* (Vrcibradic and Rocha 1996), again contrasting with *O. infrapunctatum* and *O. lineoocellatum*.

It is interesting to note that field populations of *O. infrapunctatum* and *O. lineoocellatum* show limited foraging behaviour during the first four hours after sunrise, at a time when so many other species actively search for food. Microhabitat structure and substrate temperatures may have a significant effect on skink activity in the morning at the study site. The dense vegetation cover, dominated by bracken fern (*Pteridium esculentum*) at most trapping areas of the study site, may shade out the morning sun from skink microhabitats. This may slow the rate at which the substrate temperature increased and thus prevent skinks from gaining heat via the substrate or basking. Lizard body temperatures are often similar to substrate temperatures (Smith 1997; Vrcibradic and Rocha 1998). Early morning basking is thought to be important for most diurnal lizards, since this is when diel environmental temperatures are lowest and the need to gain heat is greatest. Many skink species have been observed basking soon after sunrise in the field, such as *O. grande* and *O. otagense*, (Coddington and Cree 1997), *Niveoscincus microlepidotus* (Melville and Swain 1997a), *S. lateralis* (Smith 1997) and *M. frenata* (Vrcibradic and Rocha 1998). Early morning basking in direct sunlight may permit other species to begin actively foraging earlier in the day than *O. infrapunctatum* and *O. lineoocellatum*. 
At Lake Station *O. infrapunctatum* is generally found in closed-canopy microhabitats whereas *O. lineoocellatum* is a habitat generalist species which inhabits closed and open sites (Efford et al., in prep [b]). Sun cannot easily penetrate through the vegetation in closed areas where *O. infrapunctatum* are found because of the dense, bracken-covered canopies. The fact that slightly less *O. infrapunctatum* were captured 1-4 hours after sunrise (Fig. 4.2) than *O. lineoocellatum* may relate to habitat structure. Sunlight would not reach the substrate of closed habitats as early, which could in turn mean that *O. infrapunctatum* cannot get sufficiently warm through basking until later in the morning. This result therefore suggests that early morning sun may be important for initiating diel activity.

It would be interesting to examine the emergence times of both skink species at the study site to detect exactly what time of day most animals begin to move about. This would give more information regarding the daily activity budgets of both species and would indicate if *O. infrapunctatum* actually emerges later than *O. lineoocellatum*, given its closed, less sunny microhabitat. Timing of emergence in the field was out of the scope of the present study. However, it is clear from the evidence presented here that foraging activity does not begin until after 1100 h for the majority of animals.

In captivity individuals of both species exhibited active movements in the first four hours after sunrise (Fig. 4.3; Fig. 4.4; Fig. 4.5). Limited amounts of basking behaviour was also seen on some mornings in both species, although the majority of days during filming were overcast, thus preventing sunlight from entering the enclosure. Skinks in the field probably also began their diel activity soon after sunrise, as indicated by the captivity work, but did not begin foraging until their body temperatures were sufficiently high. Melville and Swain (1997a) reported that sympatric skinks *N. microlepidotus* and *N. metallicus* did not begin active foraging until 1100 h and 1230 h respectively during summer,
following at least two hours of full-sun basking. The skinks *O. grande* and *O. otagense* also spend a substantial period of time basking in the morning before active foraging begins (Murphy 1994; L. Marshall, pers. comm.). Foraging activity of *O. infrapunctatum* and *O. lineocellatum* may also have a strong thermal dependence. Early-evening activity was exhibited by most captive skinks but not seen in the field populations. It is likely that skinks at the field site were still active in the early evening (after 1700 h) but had ceased foraging due to insufficiently high body temperatures.

### 4.4.2 Species differences in diel activity patterns

Although the two species in the present study showed similar unimodal activity patterns, results of fine-scale observations on captive individuals gave evidence for clear activity differences. *O. infrapunctatum* spent significantly more time active than *O. lineocellatum* at all times of the day. Many *O. infrapunctatum* individuals emerged earlier and retreated later than *O. lineocellatum* individuals, even when both species were filmed on the same day. The activity of *O. infrapunctatum* appears to be more continuous than that of *O. lineocellatum* for long periods of the day. The combined field and captivity results strongly suggest that although foraging may occur at similar times of day for both species, active behaviour *per se* occurs more frequently and for a longer duration in *O. infrapunctatum*, at least during spring. This study, therefore, provides reliable evidence for temporal resource partitioning in these two syntopic skink species.

A limited number of other studies in New Zealand have also shown some evidence for temporal segregation of diel activity in sympatric skinks (Table 4.3). For example, distinct species differences in the timing of emergence and in foraging activity have been shown by *O. maccanni* and *O. n. polychroma* Freeman (1997). *O. maccanni* activity peaked in the early morning then tapered
TABLE 4.3 List of some of the sympatric species (skinks and other lizard families) studied which show temporal resource partitioning. The general location of study sites and author/s are also shown.

<table>
<thead>
<tr>
<th>Species</th>
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<td><em>Oligosoma infrapunctatum</em> and <em>O. lineocellatum</em></td>
<td>Buller Valley, New Zealand</td>
<td>Present study</td>
</tr>
<tr>
<td><em>Oligosoma grande</em> and <em>O. otagense</em></td>
<td>Eastern Otago, New Zealand</td>
<td>L. Marshall, pers. comm; Coddington and Cree 1997</td>
</tr>
<tr>
<td><em>Oligosoma maccanni</em> and <em>O. nigriplantare polychroma</em></td>
<td>Canterbury, New Zealand</td>
<td>Freeman 1997</td>
</tr>
<tr>
<td><em>Ctenotus calurus</em> and <em>C. schomburgkii</em></td>
<td>Western Australia</td>
<td>Pianka 1969</td>
</tr>
<tr>
<td><em>Egernia modesta</em> and <em>E. whitii</em></td>
<td>Southern Queensland, Australia</td>
<td>Milton and Hughes 1986</td>
</tr>
<tr>
<td><em>Niveoscincus metallicus</em> and <em>N. microlepidotus</em></td>
<td>Tasmania, Australia</td>
<td>Melville and Swain 1997a</td>
</tr>
<tr>
<td><em>Iguanidae</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Anolis cooki</em> and <em>A. cristatellus</em></td>
<td>Puerto Rico</td>
<td>Hertz 1992</td>
</tr>
<tr>
<td><em>Lacertidae</em></td>
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off, whereas *O. n. polychroma* was most active around midday. Data from observations of syntopic giant skinks show that *O. grande* is often active in the morning before *O. otagense*, while the opposite is seen in the afternoon (L. Marshall, pers. comm.). Furthermore, in marginal weather conditions (low substrate temperature, windy and damp) more *O. grande* emerged than *O. otagense* (Coddington and Cree 1997).

Several other studies have also documented temporal resource partitioning among sympatric skinks (Table 4.3). For example, *E. modesta* spent less diel time active than *E. whitii* and most of its activity occurred before midday, whereas *E. whitii* was active throughout the day (Milton and Hughes 1986). Also *N. microlepidotus* spent more time active on both a diel and seasonal basis than
Chapter Four: Temporal Resource Partitioning, Activity Patterns and Locomotor Responses

N. metallicus (Melville and Swain 1997a). Some species of Anolis and Lacerta lizards exhibit different activity regimes and temporal resource partitioning when in sympatry (Table 4.3). For example, A. cooki has continuous activity throughout the day in both summer and winter, whereas A. cristatellus has a brief and curtailed bimodal activity pattern in both seasons (Hertz 1992). L. vivipara emerges earlier, retreats later and spends longer periods of the day active than L. agilis (House et al. 1980).

Organisms generally partition resources because of factors that operate independently on different species (Toft 1985). These factors include physiological and morphological constraints. Although Freeman (1997) and Milton and Hughes (1986) did not offer suggestions as to why sympatric skinks exhibited temporal resource partitioning, or what factors may affect skink activity, other authors have proposed that physiological constraints cause temporal resource partitioning. Coddington and Cree (1997) proposed that O. grande may have a better physiological capacity than O. otagense for activity at low body temperatures or in unfavourable conditions. Melville and Swain (1997a) suggested that species activity differences exhibited by N. metallicus and N. microlepidotus may be due to altitudinal adaptations and restrictions. N. metallicus is at its upper altitudinal limit at their study site and is therefore restricted in its activity, due to poor adaptations to extreme alpine conditions. In contrast, N. microlepidotus was thought to be well adapted to alpine conditions and it can maintain longer diel and seasonal activity periods through physiological and behavioural adaptations (Melville and Swain 1997a).

Similarly, Hertz (1992) proposed that A. cristatellus has shorter activity periods than A. cooki because the species is not as well adapted physiologically to the desert habitat where the study was conducted. A lack of midday activity in A. cristatellus may be an adaptation to avoid heat stress and/or dehydration at high ambient temperatures (Hertz 1992). House et al. (1980) hypothesised that L. vivipara spent more time active than L. agilis because of its wider altitudinal
distribution and hence more efficient adaptations to low temperatures and unfavourable conditions.

In this study it was shown that *O. infrapunctatum* spent more diel time active than *O. lineoocellatum* and it is likely that environmental effects and physiological adaptations influence the species' activity patterns at the Lake Station field site. Of the many environmental factors that could influence diel activity time of these species, local climatic conditions (especially ambient temperature) are likely to be the most important. The results of the thermal sensitivity work showed that *O. lineoocellatum* was able to sprint significantly faster than *O. infrapunctatum* across a wide range (6-32°C) of body temperatures. This suggests that *O. lineoocellatum* is physiologically adapted to, and less limited by, extreme ambient temperatures. Even at low body temperatures (< 10°C) *O. lineoocellatum* is still capable of performing short bursts of rapid sprinting. In comparison, Towns (1975) reported that black shore skinks (*Oligosoma suteri*) had highly impaired movements at body temperatures below 8°C.

The physiological ability of *O. lineoocellatum* to sustain locomotion at extreme temperatures must relate to its distribution within New Zealand. The species is widespread latitudinally and altitudinally, with populations occurring above the sub-alpine zone, such as in Marlborough’s coastal ranges at altitudes of 1300 m asl (R. Cuthbert, unpubl. data). The impaired sprint-running ability of *O. infrapunctatum* at low temperatures provides evidence that this species could not survive in the high-altitude habitats where *O. lineoocellatum* populations thrive.

It is interesting to note that *O. lineoocellatum*, the species that is more tolerant of extreme ambient temperatures, spent less diel time active than *O. infrapunctatum* during spring. This result contrasts with results from a comparative study showing that *N. microlepidotus* was better adapted to alpine
conditions than *N. metallicus*, and in turn showed longer diel activity periods and was often active in cold weather (Melville and Swain 1997a). The thermal sensitivity work presented here indicates that although *O. lineoocellatum* is probably capable of more daily locomotor activity, its activity was constrained.

### 4.4.3 Factors limiting activity of *O. lineoocellatum* and *O. infrapunctatum*

Environmental and behavioural factors may limit the amount of diel time that *O. lineoocellatum* spends active. Of the environmental factors, habitat structure probably plays a major role. *O. lineoocellatum* is commonly found in exposed, open habitats with limited vegetation, not only at the study site but also at other localities such as Stephens Island (East et al. 1995), inland Marlborough (pers. obs.), the seaward Kaikoura ranges (R. Cuthbert, unpubl. data) and coastal Canterbury (Freeman 1997). Exposed habitats do not provide effective cover for skinks and are likely to carry a higher risk of predation by aerial predators such as Australasian harriers (*Circus approximans gouldi*), falcons (*Falco novaeseelandiae*) and kingfishers (*Halcyon sancta vagans*). All of these predators can be seen at the Lake Station study site. If the risk of being predated is high, a skink is likely to limit its activity to short, occasional bursts rather than continuous locomotion. Thus *O. lineoocellatum* may exhibit different activity patterns to *O. infrapunctatum* as an adaptation to the structure of its natural microhabitat whereby activity time is constrained to reduce the chance of detection by aerial predators.

Other studies have also shown that activity may be related to habitat structure and predation risk (Saint Girons et al. 1980; Bulova 1994). For example, tuatara (*Sphenodon punctatus*) on Stephens Island seldomly emerge from burrows situated in pasture areas during daylight hours (Saint Girons et al. 1980). In contrast, on forested parts of the island tuatara emerge frequently during the day
and move up to 2 m away from their burrows. It has been suggested that this activity difference was probably due to the greater risk of aerial predation in open pasture sites (Saint Girons et al. 1980). Predation on adult tuatara by Australasian harriers had been previously witnessed in pasture areas of the island.

Hertz et al. (1983) suggested that impaired sprint performance at extreme temperatures in agamid lizards could increase the risk of being captured by predators. This may apply to *O. infrapunctatum* at low body temperatures, when sprinting ability is physiologically impaired. A high risk of aerial predation in exposed habitats, coupled with an inability to rapidly escape, may restrict the distribution of *O. infrapunctatum* to closed canopy habitats, such as under bracken fern at Lake Station. *O. infrapunctatum* may also select more sheltered habitats because these offer greater thermal stability and moisture retention, both of which are characteristics preferred by a number of other New Zealand skinks (Porter 1987). On Stephens Island *O. infrapunctatum* has been found at high densities in mature bush and vineland, whereas *O. lineoocellatum* is caught more often in grasses and never in mature bush (East et al. 1995). Although *O. infrapunctatum* faces the risk of predation in mature bush on Stephens Island by nocturnal tuatara (*Sphenodon punctatus*), the skinks avoid this by being diurnal and also adopting tunnelling behaviour in soft soil and leaf litter (East et al. 1995).

A behavioural factor that may influence activity time of both species and which relates directly to microhabitat structure is foraging mode. Since it is safer for a skink to be less active in an open habitat, it follows that the species should have evolved a ‘sit-and-wait’ (or rarely active) mode of foraging (Pianka 1966). For example, foraging patterns of *Anolis* lizards show site-specific differences that are related to the structure of foraging sites (Moermond 1979). Results from the present study provide some evidence that *O. lineoocellatum* may have adopted a less active foraging mode than *O. infrapunctatum*, making it more of a sit-and-
wait predator than a widely searching forager. The sympatric lizards *Tropidurus torquatus* and *Cnemidophorus ocellifer* also show a significant difference in their times spent active. *T. torquatus* spends less time active, remaining motionless for long periods, and is known to be a sit-and-wait predator (Bergallo and Rocha 1994).

The diet of widely foraging lizards often includes fruits, sedentary invertebrates and a wide variety of prey taxa, whereas sit-and-wait predators consume a narrower range of taxa and more mobile prey such as flying insects (Huey and Pianka 1981; Bergallo and Rocha 1994; Wapstra and Swain 1996). Information on the diets of *O. infrapunctatum* and *O. lineoocellatum* populations at Lake Station, obtained from scat analysis (M. Efford, unpubl. results), has shown some important differences between the species. Considerable dietary overlap occurred, although major prey items taken differed between species in early and late summer. Furthermore, *O. infrapunctatum* consumed a wider variety and larger amounts of prey than *O. lineoocellatum* and also included more fruits/berries in its diet (M. Efford, unpubl. results). Both species are therefore dietary generalists, although the seasonal inclusion of more berries in the diet of *O. infrapunctatum* suggests that this species may be more opportunistic by taking advantage of temporarily abundant food resources. The seasonal inclusion of berries in the diet is not uncommon in skinks (Patterson 1992; Twigg et al. 1996; Wapstra and Swain 1996; Spencer et al. 1998). Therefore, the shortened diel activity period of *O. lineoocellatum* and the limited amount of fruit in its diet provide some evidence that this species may rely on a sit-and-wait mode of foraging combined with the widely searching mode adopted by *O. infrapunctatum*. However, more evidence of dietary differences between the two species is needed before foraging modes can be quantified further. It would be of interest to examine the skinks’ foraging behaviour in more detail at Lake Station and also at other sites where the species are syntopic or allopatric. The present study suggests that temporal resource partitioning may be linked to trophic and spatial factors at the study site.
A further behavioural factor which may affect the time that lizards spend active is home range. A lizard with a large home range or territory may spend more time foraging or defending within its boundaries than a lizard occupying a smaller area. Home range is difficult to assess for skinks using pitfall trapping (M. Efford, pers. comm.) and has not been calculated as yet for either species at Lake Station.

4.4.4 Conclusion

In conclusion, the results of this work show three important points. First, *O. infrapunctatum* and *O. lineoocellatum* show unimodal diel activity patterns during spring and summer, in captivity and in the wild. Foraging behaviour occurs mostly around midday which is later than for many other skink species. Second, *O. lineoocellatum* spends less diel time active than *O. infrapunctatum* during spring, suggesting that the two species show temporal resource partitioning. *O. lineoocellatum* may be limited in its activity due to habitat structure or foraging mode. Third, the two species differ in their thermal sensitivity, with *O. lineoocellatum* able to sprint faster across a range of body temperatures. This chapter of work gives a valuable insight into temporal and thermal niche partitioning in the two species. The implications of these results for trappability differences between the species are important and will be discussed in Chapter Five.
CHAPTER 5

GENERAL DISCUSSION

5.1 ECOLOGICAL DIFFERENCES BETWEEN O. INFRAPUNCTATUM AND O. LINEOCELLATUM

To date, a very limited amount of research has focused on the comparative ecology of O. infrapunctatum and O. lineoocellatum. This research has concentrated mainly on differences between syntopic populations of O. infrapunctatum and O. lineoocellatum in their microhabitat associations at two localities, Stephens Island and Lake Station in the upper Buller River valley (East et al. 1995; Efford et al. 1997, in prep [b]). The diets of both species have been described at the Lake Station site (Efford et al. 1997; M. Efford, unpubl. results). These studies suggest that syntopic populations of O. infrapunctatum and O. lineoocellatum show a limited amount of resource partitioning. The present study provides additional information regarding the comparative ecology and behaviour of O. infrapunctatum and O. lineoocellatum. Evidence from this study suggests that the two species partition temporal resources to a limited extent and that they differ in terms of their physiology, agility, escape behaviour and wariness. These findings are discussed below in relation to species differences in microhabitat and dietary associations. Understanding the ecological and behavioural differences between O. infrapunctatum and O. lineoocellatum is an essential step in determining why the species have different trappability estimates (Efford et al., in prep [a]). Factors influencing the trappability of each species are discussed later in this chapter.
5.1.1 Spatial resource partitioning

*O. infrapunctatum* and *O. lineoocellatum* appear to have somewhat different microhabitat preferences. All information on the spatial resource partitioning of these species comes from studies undertaken at Stephens Island (East et al. 1995) and Lake Station in the upper Buller River valley (Efford et al. 1997, in prep [b]). Both skink species occur on Stephens Island (Takapourewa) in the Cook Strait. This 150 ha island was once covered in dense forest which was burnt and grazed about 150 years ago, following human occupation (East et al. 1995). The island is now a fully protected Wildlife Sanctuary and contains a highly diverse assemblage of reptiles, including three species of geckos, four species of skinks and the largest population of tuatara in New Zealand. The vegetation is a mosaic of low, regenerating forest, vinelands, scrub, tall grasses and pasture (East et al. 1995).

Pitfall trapping data has shown that *O. infrapunctatum* occurs at different densities in all five habitat types on Stephens Island. Most individuals were captured in scrub, vineland and forest, with very few skinks found in grass habitats (East et al. 1995). In comparison, *O. lineoocellatum* was frequently captured in tall grass and pasture, with captures also occurring in scrub and vineland habitats. This species was not found in forested areas (East et al. 1995). Thus it appears that on Stephens Island *O. infrapunctatum* selects closed and partially closed-canopy microhabitats such as scrub and forest, whereas *O. lineoocellatum* occurs mostly in open and partially closed-canopy areas. Microhabitat overlap between the species is evident.

A similar microhabitat preference to that on Stephens Island is apparent for the two skink species at Lake Station (Efford et al., in prep [b]). This farm is a sprawling expanse of pasture with small areas of low scrub. At the terrace scarp where the lizard study site is situated, repeated burning is carried out by the land owners (B. Thomas, pers. comm.) to suppress the growth of scrub, mainly bracken fern (*Pteridium esculentum*) and weeds such as blackberry (*Rubus fruticosus*). Burning has not been undertaken at the site for more than six years because Landcare Research have been carrying out skink research. The scrub on the terrace scarp has
had sufficient time to regenerate and in some places the bracken reaches heights of over a metre. There are distinctive differences amongst the microhabitats available to skinks on the terrace scarp, ranging from 'open' to 'closed' canopy (Efford et al., in prep [b]). Capture data from pitfall trapping at the site, combined with spatial modelling using vegetation and substrate data, shows that *O. infrapunctatum* is commonly associated with microhabitats containing closed-canopy vegetation, especially bracken (Efford et al. 1997, in prep [b]). In contrast *O. lineoecellatum* seems to be more of a generalist in terms of microhabitat use, occupying areas classed as open and closed but avoiding very open sites which have bare ground.

The results from studies at Lake Station (Efford et al. 1997, in prep [b]) and Stephens Island (East et al. 1995) described here strongly suggests that syntopic populations of *O. infrapunctatum* and *O. lineoecellatum* show spatial resource partitioning, although selected microhabitats overlap to some extent. Habitat segregation among sympatric lizard species is common (Patterson 1992; Bruna et al. 1996; Vrcibradic and Rocha 1996; Melville and Swain 1997). It is difficult to determine the causes of habitat partitioning in *O. infrapunctatum* and *O. lineoecellatum*. Perhaps the two species have quite different habitat preferences, but it is just as likely that interspecific competition (Patterson 1992) or predation pressures could be responsible for their distributions among microhabitat types. Diet preferences may also play a role in determining habitat partitioning. For example, *O. infrapunctatum* consumes more seasonal fruits than *O. lineoecellatum* at Lake Station (Efford et al. 1997) and is associated with microhabitats that have an abundance of fruiting plants (Efford et al., in prep [b]). Data from experimental density manipulations of skinks at Lake Station, obtained by Landcare Research but yet to be analysed, may provide some answers regarding the role of competition in habitat partitioning. Whatever the causes of partial habitat segregation among *O. infrapunctatum* and *O. lineoecellatum*, the benefits are unmistakable: the two species are able to co-exist in syntopy in at least two locations in New Zealand and do not appear to out-compete each other at these sites.
5.1.2 Trophic resource partitioning

*O. infrapunctatum* and *O. lineoocellatum* appear to partition trophic resources at Lake Station to a certain extent (Efford et al. 1997). Diet analysis has shown that both species are opportunistic dietary generalists. However, although a wide range of invertebrates (especially Oligochaetes) and fruits/berries are taken by both species during summer, important species differences exist (Efford et al. 1997; M. Efford, unpubl. results). *O. infrapunctatum* takes a wider variety and larger amounts of prey and feeds more on shade-dwelling insects such as tiger beetles (*Neocicindela* sp. aff. *parryi*). Also, *O. infrapunctatum* takes more seasonal fruits and berries from plants such as *Coprosma* sp., *Leucopogon fraseri*, *Coriaria arborea* (tutu) and *Rubus fruticosus* (blackberry). In contrast, *O. lineoocellatum* feeds on a smaller variety of food types, concentrating mainly on two to three taxa. *O. lineoocellatum* also appears to take more invertebrate prey items such as manuka beetles (*Pyronota* sp.), millipedes, flies and larvae compared to *O. infrapunctatum* (Efford et al. 1997; M. Efford, unpubl. results).

There are several reasons why *O. infrapunctatum* and *O. lineoocellatum* might partition food resources at the Lake Station study site. The most obvious reason is that they occupy slightly different microhabitats and therefore have different assemblages of invertebrates and fruits available for consumption. Closed-canopy microhabitats such as those associated with large numbers of *O. infrapunctatum* contain more fruiting plants and shade-dwelling arthropods, and consequently substantial volumes of fruit and tiger beetles feature in the diet of *O. infrapunctatum*. Thus there appears to be a strong link between diet and habitat. It has been suggested that variation in the diet composition of the syntopic skinks *Mabuya agilis* and *M. macrorhyncha* may result from differential use of microhabitats (Vrcibradic and Rocha 1996). The same explanation has been proposed for the dietary differences shown among the sympatric skinks *Oligosoma inconspicuum*, *O. maccanni* and *O. nigriplantare polychroma* in two localities (Patterson 1992; Freeman 1997).
Before a conclusion can be made regarding the link between the diet and habitat of Lake Station skinks, quantitative data of the available food types in different microhabitats is needed. If prey types eaten by *O. infrapunctatum*, for example, are entirely representative of the prey available in typical *O. infrapunctatum* microhabitats (i.e. closed-canopy sites), it can be assumed that this species has a habitat-defined diet. *O. lineoecellatum* does not have a well-defined microhabitat preference, therefore prey/habitat relationships would be difficult to establish for this species. However, if *O. infrapunctatum* was found to consume prey items which did not commonly occur in its preferred microhabitat, this would indicate that the species selectively forages beyond its habitat boundaries. If selective foraging was detected, the trophic partitioning exhibited by skinks could be attributed to differences in food preferences rather than microhabitat differentiation. For example, the sympatric skinks *O. maccanni* and *O. n. polychroma* had diets that reflected the prey availability in their preferred microhabitats (Freeman 1997). However, a comparison of the items found in skink scats with potential prey items showed that selective foraging was occurring. Some prey types were absent or under represented in scats but very abundant in microhabitats, suggesting negative selection (Freeman 1997). In other cases skinks consumed prey that was rare or absent from their microhabitat, suggesting movement out of preferred areas and a high degree of selectivity (Freeman 1997).

For the skinks at Lake Station it would be worthwhile to conduct an extensive investigation into diet and prey availability, similar to that of Freeman (1997). This would help to determine what food types are available in the microhabitats occupied by *O. infrapunctatum* and *O. lineoecellatum* and indicate whether the skinks’ diets are determined by microhabitat type alone or include a degree of selectivity.
5.1.3 Temporal resource partitioning

The captive work conducted in the present study gives good evidence for differences in temporal resource partitioning between syntopic *O. infrapunctatum* and *O. lineoocellatum* populations. *O. infrapunctatum* spent significantly more diel time active than *O. lineoocellatum* and also tended to emerge earlier and retreat later in the day. The activity of *O. infrapunctatum* appeared to be more continuous throughout the day as opposed to *O. lineoocellatum* individuals which commonly spent 1-3 h inactive. Furthermore, a higher percentage of *O. infrapunctatum* were active at all times of the day, especially in the morning and late afternoon.

Differences between sympatric skinks in their activity patterns have been documented in a small number of diurnal species in New Zealand (Coddington and Cree 1997; Freeman 1997), but generally very few studies have fully addressed this ecological issue. It is also likely that other sympatric and syntopic lizard species in New Zealand exhibit some degree of segregation in their activity patterns. More work in this area of lizard ecology is essential for a complete understanding of how different lizard species partition their time in relation to their habitat associations, diets, foraging patterns and physiology. The constrained activity time exhibited by *O. lineoocellatum* may be an adaptation to avoid aerial predation in the exposed habitat types that this species is associated with in some localities, especially in sub-alpine, alpine and coastal areas. The larger variety and volume of prey types and fruit consumed by *O. infrapunctatum* compared to *O. lineoocellatum* (M. Efford, unpubl. results) may be a reflection of the longer duration of diel activity shown by the former species. Other aspects of the habitat and diet of the two species, with respect to their activity patterns, are further discussed in Chapter Four. Differences between the species in relation to their foraging patterns and physiology are discussed below.
5.1.4 Foraging modes

The data presented in Chapters Three and Four of this study suggest that *O. infrapunctatum* and *O. lineoellatum* may exhibit different modes of foraging. This was based on evidence from skink activity patterns, dietary preferences and microhabitat associations. Following Pianka (1966), Huey and Pianka (1981) and the work of many others who have studied foraging behaviour, *O. infrapunctatum* and *O. lineoellatum* could be tentatively categorised as 'widely searching' and 'sit-and-wait' species respectively. However, a recently published study sheds new light on the long-held theory of bimodality in lizard foraging behaviour. Perry (1999) tested the theory that foraging modes in lizards often take one of two forms: active search or sedentary ambush. By expanding the database on lizard foraging behaviour, 83 lizard species in 12 families were compared for bimodality. Interestingly, this large amount of data did not exhibit a bimodal distribution of foraging behaviours (Perry 1999). The majority of the species were found to remain relatively stationary during foraging activity. A phylogenetic comparison of foraging modes showed that phylogeny was a strong predictor of behaviour, with closely related species tending to exhibit similar foraging patterns (Perry 1999). In light of these results, bimodality of search modes in lizards was not considered to be a real phenomenon. It was suggested that historical trends in the theory of foraging behaviour may have been caused by phylogenetically biased sampling of species, pseudoreplication and the use of inappropriate methodology (Perry 1999).

The conclusions made by Perry (1999) regarding foraging activity in lizards appear to be logical and well supported by phylogenetic evidence. In light of the results presented by Perry (1999), it seems highly unlikely that *O. infrapunctatum* and *O. lineoellatum* possess significantly different foraging modes. The two species are very closely related phylogenetically (Towns et al. 1985) and therefore are likely to have similar foraging behaviours (Perry 1999). Although *O. infrapunctatum* clearly spends more diel time active than *O. lineoellatum*, this does not necessarily imply a large difference in search modes. Instead the activity differences between species may be more strongly correlated with habitat structure and the subsequent risk of
predation (see Section 4.4). The findings of the present study, combined with results from Landcare Research investigations, support the idea that *O. infrapunctatum* and *O. lineoecellatum* are opportunistic skinks which employ a range of intermediate foraging behaviours rather than just one mode. This description of foraging behaviour is common among many studies of scincid lizards (Pietruszka 1986; Taylor 1986; Lunney et al. 1989; Vrcibradic and Rocha 1996; Wapstra and Swain 1996). These studies support the hypothesis proposed by Perry (1999) which states that foraging patterns are less polarised than historically suggested by Pianka (1966, 1969), Huey and Pianka (1981) and others.

### 5.1.5 Physiological characteristics

A clear physiological difference between *O. infrapunctatum* and *O. lineoecellatum* in their locomotor response to temperature was exhibited in this study. *O. lineoecellatum* sprinted significantly faster than *O. infrapunctatum* across a wide range of body temperatures. This difference is not surprising given the variation in distributions of the two species in New Zealand. *O. lineoecellatum* inhabits a wide variety of geographic areas, ranging from the sea shore of Nelson’s boulder bank to Marlborough’s alpine scree slopes. This species is physiologically adaptable and highly tolerant of adverse conditions such as extreme temperatures. Very few skinks in New Zealand are able to survive above the sub-alpine zone (e.g. *Oligosoma waimatense* and *O. n. polychroma*). Thus *O. lineoecellatum* is an interesting species to study, in terms of its enhanced physiological capacity and its ability to survive in a wide range of habitats and altitudes.

The rapid sprint-speeds exhibited by *O. lineoecellatum* across a range of ambient temperatures are likely to be beneficial in the exposed microhabitats which this species is often associated with, particularly in sub-alpine and alpine areas. These exposed habitats carry a high risk of aerial predation (Bulova 1994). A skink must therefore be able to sprint rapidly from a predator if detected. *O. lineoecellatum* certainly appears to have the physiological capacity to run from approaching
predators at all body temperatures tested, thus ensuring that escapes are possible even in cold, high-altitude habitats. *O. infrapunctatum* appears to lack the physiological adaptations necessary for effective locomotion and predator avoidance at exposed and alpine sites.

5.1.6 **Responses to climatic conditions**

The two skink species appeared to react differently to climatic conditions during the bait experiment, in terms of their capture probabilities. The MARK analysis in the bait investigation showed that the trappability of *O. lineoocellatum* was negatively associated with adverse weather conditions such as low solar radiation and high rainfall. Coddington and Cree (1997) noted that *Oligosoma grande* and *O. otagense* also differed in their responses to unfavourable climatic conditions. Interestingly, although the variation in weather conditions affected the activity and capture probability of *O. lineoocellatum* in the field, this environmental factor was not related to daily activity patterns exhibited by either species in captivity. However, this may have been a result of keeping skinks in a sheltered enclosure during filming, where rain and direct sunlight could not penetrate the filming arena. Differences between species in their responses to weather conditions may relate to habitat structure. It is possible that *O. lineoocellatum* reacts more strongly than *O. infrapunctatum* to variation in weather conditions because the former species often occupies microhabitats which are exposed. Rain and direct sunlight would penetrate the substrate of exposed habitats more readily than the closed-canopy habitat of *O. infrapunctatum*. This may have led to the development of heightened physiological reactions in *O. lineoocellatum* to changes in weather conditions, which in turn may affect its activity, foraging and trap encounter rate.
5.1.7 Agility and wariness

Although the escape investigation in this study showed no evidence for a significant difference between species in escape rates, the two species do appear to differ in agility per se. From personal observations at the field site, *O. lineocellatum* appears to be more agile and aggressive than *O. infrapunctatum* when disturbed, handled or captured in pitfall traps. Heightened agility may be an adaptation for survival in exposed habitats such as coastal and alpine areas where the threat of aerial predation is high. The ability to run, leap and undulate rapidly, as observed for *O. lineocellatum*, would be highly advantageous to a lizard in an exposed habitat (Bulova 1994; Cooper 1997). *O. infrapunctatum* occupies sheltered, closed-canopy habitats (Efford et al., in prep [b]) which carry a low threat of aerial predation and provide a safe refuge for skinks. In addition, *O. infrapunctatum* has the ability to use tunnelling behaviour in forest habitats on Stephens Island (East et al. 1995) to avoid its only natural ground-dwelling predator, the tuatara (*Sphenodon punctatus*). *O. lineocellatum* does not appear to utilise fossorial behaviour, most probably because it does not share a forest habitat with tuatara.

In the present study it was noted that *O. lineocellatum* appears to be more wary and alert than *O. infrapunctatum*, both at the field site and in captivity. The heightened wariness shown by *O. lineocellatum* is likely to be an adaptation to an exposed microhabitat. Bulova (1994) noted that among populations of the lizard *Callisaurus draconoides*, individuals were the most wary at sites which had the least plant cover. Heightened wariness in *O. lineocellatum* may also relate to the smaller amount of time that this species spends active each day. *O. lineocellatum* may spend more of its time stationary in microhabitats with limited plant cover because it is cautious of aerial predators such as Australasian harriers (*Circus approximans gouldi*), falcons (*Falco novaeseelandiae*) and kingfishers (*Halcyon sancta vagans*). In contrast, *O. infrapunctatum* moves about more often in its preferred closed-canopy microhabitat because there is less chance of predation and therefore less need to be cautious.
5.2 FACTORS AFFECTING SKINK TRAPPABILITY

It is exceptionally difficult to determine all of the factors affecting the trappability of a species (Jolly and Dickson 1983; Bubela et al. 1998; Koper and Brooks 1998; Efford et al., in prep [a]). This difficulty is caused in part by a lack of knowledge regarding why animals enter traps in the first place. Alterio et al. (1999) suggested that stoats (Mustela erminea) entered baited traps because of hunger. A similar reason to explain the capture of red foxes (Vulpes vulpes) was proposed by Bubela et al. (1998). In the present study, it is likely that skinks entered traps because of an attraction to the bait, but it is also possible that captures were often accidental. From the main factors investigated in this study and the ecological differences between the species, a number of reasons are suggested below to partly explain trappability differences between O. infrapunctatum and O. lineoocellatum.

5.2.1 Attraction to bait

Bait type had a marked effect on the number of captures of O. infrapunctatum and O. lineoocellatum. Capture success for both species was high when pear bait was used in traps during fine weather. This result suggests that pear is an effective bait for capturing good numbers of both species, even though O. infrapunctatum appears to include a larger volume of fruit in its diet compared to O. lineoocellatum (Efford et al. 1997). This dietary difference between the species is more likely to reflect the availability of fruit in microhabitats preferred by O. infrapunctatum rather than representing a difference in food preferences. Therefore, lack of variation between species in their attraction to pear bait suggests that pear is not likely to be a major factor influencing the trappability difference. It would be worthwhile to conduct cafeteria trials using a range of food types, including pear, to determine if any fine-scale differences between the species exist in terms of food preferences. Cafeteria trials have already proved to be successful for determining fruit-colour preferences in the skink O. maccanni (J. Marshall, pers. comm.).
5.2.2 Effects of weather conditions

The MARK analysis showed that weather variables, particularly cloud and rain, were important in explaining daily variation in capture probabilities for *O. lineoocellatum* in the bait experiment. During unfavourable weather (wet, cloudy), *O. lineoocellatum* was very unlikely to be captured. Each small improvement in the weather conditions, from overcast and wet to sunny and dry, resulted in an increase in the probability of capture. The effects of weather conditions were not as important in explaining the daily variations in *O. infrapunctatum* capture probabilities. These results suggest that the lower trappability of *O. lineoocellatum* (Efford et al., in prep [a]) may be related to the way in which this species interacts with local climatic conditions. *O. lineoocellatum* may have a low trappability within a four-day trapping session (Efford et al., in prep [a]) partly because wet and cloudy weather during trapping decreases skink activity, therefore lowering the capture probability of this species. *O. lineoocellatum* may show heightened physiological sensitivity to weather conditions as an adaptation to exposed and thermally extreme habitats. The low trappability of *O. lineoocellatum* during wet weather may play a role in the overall trappability difference (Efford et al., in prep [a]) between the two species.

5.2.3 Time spent active

The activity investigation clearly showed that *O. infrapunctatum* spent significantly more diel time active than *O. lineoocellatum*. Activity time is likely to be a major factor influencing the trappability of both species. If *O. infrapunctatum* moves about in its habitat more frequently and for longer periods of the day than *O. lineoocellatum*, the former species will encounter pitfall traps in the field more often. A higher trap encounter rate is very likely to facilitate a larger number of captures, regardless of whether skinks are captured because of a bait attraction, accidentally or both. The short periods of diel activity shown by *O. lineoocellatum*, combined with limited activity in the morning and evening, could lead to limited trap
encounters in the field. This would contribute to fewer captures and a lower trappability estimate. Activity differences among ground-dwelling lizard species are seldom examined before pitfall trapping is undertaken in population studies. It is highly likely that different activity patterns among sympatric and syntopic species often confound the results of such studies by affecting trap encounter rates and hence trappability. Differences in the activity patterns of *O. infrapunctatum* and *O. lineoocellatum* are very likely to be affecting their trappability at the Lake Station site.

### 5.2.4 Predation and escapes from pitfall traps

The escape investigation in the present study aimed to determine the escape rates of each species. The proportion of *O. lineoocellatum* that went missing from pitfall traps (0.15) was significantly higher than that of *O. infrapunctatum* (0.05). One third of the missing *O. lineoocellatum* \((n = 10)\) were assumed to have escaped from traps, as no evidence of predation was found. This finding may be partly explained by an observed difference in the level of agility between the species, as *O. lineoocellatum* appears to be more agile than *O. infrapunctatum*. From evidence left near pitfall traps it appeared that escapes were not the only cause of skink disappearances. Nocturnal predation of skinks in traps, probably by ferrets (*Mustela furo*) (B. Thomas, pers. comm.), accounted for at least two thirds of the missing *O. lineoocellatum* and three of the five *O. infrapunctatum*. These results suggest that escapes and predation of skinks in traps may reduce the number of captures in a trapping session, in turn lowering the trappability estimate for a species. This is especially true for *O. lineoocellatum*, given its higher escape and predation rates. All traps where predation occurred were situated in relatively open microhabitats, suggesting that skinks in these areas are more vulnerable to mammalian predators. *O. infrapunctatum* is seldom found in open microhabitats at the study site (Efford et al., in prep [b]) and therefore may not be exposed to high predation pressures. Predation of trapped lizards by small mammals is common in New Zealand studies (Newman 1994; Towns and Elliot 1996) and may account for losses of individuals.
lesser extent trap escapes appear to be important factors influencing the trappability difference between \textit{O. infrapunctatum} and \textit{O. lineoocellatum}.

5.2.5 \textbf{Behavioural characteristics}

From personal observations, \textit{O. lineoocellatum} appears to show a higher degree of wariness and alert behaviour than \textit{O. infrapunctatum} at the field site and in captivity, which may have negative consequences for the trappability of the former species. Although these behaviours were not examined in great detail during the present study, many independent observations were made during field and captive work which provided evidence of a species difference in wariness. Heightened wariness in \textit{O. lineoocellatum} is probably an adaptation for survival in exposed habitats.

Two explanations may account for how heightened wariness in a species could affect its trappability. Firstly individuals of a wary species may be less likely to investigate new or unnatural objects (e.g. traps) in their habitat. This neophobic behaviour could contribute to low numbers of captures and low trappability estimates, as may be the case for \textit{O. lineoocellatum}. For example, Bubela et al. (1998) suggested that a high proportion of red foxes (\textit{Vulpes vulpes}) in their study were untrappable because of innate neophobia in some individuals. Secondly, \textit{O. lineoocellatum} may develop trap-shyness. The term 'trap-shy' refers to a learned negative trap response shown by individuals in a population (Pollock et al. 1990). This response usually leads to low trappability estimates because of low recapture probabilities. Bubela et al. (1998) proposed that trap-shyness in red foxes may lead to low recaptures and trappability estimates. It is possible that the heightened wariness shown by \textit{O. lineoocellatum} is a behavioural precursor to the development of trap-shyness. Even if trap-shy behaviour in a skink only persisted for a few days following initial capture, this response would still have a negative impact on the trappability estimate. The mean recapture probability within a four-day trapping period was particularly low for \textit{O. lineoocellatum} (0.494) compared to that for \textit{O.}
**Chapter Five: General Discussion**

*infrapunctatum* (0.702) at Lake Station (Efford et al., in prep [a]). This result gives some support towards the idea that short-term trap-shyness lowers the number of recaptures and the trappability of *O. lineoocellatum*. Whether the heightened wariness exhibited by this species contributes to its low recapture rate remains unclear and requires further investigation.

### 5.3 FUTURE PROSPECTS FOR *O. INFRAPOUNCTATUM* AND *O. LINEOOCELLATUM*

The present distributions of *O. infrapunctatum* and *O. lineoocellatum* appear to be stable, having changed little over the last two decades (see Pickard and Towns 1988; Gill and Whitaker 1996). Evidence suggests that the historical range of *O. infrapunctatum* was more extensive (Towns and Daugherty 1994) but has contracted possibly because of deforestation and increased predation. *O. infrapunctatum* has quite specific habitat requirements (East et al. 1995; Efford et al., in prep [b]), therefore limiting its distribution to forest and scrub areas which provide good cover and shade. This species has a limited physiological ability for sustained activity at extreme temperatures, restricting it to altitudes of less than 600 m asl. In contrast, *O. lineoocellatum* is widespread throughout eastern parts of New Zealand and occupies a wide variety of habitat types and altitudes (East et al. 1995; Efford et al., in prep [b]). This physiologically tolerant and adaptable species may have increased its distribution after humans started to undertake widespread land clearance about 150 years ago. An increasing abundance of land covered by pasture, long grasses and low scrub at all elevations has possibly provided *O. lineoocellatum* with an expanding number of suitable habitat sites.

Undoubtedly, populations of the adaptable and generalist species *O. lineoocellatum* have a very good chance of persistence in the future. However, the outlook for *O. infrapunctatum* may not be as positive. Populations of *O. infrapunctatum* are already very localised and widely separated geographically (Gill and Whitaker 1996). Future removal of native forest and scrub by humans throughout the range of *O.*
infrapunctatum could further decrease and isolate the remaining number of small, discrete populations. *O. infrapunctatum* populations should be monitored carefully where possible to determine if numbers are decreasing and if major threats to survival are present. Stephens Island and Lake Station presently provide areas of suitable habitat for *O. infrapunctatum* (East et al. 1995; Efford et al., in prep [b]). These sites will hopefully retain large populations of *O. infrapunctatum* for many years to come. It should be noted that the population at Lake Station has survived repeated burning of its habitat since at least 1970 (B. Thomas, pers. comm.). The survival of *O. infrapunctatum* at Lake Station is probably due to the length of time between burning sessions, usually about five years, which gives the vegetation time to grow dense enough to provide suitable skink habitat. Five to seven year cycles of burning also enable five-lined skinks (*Eumeces inexpectatus*) to survive in scrub and sandhill habitats (Mushinsky 1992). Preferably the small section of Lake Station which supports the *O. infrapunctatum* population should be protected by law from burning, grazing, exotic forest planting and habitat degradation. As yet, no action has been taken to formalise any type of protection for skinks at this site.

### 5.4 CONCLUSIONS

The present study aimed firstly to expand the current knowledge of the ecology and behaviour of *O. infrapunctatum* and *O. lineocellatum*. From the results presented here and those from the work of Landcare Research, it is now known that the two species exhibit spatial, trophic and temporal niche partitioning to a limited extent at the Lake Station site. Certain aspects of all three of these niche axes tend to overlap somewhat. *O. infrapunctatum* selects closed-canopy microhabitats, whereas *O. lineocellatum* shows little preference for any one microhabitat type. Although both species are opportunistic dietary generalists, *O. infrapunctatum* appears to take a wider variety and larger amounts of live prey and seasonal fruits. Although the time-dependence of foraging activity is similar for both species, *O. infrapunctatum* spends a significantly longer amount of diel time active than *O. lineocellatum*, as well as emerging earlier and retreating later in the
day. Differences between the species in their physiological responses to ambient temperature and local climatic conditions provide some evidence that they also partition the thermal niche to some extent. The two species probably rely on a similar mode of foraging behaviour, although *O. infrapunctatum* may spend more time searching. *O. lineoecellatum* has been described as being more wary and alert than *O. infrapunctatum*, perhaps as an adaptation to avoid predation in exposed habitats. In general, most of the ecological and behavioural differences between *O. infrapunctatum* and *O. lineoecellatum* may relate to specific adaptations to their preferred or common microhabitats. The present study has identified a number of important differences between the two species and has provided a great deal of detail regarding their ecology.

The second aim of this study was to determine what ecological and behavioural factors may contribute to the trappability difference between the species. Four main factors were isolated and these are all considered to affect skink trappability estimates in some way. These factors include differences between the species with respect to (1) responses to weather conditions, (2) diel time spent active, (3) the occurrence of predation in traps and (4) behavioural characteristics such as wariness and trap-shyness. The reason why *O. lineoecellatum* has a lower trappability estimate may relate to one or more of these factors. In general this species may be less likely than *O. infrapunctatum* to be caught because it is less active (especially during wet weather), it is predated on quite heavily while in traps, and it exhibits heightened wariness which may contribute to trap avoidance and/or trap-shy behaviour. It is extremely difficult to determine all of the factors affecting the trappability of a small, cryptic lizard species. However, this study provides evidence of some of the ecological and behavioural factors that may influence the trappability of these and other skink species in New Zealand.
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