Basking behaviour of a primarily nocturnal, viviparous gecko in a temperate climate

Sophie Gibson

A thesis submitted in partial fulfilment for the degree of Master of Science at the University of Otago, Dunedin, New Zealand

20 December 2013
FRONTISPIECE

An adult female Otago-Southland gecko (*Woodworthia* “Otago/Southland”) basking at Macraes Flat, Eastern Otago.
ABSTRACT

Many reptiles, commonly labelled as ‘nocturnal’, have higher selected body temperatures on a laboratory thermal gradient than are available during their night-time activity period. These purportedly ‘nocturnal’ reptiles experience similar day-time body temperatures ($T_b$) to diurnal reptiles, suggesting that nocturnal reptiles are capable of thermoregulating during the day. By basking for intermittent periods, utilizing postural adjustments and/or by selecting retreat types for specific thermal qualities, nocturnal reptiles may achieve elevated day-time $T_b$. To date, no studies have directly examined the diurnal behaviour of a nocturnal reptile in a cool-temperate climate. In this thesis, the diurnal behaviour of the viviparous (live-bearing), nocturnal Otago-Southland gecko (*Woodworthia* “Otago/Southland”) at Macraes Flat, Eastern Otago, was monitored using time-lapse photography. Time-lapse cameras were set up at deep crevice and superficial rock retreats over two seasons: spring-summer and autumn. Three aspects of behaviour were examined to infer whether the Otago-Southland gecko thermoregulates during the day: 1) basking behaviour, 2) postural adjustments and 3) retreat type selection. Operative temperature ($T_e$) was recorded throughout the study using temperature loggers inserted into copper models. Copper models were used to simulate the $T_e$ available to geckos in two basking positions (flat and ‘on-toes’) and in two retreat types (in a deep crevice and under a superficial rock). I discovered that Otago-Southland geckos exhibit a complex array of diurnal behaviours. Both females and males basked and exhibited postural adjustments, yet females had a higher incidence of basking, including the ‘on-toes’ basking behaviour, compared to males. However, there were no differences in the incidence of basking between reproductive and non-reproductive females. Furthermore, no clear differences between basking duration and retreat type were found. In spring-summer basking duration of three out of the four basking behaviours was longer overall for geckos at deep crevice retreats compared to those at superficial rock retreats. However, no differences in basking duration between geckos from different retreat types were evident in autumn. The thermal profiles of copper models indicate that models in basking and in-retreat positions exhibit two distinct profiles. The models in basking positions showed lower temperatures in the early morning and consistently reached higher temperatures in the afternoon, compared to models in retreats. The models in ‘on-toes’ and flat basking positions showed similar heating profiles and reached similar temperatures.
Collectively, these findings confirm that the Otago-Southland gecko uses a range of diurnal behaviours, including overt basking, postural adjustments and probably retreat type selection to thermoregulate during the day. The findings of my thesis suggest that more attention should be directed towards the diurnal behaviour of supposedly nocturnal reptiles. In chapter 3, I review the challenges associated with categorising the activity pattern of reptiles. I describe some of the approaches that can be used to study reptile activity patterns and conclude the review with some recommendations for future research on the activity patterns of reptiles.
ACKNOWLEDGEMENTS

Firstly, I would like to thank my supervisor Alison Cree for all the support she has given over the last two years. Thank you for making my Masters a memorable and enjoyable experience. I would also like to thank all the members of the 2012 – 2013 Cree lab group for their feedback on drafts and most importantly, their overwhelming support: Sophie Penniket, Scott Jarvie, Anne Besson, Samantha Botting, Georgia Moore, Joanne Monks and Merenia Wright.

Secondly, I would like to acknowledge that this research was approved by the Department of Conservation (34730-FAU), the University of Otago Animal Ethics Committee (45/12), the Ngai Tahu Consultation Committee and Kati Huirapa Runaka ki Puketeraki. I am grateful for all their support and permission to carry out this research. I would also like to thank the landowners Greg and Nicky Hand for access to their property.

I would like to acknowledge all of my field work volunteers for all their hard work: Les Gibson, Merenia Wright, Sophie Penniket, Alison Cree, Sara Mockett, Jenny Kitchin, Steve Adolph, Dominik Paschke, Sara Larcombe, Edward Ramirez and Scott Jarvie. I would especially like to thank Les and Merenia for their dedication throughout my field work, for all the long days in the field and cool nights spent at the DoC base at Macraes Flat.

I would also like to thank the staff at the Zoology Department, especially Kim Garrett for all his help with field work equipment, Murray McKenzie for making my ‘on-toes’ copper models and assisting with the many camera malfunctions I faced and Kenneth Miller for assistance formatting figures. Also, thank you to Christoph Matthaei and Alistair Senior for their statistical advice.

Overall, it was my friends and family who got me through these tough times. I would like to thank everyone in my office for all their support, thank you all for these amazing last two years (especially for all the procrastination breaks that helped me keep my sanity).

I would like to thank my family for their unconditional love and support. Thank you to Michael, you have supported me through thick and thin and have helped me get through some really tough times. Thank you to my parents Les and Gloria for all your
knowledge and wisdom (especially for all the quirky ideas, such as using bottle brushes to catch geckos in crevices). I would also like to thank my two brothers Graham and Blake who have been an inspiration to me. Graham, you have encouraged me so much and I will strive to be as happy and successful as you. Blake, you were a huge motivation to me, seeing you go through Masters made me realise I could do it too. I enjoy talking about all the troubles we have both faced. Most of all I appreciate all the support that has been given, thank you.
TABLE OF CONTENTS

Frontispiece .......................................................................................................................... i
Abstract ................................................................................................................................. ii
Acknowledgements ............................................................................................................. iv
Table of contents ................................................................................................................ vi
List of figures ....................................................................................................................... ix
List of tables ......................................................................................................................... xi
List of definitions and abbreviations .................................................................................. xii

Chapter 1: General Introduction ......................................................................................... 1
Thermoregulation: behaviour and body temperature in lepidosaurian reptiles ............. 1
Two modes of thermoregulation and of activity pattern ................................................. 2
Reproductive mode in reptiles ............................................................................................. 4
Thermoregulation during pregnancy in viviparous species ............................................. 5
Basking behaviour ............................................................................................................... 11
Postural adjustments .......................................................................................................... 12
Retreat type ........................................................................................................................ 16
How do we study reptiles in the field? ............................................................................ 19
Time-lapse photography ...................................................................................................... 20
Operative temperature and copper models ........................................................................ 21
New Zealand reptiles, climate and reproductive mode ..................................................... 22
The Otago-Southland gecko ................................................................................................. 23
Aims and predictions .......................................................................................................... 28

Chapter 2: Basking behaviour of the Otago-Southland gecko in Eastern Otago ........ 31
Introduction ......................................................................................................................... 31
Materials and Methods .................................................................................................... 33
Study site and species ......................................................................................................... 33
Sampling period rationale ................................................................................................. 34
Site selection for time-lapse photography ......................................................................... 35
Time-lapse photography .................................................................................................... 35
Capture methods and lizard measurements ..................................................................... 38
Gecko morphometrics, sex and reproductive status ....................................................... 39
Gecko identification .......................................................................................................... 40
Time-lapse photography image analysis .......................................................................... 41
Basking behaviour in the Otago-Southland gecko .............................................41
Environmental temperature ..........................................................................................42
Statistical analyses ........................................................................................................45
  The incidence of basking behaviour in the Otago-Southland gecko ......................45
  Effect of retreat type on basking behaviour ..............................................................45
  Effect of time of day on basking behaviour at different retreat types ....................46
  Temperature of copper models ................................................................................46
Results ..........................................................................................................................48
  General observations of basking behaviour in the Otago-Southland gecko ..........48
  The incidence of basking behaviours in the Otago-Southland gecko .................52
  The incidence of basking behaviour among reproductive and non-reproductive
  females in the Otago-Southland gecko .................................................................54
  Effect of retreat type on basking behaviour ..............................................................55
  Effect of time of day on basking behaviour at different retreat types ....................58
  Temperatures of copper models ............................................................................62
Discussion ....................................................................................................................67
  Basking behaviours in the Otago-Southland gecko ................................................67
  Effect of retreat type on basking behaviour ..............................................................71
  Effect of time of day on basking behaviour at different retreat types ....................71
  Temperature of copper models ............................................................................73
A new activity pattern for the Otago-Southland gecko? .............................................75
Recommendations for future research ........................................................................76
  Could time-lapse photography be used to monitoring other species? ....................76
  What are the thermal advantages of basking in the field? ........................................77
  What physiological mechanisms drive males with autotomized tails to bask? ....77
  Are there any differences between diurnal and nocturnal activity? .......................78
Conclusion ....................................................................................................................78

Chapter 3: Challenges associated with the definition of activity patterns in
lepidosaurian reptiles: a review using New Zealand species as examples ............79
Introduction .................................................................................................................79
  How are activity and inactivity defined? .................................................................81
  Activity patterns in lepidosaurian reptiles: two ends of a spectrum ......................82
  A brief history of the definitions used to describe the activity patterns of lepidosaurs
  ...............................................................................................................................82
Definitions and examples of current labels used to describe the activity patterns of lepidosaurs ................................................................. 84
Activity patterns in New Zealand lepidosaurs .................................................. 86
Why is defining reptiles as solely diurnal or nocturnal uninformative? New Zealand lepidosaurs as an example ........................................... 88
Are activity patterns the same for all individuals within a species? New Zealand lepidosaurs as examples ............................................. 90
Meta-analyses and activity patterns, the Otago-Southland gecko as an example ...... 92
How can we determine the activity time of different behaviours? ....................... 93
The use of multiple approaches in studies of lepidosaurs behaviour and activity patterns........................................................................ 95
Conclusions and future research ...................................................................... 97
References ........................................................................................................ 99
Appendix 1: The effects of Parafilm on temperature logger temperature records .................................................................................. 110
Introduction........................................................................................................ 110
Methods ............................................................................................................ 111
Statistical analyses ............................................................................................ 112
Results and Discussion ....................................................................................... 112
Appendix 2: Environmental temperature and copper models ......................... 115
Statistical analyses ............................................................................................ 115
Results and Discussion ....................................................................................... 116
Appendix 3: The incidence of in-retreat activity in the Otago-Southland gecko . 119
The incidence in-retreat activity among reproductive and non-reproductive females in the Otago-Southland gecko.................................................. 121
Effect of retreat type on in-retreat activity......................................................... 122
Effect of time of day on in-retreat activity at different retreat types .................. 124
Appendix 4: Thermal profiles of copper models in basking and in retreat positions over a diel cycle ................................................................. 128
LIST OF FIGURES

Figure 1.1: Two different retreat types available to reptiles in a rocky environment, A) a superficial rock slab and B) a deep crevice retreat at Macraes Flat, Eastern Otago. .......................................................................................................................................................... 18

Figure 1.2: A captive female Otago-Southland gecko in the ‘on-toes’ basking behaviour at the animal containment facility at the University of Otago, Department of Zoology. .................................................................................................................................................. 27

Figure 2.1: Tussock grasslands and rock outcrops at Macraes Flat, East Otago, New Zealand.................................................................................................................................................................................. 34

Figure 2.2: Time-lapse camera and solar panel set up at a superficial rock retreat in autumn........................................................................................................................................................................... 37

Figure 2.3: ‘On-toes’ copper model showing the crimped head end of the model and open, un-sealed tail end................................................................................................................................................................................. 44

Figure 2.4: Time-lapse photographs of the basking behaviours of a female Otago-Southland gecko at Macraes Flat, Eastern Otago. ....................................................................................................................... 49

Figure 2.5: Time-lapse photography of the daily movements of a female Otago-Southland gecko during spring-summer at Macraes Flat................................................................. 51

Figure 2.6: The incidence of basking behaviours of female and male Otago-Southland geckos in spring-summer and autumn. ............................................................................................. 53

Figure 2.7: The incidence of basking behaviour of reproductive and non-reproductive female Otago-Southland geckos in spring (October-December 2012). ............................... 55

Figure 2.8: Average duration of basking behaviour of female Otago-Southland geckos photographed by time-lapse cameras at superficial rock (n=6) and deep crevice (n=6) retreats in A) spring-summer and B) autumn. ................................................................. 56

Figure 2.9: Average duration of basking (across all behaviours) of female Otago-Southland geckos photographed by time-lapse cameras at superficial rock (n=6) and deep crevice (n=6) retreats in spring-summer and autumn. .................................................... 57

Figure 2.10: Effect of time of day on basking behaviour of female Otago-Southland geckos from deep crevice and superficial rock retreats in spring-summer (October 2012 – February 2013). ................................................................................................................................. 59

Figure 2.11: Effect of time of day on basking behaviour of female Otago-Southland geckos from deep crevice and superficial rock retreats in autumn (February – April 2013). .................................................................................................................................................. 62
**Figure 2.12:** Copper model temperature profiles of four different positions available to geckos in the field for basking (A, C, E) and non-basking days (B, D, F) for three bi-monthly periods. ........................................................................................................................................63

**Figure 3.1:** Hypothetical diel activity of lepidosaurs illustrating five different activity patterns. Shaded bars indicate the timing of activity over 2400 h. ..............................85
LIST OF TABLES

Table 1.1: Examples of squamates that show increased, decreased, or no change in $T_b$, $T_{sel}$ and/or basking behaviour during pregnancy (or gravidity for oviparous species)..............................................................................................................................7

Table 1.2: Studies that have labelled the Otago-Southland gecko *Woodworthia* “Otago/Southland”, as nocturnal (n=5) or primarily nocturnal (n=8). ...............25

Table 2.1: Probabilities for the effect of retreat type on duration of basking behaviour of female Otago-Southland geckos in spring-summer and autumn.....................58

Table 2.2: Significance of retreat type on average basking duration in relation to time of day.........................................................................................................................61

Table 2.3: Statistical probabilities for the significance of changes in temperature of copper models in basking positions (flat or ‘on-toes’) and in-retreats (in deep crevices or under superficial rocks) over the heating phase (0600-1400 h) of the day.................................................................................................................................65

Table 2.4: Rate of temperature increase / hour for four types of copper models from 0600 to 0900 h.........................................................................................................................66
**LIST OF DEFINITIONS AND ABBREVIATIONS**

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Autumn</strong></td>
<td><em>In time-lapse photography.</em> The second field season, spanning from 18 February until 25 April 2013.</td>
</tr>
<tr>
<td><strong>Basking behaviour</strong></td>
<td>A behaviour in which a gecko is emerged from its retreat and basking was defined by either: 1) partial or full emergence from a retreat in direct sunlight, or 2) emergence from its retreat in a position where it has the potential to be exposed (i.e. this includes situations when the gecko has emerged from its retreat and the weather is overcast).</td>
</tr>
<tr>
<td><strong>Basking days</strong></td>
<td><em>In temperature of copper models.</em> Days when basking was observed using time-lapse photography.</td>
</tr>
<tr>
<td><strong>Caudal autotomy</strong></td>
<td>Caudal autotomy is the ‘voluntary’ loss of the tail that can occur as 1) an anti-predator behaviour, or 2) a result of intraspecific conflict (Bateman and Fleming 2009). Autotomy is a trait that is conserved among 13 of c. 20 lizard families (Downes and Shine 2001).</td>
</tr>
<tr>
<td><strong>In-retreat activity</strong></td>
<td><em>In Appendix Three.</em> A behaviour in which a gecko is observed as active whilst remaining in the shade of the retreat.</td>
</tr>
<tr>
<td><strong>Non-basking days</strong></td>
<td><em>In temperature of copper models.</em> Days when no basking, or only retreat activity, was observed using time-lapse photography.</td>
</tr>
<tr>
<td><strong>Oviparity</strong></td>
<td>A mode of reproduction where the female lays eggs. The vast majority of modern reptiles are oviparous (Spellerberg 1982); however, only a few New Zealand reptiles are oviparous (King <em>et al.</em> 2009).</td>
</tr>
<tr>
<td><strong>Retreat</strong></td>
<td>A term used describe two of the main habitat types available to geckos at Macraes Flat: deep crevice and superficial rock retreats.</td>
</tr>
<tr>
<td><strong>Shuttling</strong></td>
<td>The movement of an animal between habitats (or retreat types) that offer different thermoregulatory opportunities.</td>
</tr>
<tr>
<td><strong>Spring-summer</strong></td>
<td><em>In time-lapse photography.</em> The first field season, spanning from 20 October 2012 until 17 February 2013.</td>
</tr>
<tr>
<td><strong>T_b</strong></td>
<td>Body temperature, a measure of internal body temperature of a lizard.</td>
</tr>
</tbody>
</table>
**$T_e$** \( (In temperature of copper models.\) Operative temperature, a measure of temperatures – using simulations such as copper models – of an inanimate object of the same size, shape and reflectivity, as an animal situated in the same microenvironment (Bakken and Gates 1975).

**Thermoregulation** The maintenance of body temperature within a specific range (irrespective of environmental temperature) that is optimal for physiological processes (Zug *et al.* 2001; Pianka and Vitt 2003).

**Thigmothermy** A form of thermoregulation involving gaining heat by conduction through contacting warm surfaces (Pough and Gans 1982).

**$T_{set}$** Selected body temperature, a measure of the preferred temperature of a reptile on a laboratory thermal gradient (Pough and Gans 1982; Zug *et al.* 2001).

**Viviparity** A mode of reproduction where the female gives birth to live young. This reproductive mode is often associated with temperate climates (Spellerberg 1982) and has supposedly evolved to enhance the exposure of young to preferred body temperatures.
Chapter One

General Introduction

Thermoregulation: behaviour and body temperature in lepidosaurian reptiles

As ectotherms (‘cold blooded’ animals), reptiles from the superorder Lepidosauria (squamate and rhynchocephalian reptiles) rely on external heat sources to achieve body temperatures (T_b) that exceed environmental temperature (Davenport 1992; Seebacher and Franklin 2005). Environmental temperature is the main determinant that influences reptile T_b (Huey and Kingsolver 1989). Consequently, physiological processes have little influence on an ectotherm’s T_b (Seebacher and Franklin 2005). The resulting T_b of an ectotherm at a given time is influenced by the surrounding environment and by thermoregulatory behaviour (Seebacher and Franklin 2005).

Thermoregulation is a complex process in which an organism maintains its T_b within a certain range that is optimal for physiological processes (Pianka and Vitt 2003; Rock 2006). The ability of an ectotherm to thermoregulate rather than thermoconform (match T_b to environmental temperature) is highly adaptive (Cowles and Bogert 1944). While squamates are able to thermoregulate by behavioural means (Frears et al. 1997), accurate thermoregulation involves sensing climatic conditions on both a temporal and spatial scale and integrating thermal variation with behavioural and physiological responses (Kearney 2001). In this respect, an animal’s ability to sense its environment is particularly important and these responses allow an ectotherm to remain within a narrow range of T_b, despite large fluctuations in environmental temperature (Seebacher and Franklin 2005).

As chemical reactions and processes within the body are temperature-dependent, it is vital that reptiles achieve a T_b suited for their current physiological requirements (Pianka and Vitt 2003; Seebacher and Franklin 2005). This is particularly important for reptiles as virtually all biological processes are sensitive to temperature (Huey and
Kingsolver 1989; Dorcas and Peterson 1998). In reptiles, T_b influences growth rates, foraging behaviour and embryonic development, in addition to many other physiological processes (Werner and Whitaker 1978; Rock et al. 2000; Besson and Cree 2010). As extreme fluctuations in T_b can damage tissues and can be potentially lethal (Arnold 1988), behavioural mechanisms can act to buffer these extremes (Huey and Kingsolver 1989), allowing an individual to avoid physiologically damaging temperatures (Kearney 2002).

Even though reptiles are able to thermoregulate, they still have restricted capacity to maintain T_b (Kearney 2001). Therefore, T_b varies temporally on a diel (daily) and annual (yearly) cycle; thus, there are changes in thermoregulatory effort over time (Seebacher and Franklin 2005). Through exploiting spatial and temporal variation through behavioural means, reptiles are able to achieve selected body temperatures (T_sel, preferred body temperature in a laboratory thermal gradient) and maintain T_sel within a certain range that is optimal for physiological performance (Rock et al. 2000; Kearney 2001). These temperatures are not constant and can change over time (Rock et al. 2000). In addition, different reproductive conditions and sexes have different T_sel to maximise performance (Rock et al. 2000). Subsequently, T_sel can change over the course of the day, between sites and over seasons (Rock et al. 2000).

Two modes of thermoregulation and of activity pattern

Thermoregulatory mode is predominantly dependent on life history (Pianka and Vitt 2003). There are two main thermoregulatory mechanisms utilised by squamates – heliothermy and thigmothermy. Heliotherms achieve T_sel by gaining heat from direct basking (exposing the body to the sun), via heat transfer in the form of solar radiation and conduction (Braña 1993; Pianka and Vitt 2003). Therefore, heliothermic animals are typically active during the day (diurnal) and bask overtly to achieve T_sel (Pianka and Vitt 2003). Thigmothermy, on the other hand, involves drawing heat from solid surfaces by physical contact (Pianka and Vitt 2003). Thigmothermic animals do not need to expose themselves to radiation or emerge from their retreat. Thigmothermy is particularly important for nocturnal species (Wilson 2012). Animals that are thigmothermic are commonly active outside their retreats during the night (nocturnal)
(Rock et al. 2002; Rock and Cree 2008) and do not bask – or at least not conspicuously during the day.

Many studies classify the activity patterns of squamates in a binary way, as either nocturnal or diurnal. For example, some squamate species, including the leopard gecko *Eublepharis macularius* (Autumn and De Nardo 1995), the tropical house gecko *Hemidactylus mabouia* (Vitt 1986) and the black false boa *Pseudoboa nigra* (Vitt and Vangilder 1983) are labelled as ‘strictly nocturnal’, while Kluge’s dwarf gecko *Lygodactylus klugei* (Vitt 1986), the montpellier snake *Malpolon monspessulanus* (Jaksić et al. 1982) and the parrot snake *Leptophis ahaetulla* (Vitt and Vangilder 1983) are labelled as ‘strictly diurnal’. These classifications suggest that these species will not be active outside their activity period (or at least not in the same way they are active during their activity period) (Pianka and Vitt 2003). However, some studies have shown labelling species via activity pattern is not as clear-cut as previously thought (Brattstrom 1952; Rock et al. 2002). It is possible for animals to exhibit both heliothermic and thigmothermic behaviours (Rock and Cree 2008). Consequently, animals can therefore be active during both the day and the night (Brattstrom 1952). Researchers now use ‘primarily’ or ‘partially’ to explain activity times (Vitt 1986). For example, the activity pattern of the naked-toed gecko *Gymnodactylus geckoides*, is described as ‘partially’ diurnal, as this species is active both during the day and night (Vitt 1986). Similarly, the Brazilian gecko *Phyllopezus pollicaris* is described as ‘primarily’ nocturnal (Vitt 1986).

Some species even show changes in activity pattern over seasons (Szczerbak and Golubev 1996). At high-altitudes geckos from the genus *Tenuidactylus* show variations in activity pattern over the course of a year (Szczerbak and Golubev 1996). During cooler months, geckos become heat seeking and bask, whereas during warmer months, geckos remain in retreats during the day and only emerge at night (Szczerbak and Golubev 1996).

In general, more is known about behavioural thermoregulation of diurnal species and less is known about nocturnal species (Huey 1982; Kearney 2001). In the past, the opportunities for regulating $T_b$ for nocturnal species were thought to be restricted to night-time activity. Consequently, the $T_b$ of nocturnal lizards was commonly
considered as low and variable (Kearney 2001; Pianka and Vitt 2003). This suggested that in nocturnal reptiles, a physiological shift would optimize performance at lower $T_b$ (Pianka and Vitt 2003). Yet in fact, optimal $T_b$ and temperature for sprinting for several nocturnal geckos are similar to those of diurnal species (Huey et al. 1989a). Such a high thermal optimum for sprinting is evident in five species of nocturnal geckos, *Coleonyx brevis, C. variegatus, Hemidactylus frenatus, H. turcicus* and *Lepidodactylus lugubris* (Huey et al. 1989a). This result suggests that these geckos have similar thermal dependencies for sprinting as many other diurnal lizards (Huey et al. 1989a).

*Reproductive mode in reptiles*

There are two main reproductive modes in squamates – oviparity and viviparity. In oviparous (egg-laying) reptiles, incubation (e.g. in soil) is used to accelerate embryonic development external to the maternal environment (Shine 1983). Therefore the success of the clutch is dependent on environmental conditions (Robb 1986). Oviparity is common in tropical climates and is often viewed as the ancestral reproductive mode (Arrayago et al. 1996). In viviparous (live-bearing) species, embryonic development is completed *in utero* and females give birth to live young (Shine 1983). Thus the success of a clutch is primarily dependent on maternal (internal) conditions (Jewell and Morris 2008).

A prevailing hypothesis for the evolution of viviparity – the ‘cold-climate’ hypothesis – suggests that viviparity developed predominantly in temperate climates to enable females to control the $T_b$ of their developing young, through increased maternal control over developmental conditions (Shine 2004). For example, laying eggs in cool climates may be disadvantageous as the eggs may be exposed to extreme fluctuations in temperature that may inhibit embryonic development (Robb 1986). On the other hand, in viviparous species, the thermoregulatory behaviours exhibited by the mother can buffer extremes and protect developing offspring from harsh environmental conditions (Shine 1985; Pianka and Vitt 2003). Thus, neonates that are retained within the body are exposed to higher and more stable temperatures (Robb 1986).
Among viviparous species, gestation lengths differ. Some viviparous species exhibit annual reproductive cycles in which gestation takes 4-5 months (Holmes and Cree 2006; Cree and Hare 2010). For example, McCann’s skink *Oligosoma maccanni*, reproduces on an annual cycle, has small clutch sizes and a low reproductive output (Holmes and Cree 2006).

Similarly to the evolution of viviparity, biennial reproduction may be a solution to counter the problems of reproduction in temperate climates (Cree and Guillette 1995). Some species, particularly in cool climates, exhibit prolonged biennial cycles (Cree and Guillette 1995). Such an extended reproductive cycle has only been documented in a few species. Cope’s alligator lizard *Barisia monticola* exhibits biennial reproduction, in which gestation lasts from 10-12 months (Vial and Stewart 1985), whereas the southern snow skink *Niveoscincus microlepidotus*, has a biennial-triennial reproductive cycle, in which females produce one litter every 2 years (biennial) or in some cases every 3-4 years (triennial) (Olsson and Shine 1999). Furthermore, environmental factors influence gestation length. For example, in the laboratory the southern snow skink is able to reproduce on an annual cycle, given favourable conditions (Olsson and Shine 1999). This demonstrates that in this species favourable conditions can dramatically reduce gestation length.

*Thermoregulation during pregnancy in viviparous species*

During pregnancy, viviparous species may manipulate their behaviour and/or physiology (Schwarzkopf and Andrews 2012). The maternal manipulation hypothesis posits that alterations in maternal behaviour and/or physiology during pregnancy may buffer environmental conditions and lead to increased offspring fitness (Schwarzkopf and Andrews 2012). Mothers can alter their basking behaviour to regulate $T_b$ and the temperatures their offspring are exposed to, and even select specific habitats for their thermal qualities (Schwarzkopf and Andrews 2012). Such changes in behaviour can have significant effects on pregnancy outcomes (Hare and Cree 2010).

Many studies have noted shifts in $T_b$ and behaviour associated with changes in reproductive status in viviparous reptiles (Werner and Whitaker 1978; Beuchat 1986;
Rock et al. 2000; Rock et al. 2002) (Table 1.1). Maternal behaviour and thermoregulatory effort can affect the outcome of pregnancy (Schwarzkopf and Andrews 2012). During pregnancy the thermal requirement of the offspring may differ from that of the mother, subsequently leading to commonly observed shifts in $T_b$ or behaviour. This provides a proximate reason (embryonic demand) for shifts in $T_b$ during pregnancy (Shine 2006). The majority of squamates shown to alter their $T_b$ during pregnancy have increased $T_b$, however some species show either a decrease in $T_b$, or no change (Table 1.1).
Table 1.1. Examples of squamates that show increased, decreased, or no change in $T_b$, $T_{set}$, and/or basking behaviour during pregnancy (or gravidity for oviparous species). Viviparous species have been extracted from Table 1 by Shine (2006). Additional information on oviparous species, as well as context for the studies on viviparous species has also been added. ‘Reproductive mode’ is shown as either viviparous or oviparous. ‘Study comparison’ shows which reproductive groups each study compared, defined as either pregnant (or gravid, if oviparous) females – male (PF, M), pregnant females – non-pregnant females (PF, F), or pregnant female – non-pregnant female – male (PF, F, M). ‘Study design’ is described as field, laboratory or both. The ‘maternal effect’ indicates how females change their thermoregulatory behaviour while pregnant (or gravid). ‘Geographical area’ and original ‘reference’ are also shown.

<table>
<thead>
<tr>
<th>Species</th>
<th>Family</th>
<th>Reproductive mode</th>
<th>Study comparison</th>
<th>Study design</th>
<th>Maternal effect</th>
<th>Geographical area</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Antaresia childerni</em></td>
<td>Pythonidae</td>
<td>Oviparous</td>
<td>PF, F, M</td>
<td>Laboratory</td>
<td>Increased $T_b$, increased precision</td>
<td>Australia</td>
<td>(Lourdais <em>et al.</em> 2008)</td>
</tr>
<tr>
<td><em>Bassiana duperreyi</em></td>
<td>Scincidae</td>
<td>Oviparous</td>
<td>PF, F, M</td>
<td>Laboratory</td>
<td>Increased $T_b$</td>
<td>Australia</td>
<td>(Shine 2006)</td>
</tr>
<tr>
<td><em>Chalcides ocellatus</em></td>
<td>Scincidae</td>
<td>Viviparous</td>
<td>F, M</td>
<td>Laboratory</td>
<td>Increased $T_b$, increased basking</td>
<td>North Africa</td>
<td>(Daut and Andrews 1993)</td>
</tr>
<tr>
<td><em>Crotalus viridis</em></td>
<td>Viperidae</td>
<td>Viviparous</td>
<td>PF, F</td>
<td>Laboratory</td>
<td>Increased $T_b$, increased precision</td>
<td>Canada</td>
<td>(Charland and Gregory 1990)</td>
</tr>
<tr>
<td><em>Eulamprus tympanum</em></td>
<td>Scincidae</td>
<td>Viviparous</td>
<td>PF, F, M</td>
<td>Field and Laboratory</td>
<td>Increased basking, no change in $T_b$</td>
<td>Australia</td>
<td>(Schwarzkopf and Shine 1991)</td>
</tr>
<tr>
<td>Species</td>
<td>Family</td>
<td>Reproductive</td>
<td>Sex</td>
<td>Environment</td>
<td>Body Temperature</td>
<td>Location</td>
<td>Reference</td>
</tr>
<tr>
<td>--------------------------</td>
<td>---------------------</td>
<td>----------------</td>
<td>--------</td>
<td>-------------</td>
<td>------------------</td>
<td>-----------------------</td>
<td>--------------------------------</td>
</tr>
<tr>
<td><em>Lacerta vivipara</em></td>
<td>Lacertidae</td>
<td>Viviparous</td>
<td>PF, F</td>
<td>Laboratory</td>
<td>Decreased T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>Eurasia</td>
<td>(Le Galliard et al. 2003)</td>
</tr>
<tr>
<td><em>Oligosoma maccanni</em></td>
<td>Scincidae</td>
<td>Viviparous</td>
<td>PF, M</td>
<td>Field</td>
<td>No change in T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>New Zealand</td>
<td>(Hare et al. 2009)</td>
</tr>
<tr>
<td><em>Podarcis muralis</em></td>
<td>Lacertidae</td>
<td>Oviparous</td>
<td>PF, F, M</td>
<td>Field and Laboratory</td>
<td>Decreased field T&lt;sub&gt;b&lt;/sub&gt;, no change in laboratory T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>Europe, North America</td>
<td>(Braña 1993)</td>
</tr>
<tr>
<td><em>Pseudemoia entrecasteauxii</em></td>
<td>Scincidae</td>
<td>Oviparous</td>
<td>PF, M</td>
<td>Field and Laboratory</td>
<td>Increased basking</td>
<td>Australia</td>
<td>(Shine 1980)</td>
</tr>
<tr>
<td><em>Sceloporus cyanogenys</em></td>
<td>Phrynosomatidae</td>
<td>Viviparous</td>
<td>PF, M</td>
<td>Laboratory</td>
<td>Decreased T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>North America</td>
<td>(Garrick 1974)</td>
</tr>
<tr>
<td><em>Sceloporus grammicus</em></td>
<td>Phrynosomatidae</td>
<td>Viviparous</td>
<td>PF, F, M</td>
<td>Field</td>
<td>Decreased T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>North America</td>
<td>(Andrews et al. 1997)</td>
</tr>
<tr>
<td><em>Sceloporus jarrovi</em></td>
<td>Phrynosomatidae</td>
<td>Viviparous</td>
<td>PF, F, M</td>
<td>Field</td>
<td>Decreased T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>North America</td>
<td>(Beuchat 1986)</td>
</tr>
<tr>
<td><em>Sceloporus virgatus</em></td>
<td>Phrynosomatidae</td>
<td>Oviparous</td>
<td>PF, F, M</td>
<td>Field</td>
<td>Decreased T&lt;sub&gt;b&lt;/sub&gt;</td>
<td>North America</td>
<td>(Smith and Ballinger 1994)</td>
</tr>
<tr>
<td><em>Woodworthia “Otago/Southland”</em></td>
<td>Diplodactylidae</td>
<td>Viviparous</td>
<td>PF, F, M</td>
<td>Field</td>
<td>Increased T&lt;sub&gt;sel&lt;/sub&gt;</td>
<td>New Zealand</td>
<td>(Rock et al. 2000)</td>
</tr>
</tbody>
</table>
Generally, species that inhabit warm climates such as Africa, South America and Australia often experience high $T_b$. For example, the $T_b$ of Yarrow’s spiny lizard *Sceloporus jarrovi* (Beuchat 1986) and the blue spiny lizard *Sceloporus cyanogenys* (Garrick 1974), can reach highs of 35°C. In such species, once a female becomes pregnant there is often a marked decrease in $T_b$. This reduction in $T_b$ enhances embryonic development and survival (Beuchat 1986; Mathies and Andrews 2003), shifting the thermal optimum for the mother to a range that is suitable for the development of offspring (Beuchat 1988; Lourdais *et al.* 2008). This avoids reaching the upper thermal limits for both the offspring and the mother (Beuchat 1988). The relationship between pregnancy and $T_b$ is evident in many other viviparous species, such as the mesquite lizard *Sceloporus grammicus* (Andrews *et al.* 1997), the common lizard *Lacerta vivipara* (Le Galliard *et al.* 2003), as well as oviparous species, such as the western fence lizard *Sceloporus virgatus* (Smith and Ballinger 1994) and the common wall lizard *Podarcis muralis* (Braña 1993). There are exceptions to this general pattern of decreased $T_b$ in warm climates during pregnancy. For example, the viviparous ocellated skink *Chalcides ocellatus* from North Africa (Daut and Andrews 1993) and the oviparous southern grass skink *Pseudemoia entrecasteauxii* from Australia (Shine 1980), show an increase in $T_b$ during pregnancy.

On the other hand, temperate regions are characterised by cooler temperatures and greater environmental variability (Rock 2006). In temperate environments – as opposed to tropical environments – the opposite trend is evident: reptiles often experience elevated $T_b$ during pregnancy (Werner and Whitaker 1978; Daut and Andrews 1993; Rock *et al.* 2000; Rock *et al.* 2002). Laboratory experiments on the $T_{sel}$ of the Otago-Southland gecko *Woodworthia* “Otago/Southland” demonstrated that pregnant females select higher $T_b$ (up to 8°C) on a thermal gradient, compared to non-pregnant conspecifics (Rock *et al.* 2000). Another study examined the gestation length of the Otago-Southland gecko under a warm and cool artificial thermal cycle (Rock and Cree 2003). Temperature was shown to have a profound effect on the success of pregnancies, in addition to gestation length (Rock and Cree 2003). In the warm regime, the amount of time females were physically burdened by offspring was decreased and the rate of embryonic development was increased (Deeming and Ferguson 1991; Rock and Cree 2003). Furthermore, a shorter pregnancy may also allow parturition at a more
favourable time of year, when food is abundant and temperatures are stable (Duvall 1982).

In addition to elevated $T_b$ during pregnancy, some species also show changes in thermoregulatory precision. A study examining the thermoregulatory behaviour of the viviparous western rattle-snake *Crotalus viridis*, revealed that pregnant snakes not only had higher $T_b$, but were also able to thermoregulate with greater precision (Charland and Gregory 1990). This precision was evident as there was reduced variability around $T_{set}$ (Charland and Gregory 1990). A similar relationship between gravidity and thermoregulation has been documented in oviparous species. In the children’s python *Antaresia chilreni*, one fourth of embryonic development is completed in the oviduct (Lourdais et al. 2008). Thus, maternal behaviour prior to oviposition (a period of early development before eggs are laid) may regulate thermal conditions for developing offspring (Lourdais et al. 2008). It was evident that gravidity during this short developmental window has strong influences on thermoregulation, as gravid females had higher $T_b$ and thermoregulated with greater precision than non-gravid females (Lourdais et al. 2008).

Charland and Gregory (1990) noted that many studies documenting increased $T_b$ during pregnancy assumed that non-pregnant females did not require elevated $T_b$. Presumably, pregnant females maintain such temperatures to promote embryonic development (Daut and Andrews 1993). There is, however, some evidence that even non-pregnant females might achieve higher $T_b$ than males (Shine 2006; Rock and Cree 2008). In the oviparous, eastern three-lined skink *Bassiana duperreyi*, non-gravid females experience $T_b$ closer to those of gravid females, compared to males (Shine 2006). This was evident as non-gravid females showed similar basking behaviours as gravid females when in an eight-hour basking treatment (Shine 2006). In a recent study on the viviparous Otago-Southland gecko *W. “Otago/Southland”*, non-pregnant females select $T_b$ close to those of pregnant females (Rock and Cree 2008). Elevated $T_b$ may enable non-pregnant females to maintain body condition under higher temperatures and could subsequently prepare females for the next reproductive cycle (Bonnet et al. 2001). In such cases each of the three reproductive groups in a population (pregnant and non-pregnant females,
and males) may exhibit different $T_{\text{sel}}$ as they are subject to different physiological demands.

Conversely, some squamate species such as the yellow-bellied water skink *Eulamprus tympanum* (Schwarzkopf and Shine 1991) and McCann’s skink *O. maccanni* (Hare et al. 2009), show no changes in $T_b$ during pregnancy. In *E. tympanum*, gestation is accelerated by spending longer periods of time basking at 32 °C, rather than selecting higher temperatures (Schwarzkopf and Shine 1991). As there is no change in $T_b$, the thermal optimum for both the mother and the neonate must overlap. Therefore both can perform various physiological processes under the same optimal $T_b$.

In viviparous species, the relationship between thermoregulation and reproduction is stronger than that in oviparous species. As viviparous species carry embryos for a full term and embryonic development is completed *in utero*, maternal basking can increase the rate at which offspring develop (Pianka and Vitt 2003). Yet the question remains as to how pregnant females in cool climates (especially nocturnal species) achieve elevated $T_b$ suited for embryonic development. This question will be explored by considering three aspects of behavioural thermoregulation: basking behaviour, postural adjustments and retreat type.

*Basking behaviour*

Basking is one of the most common forms of thermoregulation in reptiles (Seebacher and Franklin 2005). The process of basking involves exposing the body to warmth and light, which in nature is in the form of solar radiation. Basking behaviour provides a means to control the three routes of heat exchange (radiation, conduction and convection) and therefore $T_b$ (Seebacher 1999). As reptiles rely on environmental temperature to influence $T_b$, basking allows reptiles to gain heat rapidly (Pianka and Vitt 2003). Many species of reptiles (especially heliotherms) use basking as their main method of heating (Cowles and Bogert 1944; Heath 1962; Huey and Pianka 1977; Muth 1977; Hertz and Huey 1981; Waldschmidt and Tracy 1983). This group of diurnal reptiles exhibits a diverse assemblage of basking behaviours and such behaviours are sometimes species-specific.
On the contrary, little is known of the basking behaviours of some purportedly ‘nocturnal’ species. Given the limited opportunity for thermoregulation during the night, nocturnal species are typically active at lower temperatures than diurnal species (Autumn and De Nardo 1995). However, nocturnal species have retained some of the same traits as diurnal species. That is, they still require high $T_b$ to aid physiological processes such as digestion and growth (Autumn and De Nardo 1995). Some nocturnal geckos bask directly during the day whilst remaining close to a retreat (Pianka and Vitt 2003). For example, at high altitudes (1550 metres above sea level), individuals of the nocturnal Boettger’s wall gecko *Tarentola boettgori*, have been observed basking within rock fissures (Brown 1996). In addition, some nocturnal species have been shown not only to thermoregulate during the day, but have also been observed basking in the laboratory (Cree et al. 2003; Rock and Cree 2003; Preest et al. 2005). Yet it remains unclear to what extent basking also occurs in the field. Field biologists have occasionally reported direct basking of ‘nocturnal’ species in the field, however these claims have not been quantified in many of these studies (Werner and Whitaker 1978; Rock and Cree 2008).

*Postural adjustments*

Postural adjustments as a factor contributing to behavioural thermoregulation have been thoroughly studied in reptiles from arid climates (Muth 1977). The postural adjustments assumed by reptiles are dependent on thermal requirements and allow fine-tuned control of $T_b$ (Kearney 2001; Zug et al. 2001). Reptiles can use subtle postural adjustments to regulate $T_b$ in a variety of ways (Muth 1977; Kearney 2001). Postural adjustments can be used to increase heat absorption or heat loss (Zug et al. 2001). A reptile that requires increased $T_b$ will utilize different routes of heating compared to a reptile trying to decrease $T_b$. As thermal regimes fluctuate on diel as well as annual cycles, on any given day, a range of basking behaviours and postural adjustments can be employed to increase, decrease or maintain $T_b$. For reptiles living in arid or tropical climates postural adjustments are commonly used to decrease $T_b$ throughout the hottest periods of the day (DeWitt 1967). A example of a species that exhibits an elevated, or erect-posture, is the Californian zebra-tailed lizard *Callisaurus draconoides* (Muth
1977). In the field, individuals of *C. draconoides* exhibit three distinctive postures associated with behavioural thermoregulation: the prostrate (body flat on substrate), tail-down (front leg extension) and elevated (complete extension with all legs) posture (Muth 1977). These postures are closely linked to $T_b$. In the field, the prostate posture may be assumed at low $T_b$ as it maximises the amount of conductive heat gain through the substrate, while decreasing convective heat loss (through wind). The tail-down posture may be assumed when $T_b$ is close to $T_{sel}$ to decrease the rate of heat gain. The elevated posture may be assumed when the $T_b$ exceeds $T_{sel}$, raising the body of the lizard off the substrate to increase convective heat loss (Muth 1977). The Australian Yinnietharran rock dragon *Ctenophorus yinnietharra*, exhibits a similar elevated posture with only their claws and feet in contact with hot sand (Wilson 2012). An elevated posture allows an animal to avoid extreme temperatures and thermal limits by increasing wind contact (heat loss by convection) and decreasing heat absorption through conduction with the substrate (Muth 1977).

Little focus, however, has been directed towards the postural adjustments exhibited by nocturnal lizards in temperate climates. In temperate climates, night-time temperatures are typically low and suboptimal (Pianka and Vitt 2003). Postural adjustments by nocturnal lizards during the day can increase day-time $T_b$ (Muth 1977) and subsequently bring an animal’s $T_b$ closer to optima for biological processes (Kearney 2001). Therefore, day-time thermoregulation by something as minute as postural adjustments (Kearney 2001) may be particularly important for nocturnal species.

A postural adjustment of particular interest is the ‘on-toes’ basking behaviour. The ‘on-toes’ behaviour occurs when the legs of an animal are partially or completely extended, elevating the abdomen off the substrate (A. Cree *pers. comm.*). This posture is hypothesised to increase the rate of heating, in a cool climate, through both bringing the body of an animal closer to a radiant heat source and decreasing the amount of heat loss through conduction to the cool substrate. This postural adjustment may be particularly important for animals in temperate climates, especially during the early morning. Many studies have observed similar postural adjustments in diurnal species from arid climates (DeWitt 1967; DeWitt 1971; Muth 1977), yet in these studies this behaviour was exhibited for a completely different reason. For example, in the desert iguana
Dipsosaurus dorsalis, changes in posture are used to maintain a constant $T_b$ (DeWitt 1967); while in C. draconoides an elevated posture exposes the body to convective heat loss and may be used in the field as a cooling mechanism (Muth 1977).

The ‘on-toes’ postural adjustments may be exhibited by individuals exposed to direct sunlight, or can occur in the shade within a retreat (A. Cree pers. comm.). These two strategies, however, yield completely different heating methods. When an animal exposes its body to the sun in the ‘on-toes’ position, solar radiation and convection are the main routes of heat exchange (Wilson 2012). Whereas, when an animal is in a shaded retreat that little radiation and wind can penetrate, contacting the surface of the rocks above, conduction becomes an important route of heat exchange. Conduction involves the transfer of heat through solid surfaces and is the basis of thigmothermy (Wilson 2012). However, this thermoregulatory mode is only possible through the heating of surfaces via solar radiation (Pianka and Vitt 2003). The importance of solar radiation for heating surfaces is evident for the Galápagos marine iguana Amblyrhynchus cristatus. This species gains high daytime $T_b$ through diurnal basking, in addition to conduction with black basalt (Pianka and Vitt 2003). When the $T_b$ of an animal is less than air (or substrate) temperature the animal is able to draw heat from the air (or substrate), increasing $T_b$ (Pianka and Vitt 2003). As the substrate in this example is black volcanic rock, the rock absorbs heat rapidly, providing a valuable heat source to the iguana.

Nocturnal lizards are active at night; therefore most of a nocturnal species’ social and foraging behaviours occur at this time. It is through postural adjustments that nocturnal species are able to achieve day-time $T_b$ similar to diurnal species that openly bask (Werner and Whitaker 1978; Kearney and Predavec 2000; Rock et al. 2000; Kearney 2001). Many studies have revealed that the $T_b$ of reptiles is influenced by postural adjustments (Muth 1977; Kearney 2001; Kearney 2002). A study by Kearney (2001) demonstrated that in the laboratory, two species of Australian geckos Christinus marmoratus and Nephurus milii, exhibited an erect postural adjustment (similar to the ‘on-toes’ postural adjustment) while residing in retreats. By pressing their backs against the upper slab of rock, both C. marmoratus and N. milii achieved $T_b$ that were c.
10 °C higher than geckos in resting postures (body resting flat on the substrate) (Kearney 2001).

The use of postural adjustments in rocky environments provides nocturnal reptiles with some means to thermoregulate and take full advantage of temperatures within a retreat (Kearney 2001; Rock et al. 2002). In light of similarities between the day-time $T_b$ of diurnal and nocturnal species (Werner and Whitaker 1978; Kearney and Predavec 2000; Kearney 2001), postural adjustments may be a key to understanding how nocturnal reptiles thermoregulate during the day while in retreats. Collectively, postural adjustments and retreat type selection may enable nocturnal species to achieve higher day-time $T_b$ (Kearney 2002).

Postural adjustments also have a social context (Brattstrom 1974; Gans et al. 1984). Adjustments for thermoregulation and intraspecific communication involve similar mechanical movements, yet they have evolved in completely different contexts. Changes in posture can be used to communicate through courtship (males to females, vice versa) and territorial/competitive displays (male to male) (Brattstrom 1974; Martins et al. 1998). For example, male tuatara *Sphenodon punctatus*, defend their territory using competitive displays when threatened by intruding males (Gillingham et al. 1995). In this display, males elevate their bodies off the substrate, extending their legs into a ‘pushup’ posture, making the defending male appear larger and more threatening (Gillingham et al. 1995). In addition, male tuatara also exhibit a similar ‘pushup’ display while courting (Gillingham et al. 1995). The western fence lizard, *Sceloporus occidentalis* (Sheldahl and Martins 2000) and sagebrush lizard, *Sceloporus graciosus* (Martins et al. 1998), exhibit a similar territorial display. These two North American species use this display to communicate to others within their populations. However, due to the rapid evolution of display behaviours in *S. graciosus*, these displays cannot be used to communicate between populations of the same species (Martins et al. 1998). As this behaviour is important for same-species recognition, a modification in display behaviour may lead to speciation (Martins et al. 1998).
Retreat type

The microhabitat available to a reptile is primarily dependent on life history. Whether a species is diurnal or nocturnal, arboreal (tree dwelling) or terrestrial, dictates what kinds of habitat that animal can utilise. Retreat selection is particularly important for reptiles, as different retreats offer different thermoregulatory opportunities (Huey et al. 1989b). As the thermoregulatory conditions of a retreat can change over the course of a day (Pianka and Vitt 2003), an optimal basking spot in the early morning may become inhospitable during the afternoon (Zug et al. 2001). Therefore, it is important that lizards are able to efficiently and rapidly select retreats for their current thermal qualities.

A particularly good example of life-history having dramatic effects on microhabitat is evident in two diurnal lizards *S. occidentalis* and *S. graciosus* (Adolph 1990). These two species inhabit different altitudinal gradients – *S. occidentalis* inhabits low elevations, while *S. graciosus* inhabits high elevations, yet at intermediate elevations their distributions overlap (Adolph 1990). There was a striking difference of 10.3°C between the air temperature at low and high altitude sites (Adolph 1990). However, the $T_b$ of these two species varied minimally (1.8°C) with altitude (Adolph 1990). It was evident that both species compensated for the differences in thermal environments by modifying basking behaviour and microhabitat use (Adolph 1990). At low elevations, *S. occidentalis* was arboreal, while at intermediate elevations – where the distributions of both species overlapped – both species were partially arboreal and at high elevations *S. graciosus* was primarily terrestrial (Adolph 1990). Behavioural thermoregulation appears to be a controlling factor determining the microhabitat of these species over an altitudinal gradient.

Prolonged periods spent in retreats may have deleterious effects on reptile thermal biology. One study has shown that inhabiting retreats for long periods, limiting the exposure of juvenile broad-headed snake *Hoplocephalus bungaroides* to $T_{sel}$, often leads to decreased growth rates and survival (Webb and Shine 1998). On a typically sunny day, juveniles of this nocturnal species were only able to achieve $T_{sel}$ for less than five hours, due to strong predation pressures (Webb and Shine 1998). However,
this apparent lack of basking and increased use of retreat sites during the day entails costs related to decreased activity during the day and subsequently limited opportunities for thermoregulation, foraging and reproduction (Webb and Whiting 2005).

Despite the differences in heating profiles and thus thermoregulatory opportunity in different habitat types, many studies continue to focus on sampling individuals from the most convenient habitat. For example, in rocky habitats, rock turning is the most widely used method to sample reptiles (McDiarmid et al. 2011). This is primarily because individuals in these habitats are easily accessible. Other habitats, however, are often ignored. Deep crevices in large rock tors are a prime example of such a habitat. Deep crevices (Fig. 1.1 B), unlike loose superficial rock slabs (Fig. 1.1 A), cannot be lifted, so individuals residing in this habitat are difficult to extract (McDiarmid et al. 2011). Rock tors provide extensive opportunities for thermoregulation (Werner and Whitaker 1978; Kearney 2002; McDiarmid et al. 2011), protection from predators (Dorcas et al. 1997) and breeding, foraging and denning sites (McDiarmid et al. 2011). Superficial rocks exhibit extreme fluctuations in their thermal profiles (Rock and Cree 2008; Hare et al. 2009). On a typical summer’s day, during sunrise in the early morning the rock heats rapidly (heating phase, 0600-1000 h), reaches a high, stable temperature (1000-1600 h), then undergoes rapid cooling following sunset (cooling phase, 1600-2000 h) (Rock et al. 2002; Hare et al. 2009). Deep crevices, on the other hand, buffer environmental extremes, maintain stable temperatures (Rock et al. 2002; Pianka and Vitt 2003) and act as moisture-barriers (Dial 1978). In addition, during winter when temperatures reach freezing, lizards can move deeper into crevices and become dormant in a state of torpor (Wilson and Cree 2003). This unintentional habitat sampling bias is primarily because individuals in crevices are difficult to extract. This has probably resulted in an uneven representation of individuals from different habitat types in the scientific literature.
Figure 1.1. Two different retreat types available to reptiles in a rocky environment, *A*) a superficial rock slab and *B*) a deep crevice retreat at Macraes Flat, Eastern Otago.

The current microhabitat of an animal is, however, not the animal’s definitive habitat choice – that is, the animal’s sole habitat. Shuttling between habitats that offer different thermal conditions is common in many reptiles (Bowker and Johnson 1980; Bowker 1984; Rock and Cree 2008). The transition between habitats or retreat types over the course of a day may enable an animal to reach and sustain \( T_{\text{sel}} \), compared to animals that are confined to one habitat type (Rock and Cree 2008).

It is unknown how retreat type affects basking behaviour, especially between superficial rock slabs that experience rapid heating and cooling, compared to deep crevices, which are thermally buffered (Rock *et al.* 2002). In synergy, a combination of
basking behaviour, postural adjustments and retreat type selection are important components for thermoregulation in reptiles (Kearney et al. 2001). These allow reptiles to maximise heat gain – as heat is particularly important for all biological functions – increasing survival and fitness.

**How do we study reptiles in the field?**

Previous studies relied on surveys to study reptile behaviour in the field (Díaz 1991; Lefevre and Brooks 1995; Carrière et al. 2008). Kerr et al. (2004) noted that many field based surveys assume that observer presence has little or no effect on reptile behaviour. However, observer presence (or disturbance) may lead to biases in animal behaviour and this is known to affect some reptiles (Martín and López 1999; Kerr et al. 2004).

A recent study recorded the effects of observer presence and handling on the Australian sleepy lizard *Tiliqua rugosa* (Kerr et al. 2004). Once handled, *T. rugosa* altered its behaviour and increased its average stride frequency for up to an hour, significantly increasing activity time (Kerr et al. 2004). Such a behaviour may be an escape response – increasing activity, removing the lizard from a potential predator or threat – then resuming normal activity once the threat is gone (Kerr et al. 2004).

Observer presence may also result in longer periods spent in retreats and subsequently, reduced thermoregulatory opportunities (Martín and López 1999). Such a relationship between observer presence and decreased thermoregulatory opportunity is evident in the wall lizard *Podarcis muralis* (Martín and López 1999). This in turn, can lead to alterations in activity patterns (Martín and López 1999) and may reduce fitness and survival.

Technological advances have enabled researchers to automatically record data irrespective of human presence (Kucera and Barrett 2011). Time-lapse photography can be used to examine the emergence and thermoregulatory behaviour of reptiles, with minimal effects on reptiles from observer presence; while, temperature loggers can be used to measure environmental temperature and reptile $T_b$. Both of these technologies limit the amount of time spent in the field and keep the effects of observer presence
low. The use of time-lapse photography may be a solution to avoid observer-induced disturbance.

*Time-lapse photography*

Time-lapse photography may prove to be an invaluable method for examining reptile behaviour. Time-lapse cameras were used to study the behaviour of the endangered striped skink *Oligosoma striatum* (Neilson et al. 2004). This species is rarely seen in the wild; however, researchers were unsure whether it was because this species is difficult to detect, or because it is very low in numbers (Neilson et al. 2004). Time-lapse cameras were used to monitor the arboreal tendencies and activity period of *O. striatum* under laboratory conditions. Through monitoring behaviour over a diel cycle, it was clear that this species has arboreal tendencies, climbing higher compared to the brown skink *Oligosoma zelandicum* (Neilson et al. 2004). The use of time-lapse photography in Neilson et al. (2004) led to the conclusion that current monitoring of *O. striatum* is not sufficient and that new survey and capture techniques are needed to monitor this species on a long-term scale (Neilson et al. 2004). This study also revealed many behaviours of *O. striatum* that surveying alone could not detect, stressing the importance of behavioural observations irrespective of human presence.

Time-lapse photography has also been used to monitor repeated nest site use of the Mary River turtle *Elusor macrurus* over several years (Micheli-Campbell et al. 2013). Infrared time-lapse photography allowed the examination of nocturnal nesting behaviour in *E. macrurus*. Photography revealed that some individuals of *E. macrurus* showed nesting site fidelity between years and consistently returned to the same nesting site; however, others did not show any site preference (Micheli-Campbell et al. 2013). This study revealed that more intensive investigation of nest site selection for *E. macrurus* is needed to understand the abiotic factors that influence nest site selection. It is vital to determine favourable physical characteristics for future management and conservation of this endangered species.
Operative temperature and copper models

Operative temperature ($T_e$) has been used in many studies examining aspects of ectotherm thermoregulation (Bakken and Gates 1975; Rock et al. 2000; Shine and Kearney 2001). Operative temperature is defined as the temperature of an inanimate object of the same size, shape and reflectivity, as an animal situated in the same microenvironment (Bakken and Gates 1975). This measure provides a useful means to study thermoregulatory opportunity, providing more meaningful estimates than simple measurements, such as air or soil temperature (Shine and Kearney 2001).

Temperature-loggers inserted into copper models are one of the most commonly used methods to examine $T_e$ and thus thermoregulatory opportunities in reptiles, without the need to take invasive $T_b$ measurements (Shine and Kearney 2001). These models, unlike simple measurements, can integrate the three routes of heat exchange: radiation (both solar radiation and thermal radiation from surfaces), conduction (heat exchange through solid surfaces, such as rock) and convection (air temperature and wind) (Shine and Kearney 2001). A balance between these three routes produces the model’s $T_e$ (Shine and Kearney 2001). Models can also be adapted for different species by modifying the heat capacity of the model through altering the colour and size of the model (Shine and Kearney 2001). Although these models can estimate the $T_e$ of a reptile they cannot mimic that reptile’s behaviour. Therefore care must be taken when using these measurements as these models are capable of reaching extreme temperatures that are biologically unrealistic and often lethal to reptiles.

Previous studies have used copper models to provide information about thermal opportunities in a variety of habitats (Hertz 1992; Kearney and Predavec 2000; Hare et al. 2009). A recent study used copper models to examine trends in temperature and basking opportunities for the Otago-Southland gecko, over an altitudinal gradient (Penniket 2012). A similar study used copper models to study how elevation influences thermoregulation in the Otago-Southland gecko (previously *Hoplodactylus maculatus*) and *O. maccanni* (previously *Leirolopisma maccanni*) (Spencer and Grimmond 1994). In addition, copper models have been used to study a range of microhabitats to examine thermal environments (Rock et al. 2000; Rock et al. 2002; Hare et al. 2009), postural
adjustments (Adolph 1990), as well as calculate the activity patterns (Grant and Dunham 1988) of a variety of reptiles. Collectively, the use of copper models in herpetological studies has greatly increased our understanding of the behaviour and physiology of reptiles.

*New Zealand reptiles, climate and reproductive mode*

New Zealand reptiles belong to three families within the superorder Lepidosauria: Diplodactylidae (a family of geckos), Scincidae (skinks) and Sphenodontia (tuatara). Geckos within the family Diplodactylidae are exclusively found in Australia, New Zealand and New Caledonia (Han et al. 2004). Within the family Diplodactylidae, New Zealand geckos have adapted to live in a range of habitats, ranging from rain forests to tussock grasslands (Robb 1986). New Zealand geckos have significantly lower annual reproductive output compared to oviparous geckos in warm climates (Cree 1994). Skinks are also found in many countries and are one of the most diverse lizard families worldwide. Within the family Scincidae, New Zealand skinks exhibit a similar pattern of annual reproduction observed in other skinks (Cree 1994). New Zealand reptiles have disparate life-histories and are predominantly viviparous (all but one species of skink – *Oligosoma suteri* are live-bearing (King et al. 2009). New Zealand is home to the only living member of the order Rhynchocephalia, suborder Sphenodontia (tuatara). The tuatara – *S. punctatus*, are oviparous (Cree 1994).

Differences between these families are reflected by different methods of behavioural thermoregulation. Previously, New Zealand geckos were split into two genera: *Hoplodactylus* (Fitzinger 1843) and *Naultinus* (Gray 1842). Species within the genus *Hoplodactylus* are typically brown or gray in colour and are nocturnal (Gill and Whitaker 1996; Lindsey and Morris 2011). However, this genus has been under recent scientific scrutiny (Nielsen et al. 2011). A review of the phylogenetic relationships of New Zealand herptofauna by Nielson et al. (2011) resulted in the repositioning of some species within the genus *Hoplodactylus* into the genus *Woodworthia*, due to ecological and behavioural divergence (Nielsen et al. 2011). New Zealand species from the family Diplodactylidae have been split into seven genera: *Hoplodactylus, Naultinus,*
**CHAPTER ONE**

Woodworthia, Dactylocnemis, Tukutuku, Toropuku and Mokopirirakau, each of which is endemic to New Zealand (Nielsen *et al.* 2011). Geckos in the genus Naultinus (green geckos) are typically green in colour, arboreal and diurnal (Nielsen *et al.* 2011). Species in the genus Woodworthia are widely distributed across both the North and South Island of New Zealand (Jewell and Morris 2008; Nielsen *et al.* 2011). Woodworthia are purportedly ‘nocturnal’ (Nielsen *et al.* 2011; Penniket 2012), implying that thigmothermy is the main method of thermoregulation (Spencer and Grimmond 1994; Cree and Guillette 1995; Wilson and Cree 2003). Many species within the newly recognised genus Woodworthia are yet to be formally described.

On the other hand, New Zealand skinks belong to a single genus within the family Scincidae, Oligosoma (Chapple *et al.* 2009). The genus Oligosoma contains a diverse assemblage of species that are endemic to New Zealand. Most species from the family Scincidae are diurnal, thus heliothermy is the dominant thermoregulatory mechanism (Hare *et al.* 2007a). However, there are some exceptions. For example, within the genus Oligosoma there are several nocturnal skinks, such as Oligosoma macgregori (Hare *et al.* 2007a), Oligosoma whitakeri (Hoare *et al.* 2007) and O. suteri (Hare *et al.* 2008). At present it remains unclear through which thermoregulatory mechanisms these distinctive species achieve $T_{sel}$.

**The Otago-Southland gecko**

The Otago-Southland gecko *Woodworthia “Otago/Southland”* (previously referred to as one of several members of the species complex *Hoplodactylus maculatus*; Nielsen *et al.* 2011), is commonly found in Central and Eastern Otago (Jewell and Morris 2008). The Otago-Southland gecko is a flat-bodied, medium sized lizard, with an average snout-vent length of 70-85 mm once mature (Jewell and Morris 2008). This species has a distinctive pattern (similar to other Woodworthia species) that allows it to camouflage amongst rock lichen. This species inhabits one of the driest locations in New Zealand; it is subject to extremely hot summers and cool winters. At Macraes Flat, the Otago-Southland gecko is found at altitudes of up to 600-710 metres above sea level, under slabs of rock and in schist and greywacke rock tors (Jewell and Morris 2008).
This species was previously thought to be an obligate nocturnal thigmotherm – restricted to nocturnal activity and thermoregulating during the day while in a retreat (Rock and Cree 2008). Many studies have labelled this species as ‘nocturnal’ or ‘primarily nocturnal’ (Table 1.2). However, an influential study stated that members of the species complex *H. maculatus*, may be better described as diurno-nocturnal (Werner and Whitaker 1978). This status suggests that this species is nocturnally active as well as basks during the day. The populations of *H. maculatus* Werner and Whitaker (1978) described as diurno-nocturnal are located at Stephens Island (Marlborough Sounds) and Motunau Island (Pegasus Bay), off the coast of the South Island of New Zealand; however, this activity pattern may also be appropriate for the Otago-Southland gecko. Other studies have formed supporting evidence of this status for the Otago-Southland gecko, with basking observed both in the laboratory (Cree *et al.* 2003; Rock and Cree 2003; Preest *et al.* 2005) and in the field (Rock *et al.* 2002; Rock and Cree 2008; Besson *et al.* 2009).
Table 1.2. Studies that have labelled the Otago-Southland gecko *Woodworthia* “Otago/Southland”, as nocturnal (n=5), or primarily nocturnal (n=8). In addition this table also shows a number of studies that have observed basking both in the field (n=3) and in the laboratory (n=3). The locations of the study sites were used to identify the study species as *W*. “Otago/Southland” for studies that were conducted before the reclassification of the *H. maculatus* species complex by Nielsen *et al.* (2011).

<table>
<thead>
<tr>
<th>Nocturnal</th>
<th>Primarily nocturnal</th>
<th>Basking in the field</th>
<th>Basking in the laboratory</th>
</tr>
</thead>
</table>

We have limited understanding about how viviparous lizards from cold climates (especially nocturnal species) achieve sufficient warmth during pregnancy. The basking behaviour of the Otago-Southland gecko is cryptic, thus individuals conceal and/or camouflage their behaviour. For example, individuals have occasionally been observed basking at the mouths of crevices, exposing themselves to direct solar radiation (Rock *et al.* 2002; Rock and Cree 2008). However, no study has quantified the diurnal behaviour of this gecko, or discerned weather basking behaviour differs between sexes (females and males), reproductive conditions (reproductive-females and non-reproductive females) or retreat types (superficial rock slabs and deep crevice retreats).

In addition, the Otago-Southland gecko is a long-lived species that reproduces biennially at Macraes Flat (Cree and Guillette 1995). In this form of reproduction, pregnancy can last up to fourteen months resulting in effectively constant ovarian activity, with less than one litter/year (Cree and Guillette 1995). Vitellogenesis occurs from autumn until spring; pregnancy then extends through summer. Fully developed
embryos remain *in utero* until the following spring when parturition occurs (Cree and Guillette 1995). This biennial cycle results in three different reproductive groups existing simultaneously at Macraes Flat at any given time; these are non-reproductive females (classified as either negative or postpartum), reproductive females (late vitellogenic or pregnant) and males (Rock and Cree 2008). This gestational cycle is an unusual phenomenon among lizard species (both in New Zealand and overseas) (Cree and Guillette 1995) and may be due to the temperate climate at Macraes Flat (Rock and Cree 2003). In contrast, the closely related *Woodworthia “Central Otago”* located at Alexandra exhibits annual reproduction, with pregnancies lasting from 3-5 months (Cree and Guillette 1995). This difference in reproductive output between *W “Otago/Southland”* and *W. “Central Otago”* may be a result of cooler temperatures at Macraes Flat, particularly from spring-autumn prolonging gestation (Cree and Guillette 1995).

Some studies have suggested that Otago-Southland geckos were diurnal thigmotherms, thermoregulating during the day through postural adjustments, retreat type selection (shuttling between retreats) and opportunistic periods of direct basking (Rock *et al.* 2002; Rock and Cree 2008). Geckos may select high-temperature diurnal retreats, to maximise physiological processes (Pianka and Vitt 2003) or may select cooler retreats to avoid extreme temperatures. Thermoregulatory effectiveness has been shown to differ among reproductive groups, where pregnant females show the most effective thermoregulation (Rock *et al.* 2002). Rock *et al.* (2002) proposed an alternative thermoregulatory strategy of remaining in large, thermally stable rock tors, similarly to that employed by pregnant garter snakes *Thamnophis elegans* (Huey *et al.* 1989b). Radio telemetry indicated that geckos move within rock tors during the day and are therefore, active diurnally (Rock and Cree 2008). This was evident through changes in radio signal strength, as geckos moved deeper into the tors (Rock and Cree 2008). This suggests that geckos are capable of shuttling between a variety of microhabitats over the course of a day, allowing the gecko to maximise $T_b$ in a highly stratified thermal environment (Rock and Cree 2008).

In the laboratory, geckos have also been observed basking flat on the surface of the tiles under heat lamps (Cree *et al.* 2003; Rock and Cree 2003). In addition, some
pregnant geckos have been observed basking ‘on-toes’, with their abdomen raised off the substrate (A. Cree, *pers. comm.*; Fig. 1.2). This behaviour has the potential to increase $T_b$ as it raises the body closer to a radiant heat source, as well as decreasing the amount of heat lost to surface rock through conduction. It is unclear, however, to what extent this behaviour occurs in the field.

Figure 1.2. A captive female Otago-Southland gecko in the ‘on-toes’ basking behaviour at the animal containment facility at the University of Otago, Department of Zoology.

Within a rocky habitat, the position of a reptile should reflect the reptile’s current thermoregulatory requirements (Huey *et al.* 1989b). Macraes Flat is composed of tussock grasslands and rock outcrops. Among these outcrops there are a variety of retreats that offer different thermoregulatory opportunities. Superficial rock slabs heat quickly, reaching surface temperatures up to 40°C (*pers. obs.*), exceeding the range of field $T_b$ of 7.5 – 31.7°C for Otago-Southland geckos (Rock *et al.* 2002; Rock and Cree 2008). Superficial rock retreats are also subject to extreme fluctuations in temperature.
and can experience differences in temperature of up to 25°C over consecutive days (Rock et al. 2000). This extreme temperature variation is similar to high altitude environments, making it difficult for geckos to maintain $T_{sel}$.

A bias in sampling has led to gaps in our knowledge of the natural distribution and possible differences between thermoregulatory behaviour of geckos inhabiting superficial rock slabs and those occupying deep crevice retreats. As geckos living under superficial rock slabs are easily accessible, field studies on the Otago-Southland gecko have focused on sampling these geckos. This focus on catching geckos from under superficial rocks has resulted in a large knowledge gap of the behaviour of geckos residing in deep crevices.

**Aims and predictions**

Firstly, I aimed to determine if the nocturnal Otago-Southland gecko at Macraes Flat was active and basked diurnally. If geckos were active diurnally, I then aimed to establish which sexes (females and males) and reproductive conditions (reproductive and non-reproductive females) basked, in addition to when basking occurred over a diel cycle. I also explored the postural adjustments that geckos exhibit while basking in the field, including the ‘on-toes’ posture. The influence of retreat type on basking behaviour was investigated by comparing the basking behaviours of geckos from deep crevice and superficial rock retreats. Time-lapse photography was used to examine basking behaviour of this purportedly nocturnal lizard, from spring (2012) to mid-autumn (2013) to address these aims. I also aimed to examine the thermal profiles of lizard models in two different basking behaviours (‘on-toes’ and flat basking) and in two retreat types (under a superficial rock slab and in a deep crevice). Furthermore, I aimed to establish whether basking ‘on-toes’ or basking flat on the substrate achieved the highest day-time temperatures. Temperature loggers inserted into copper models were used to measure $T_c$ from 0600-1400 h throughout the filming period.
The specific predictions that I test in Chapter Two are as follows:

1. That females will have a higher incidence of basking than males in both spring-summer and in autumn.

2. That pregnant females, but not non-pregnant females and males, will exhibit ‘on-toes’ basking in both spring-summer and in autumn.

3. That pregnant females will have a higher incidence of basking compared to non-pregnant females in both spring-summer and in autumn.

4. That a higher incidence of basking will be observed in spring-summer, compared to in autumn for both females and males.

5. That the duration of basking will be longer for females inhabiting deep crevice retreats than those from superficial rock retreats in both spring-summer and in autumn.

6. That all basking behaviours (including the ‘on-toes’ behaviour), will be most commonly seen in the early morning and will decrease throughout the day until early afternoon.

7. That copper models in deep crevice and under superficial rock retreats will experience little thermal variability, with warm early morning temperatures and only a small increase in temperature throughout the heating phase.

8. That copper models in the ‘on-toes’ and flat basking positions will experience the greatest thermal variability, with lower temperatures in the early morning and higher temperatures in the early afternoon, than models in retreats.

9. That copper models in the ‘on-toes’ basking position would achieve warmer temperatures in the early morning while the rocks are cool, and cooler temperatures in the early afternoon once the rocks have warmed, compared to models in flat basking positions.
I conclude Chapter Two by suggesting the most appropriate activity pattern for the Otago-Southland gecko and provide some directions for future research.

In Chapter Three I review some of the challenges associated with defining activity patterns in reptiles, a history of the definitions used in studies on activity patterns and how they are currently defined for reptiles. I provide some comments on how the use of activity patterns can be improved and discuss some approaches that could be used to more accurately describe the activity patterns of reptiles in future studies.
Chapter Two

Basking behaviour of the Otago-Southland gecko in Eastern Otago

Introduction

Some reptiles, described as nocturnal, select a higher body temperature ($T_{sel}$) on a laboratory thermal gradient than they can achieve in the field during their night-time activity period (Dial 1978; Kearney and Predavec 2000). Likewise, some purportedly nocturnal species reach day-time body temperatures ($T_b$) exceeding 25°C, close to the $T_b$ of diurnal lizards (Werner and Whitaker 1978; Huey and Bennett 1987; Tocher 1992; Kearney and Predavec 2000). These high $T_{sel}$ suggest that some reptiles described as nocturnal are capable of thermoregulating during the day (Dial 1978; Kearney and Predavec 2000; Anderson et al. 2005). These supposedly nocturnal species may achieve elevated $T_b$ through thermoregulating while in their retreats (Dial 1978; Kearney and Predavec 2000) and/or basking through exposing themselves to brief periods of solar radiation (Werner and Whitaker 1978; Anderson et al. 2005). The diurnal thermal ecology of reptiles has been studied in supposedly nocturnal species from warm climates (Dial 1978; Kearney and Predavec 2000). However, to date, no study has examined the diurnal behaviour of a ‘nocturnal’ lizard in the field in a cool-temperate climate.

Viviparous nocturnal geckos from cool-temperate climates face an additional challenge to low night-time temperatures: through which behavioural mechanism can females achieve sufficient warmth during pregnancy? The Otago-Southland gecko Woodworthia “Otago/Southland” is one species where the answer to this question is incomplete. At Macraes Flat, East Otago, a habitat susceptible to cool temperatures and environmental variability (Rock 2006), female Otago-Southland geckos reproduce on a biennial reproductive cycle, with pregnancies lasting up to fourteen months (Cree 1994; Cree and Guillette 1995). In contrast a nearby population of Otago-Southland geckos at Middlemarch (44 km from Macraes Flat) reproduces on an annual cycle (Penniket 2012). For both species, each of the female’s ovaries is only able to recruit one
vitellogenic follicle per reproductive cycle; therefore, females have a maximum clutch size of two (Cree 1994). For females at Macraes Flat, this results in c. 0.85 offspring per clutch per year – one of the lowest reproductive frequencies of lizards globally (Cree 1994; Cree and Guillette 1995).

Previous studies provide evidence that female Otago-Southland geckos bask both in the laboratory (Cree et al. 2003; Rock and Cree 2003; Preest et al. 2005) and occasional observations and inferences through Tb measurements suggest that geckos also bask in the field (Rock et al. 2002; Rock and Cree 2008). Diurnal basking in supposedly ‘nocturnal’ geckos has also been observed for other members of the Hoplodactylus maculatus species complex (now Woodworthia spp.) from Stephens Island and Motunau Island (Werner and Whitaker 1978).

As well as basking flat on their abdomens, pregnant female geckos also exhibit an ‘on-toes’ basking behaviour in captivity, in which the legs of the gecko are extended and the abdomen is raised off the substrate (Fig. 1.2). This postural adjustment may be beneficial for a gecko trying to gain heat rapidly in the early morning by removing its abdomen from the cool substrate and pushing it towards a radiant heat source. It is unclear, however, whether pregnant females exhibit this ‘on-toes’ behaviour in the field and for how long.

The incidence and duration of basking in the field is unknown. It is unclear if basking behaviour differs between the sexes (females and males) or between reproductive conditions (reproductive females and non-reproductive females) in the field. In addition, the role of season and retreat type, on the basking behaviour of geckos is unknown.

This study describes a relatively novel way of studying reptile behaviour through the use of time-lapse photography. As Otago-Southland geckos are reclusive in nature, time-lapse photography was used to document diurnal activity of this gecko without the disturbance caused by human presence. In addition, temperature loggers inserted into copper models were used to simulate the thermal profiles of four behavioural positions available to geckos during the heating phase of the day (0600-1300 h). Loggers recorded operative temperature (T₀) – the Tb that is potentially available in a given
habitat (Huey 1991) – of models in two retreat types (deep crevices and under superficial rock) and models outside retreats in two basking behaviours (‘on-toes’ and flat basking). Together, the use of time-lapse cameras and temperature loggers provides insight into the diurnal behaviour of the ‘nocturnal’ Otago-Southland gecko.

The aims of this chapter were: 1) to describe diurnal emergence and basking behaviour in the apparently nocturnal Otago-Southland gecko, 2) to determine how basking behaviour differs between geckos from two thermally different retreat types (deep crevice and superficial rock retreats) and 3) to determine which position (‘on-toes’ versus flat) is more beneficial for geckos in terms of heating rate.

**Materials and Methods**

*Study site and species*

This study was carried out on private owned land near Macraes Flat, Eastern Otago, New Zealand. The habitat at Macraes Flat ranges from 600-710 metres above sea level and is characterized by rolling tussock grassland and schist rock outcrops (Fig. 2.1). At this site the Otago-Southland gecko is abundant and can be found in deep crevices within rock tors, in addition to under superficial rock slabs.
Sampling period rationale

Initially, field seasons were divided to incorporate the basking behaviour of early pregnant (the first, spring-summer season) and late pregnant (the second, autumn season) females. The ‘spring-summer’ season was planned to span from mid-October 2012 to late January 2013 and has been identified by previous studies as the period when reproductive females are in early pregnancy, from stages 1-25 (Cree 1994; Cree and Guillette 1995). The ‘autumn’ season was planned to span from February to April 2013. A previous study by Cree and Guillette (1995) demonstrated that during this period, biennially reproducing females are in mid-late pregnancy (stage 26-40 of embryonic development). However, I was unable to follow this schedule due to equipment malfunction in spring-summer. As a result, spring-summer extended from 20 October 2012 until 17 February 2013 (four months). This season encompasses stage 1-36 of embryonic development, approximately. The autumn season extended from 18 February 2013 until 25 April 2013 (over two months). During this period embryos were inferred to be close to, or fully developed, remaining in utero. Winter was excluded.
from this study as geckos retreat into inaccessible crevices (Rock et al. 2000; Rock and Cree 2003).

Site selection for time-lapse photography

In spring-summer cameras were set up from 19 October and 9 December 2012, while in autumn cameras were set up on 17 February and 24 March 2013. In spring-summer each camera site was selected according to one or more of the following criteria: 1) a minimum of two geckos were seen while searching for sites, 2) one of the geckos appeared to be a mature female and/or 3) evidence of geckos inhabiting the retreat e.g. fresh fecal matter or shed skin (Whitaker 1994b). For the first criterion, sites were checked for geckos by looking into deep crevices and under superficial rock retreats. Care was taken not to disturb the animals and the rocks were not moved. Due to fewer sightings of geckos in autumn, only the second criterion – sighting a mature female – was used when selecting camera locations. When selecting deep crevice camera sites, only horizontal crevices facing north to northwest were selected. This was due to the assumption that the positioning of the sun would enable solar energy to be available to geckos inhabiting northwest facing crevices during the morning and later in the afternoon. Deep crevices were visually identified as crevices with a minimum vertical rock depth of ≥300 mm. When selecting superficial rock slabs for camera sites a maximum rock thickness of 50 mm was required to classify the retreat as superficial. In autumn cameras were moved to an adjacent site. The GPS coordinates of each retreat site were recorded throughout the study. However, due to the increasing threat of poaching, no GPS coordinates are provided here.

Time-lapse photography

Two models of time-lapse cameras were used in this study: three TimelapseCam 8.0 (Wingscapes, USA) and three Scouting Camera UV565 “BLACK OPS” Series (UOVISION, Australia), attached to Moultrie Game 12 V PowerPanel (Moultrie Feeders, Australia). Each model type was part of a set; the TimelapseCam set were purchased in mid 2012, while in late 2012 the TimelapseCam set was no longer offered, therefore, the Scouting Camera set was purchased.
When purchasing the three Scouting Camera UV565 “BLACK OPS” Series, the supplier provided three 6 V solar panels (Solar Power Panel, UOVISION, Australia). This model of solar panel was sold as part of the Dual Pro-Cam Time Lapse Kit; however, the supplier did not properly match the solar panel and camera voltage. This resulted in two of the Scouting Cameras powered by the 6 V Solar Power Panel receiving the incorrect voltage, blowing the fuse of both cameras. This damaged the cameras beyond repair. The supplier replaced the two Scouting Cameras and supplied three new Moultrie Game 12 V PowerPanel at no additional cost. The broken cameras and inoperative solar panels led to many delays and over three weeks of data were lost in October and November 2012.

For the filming, retreat sites where pregnant females were likely to reside were monitored using time-lapse cameras for an initial period of seven days. These retreats were monitored before any attempt to capture and measure the animals was made, to ensure that habitat disturbance and handling did not have any major effects on the geckos’ behaviour (thus, if the retreats were later abandoned, there would still be data for the initial seven days).

Time-lapse cameras attached to posts were initially set up to record from 0600 h (in spring-summer sunrise was at c. 0600 h, whereas in autumn sunrise was at c. 0700 h) every day until 1200 h. During spring-summer the period that photographs were taken was extended to the afternoon (1400 h) as many geckos were still exhibiting flat basking at 1300 h. One frame was taken every minute and I assumed that behaviours observed during the film lasted for the full minute. The distance from the camera to retreat site was measured and coordinated with focus level for each location to ensure picture quality. The view finder was used to focus images on an area of approximately 2 m away, providing a field of view of 1×0.5 m surrounding the retreat. This allowed me to determine relationships between retreat type and the basking behaviours observed. Solar panels were either secured on the ground using rocks and duct tape or attached to the top of a post that supported the camera using cable ties (Fig. 2.2). Cameras were directed towards superficial rock (n=3) and deep crevice (n=3) retreats.
Figure 2.2. Time-lapse camera and solar panel set up at a superficial rock retreat in autumn.

In spring-summer camera interference by live stock led to data loss. Camera malfunction was predominantly through cows rubbing against camera posts, changing the cameras field of view away from the geckos retreat. This interference did not damage the camera or any equipment; however, while the cameras were filming within the paddocks with livestock, data was lost. The date and time of malfunction as well as an explanation for why the camera failed (if known) was noted.

Some decision criteria were put in place after both highly successful and unsuccessful filming. The criteria were as follows: 1) if examining the basking behaviour of geckos at a given site was successful, the filming period was extended for up to 50 days; 2) if a site was filmed for six days, including at least four days of sunny weather and no geckos were seen basking, the camera was shifted to a new location. After retreats were monitored for an average of c. 27 days (for both seasons), time-lapse cameras were then moved to additional sites for each retreat type in spring-summer. The same procedure was followed in autumn.
Capture methods and lizard measurements

Due to the changeable nature of the climate at this study site, the day that lizards were first caught and measurements taken was subject to extreme plasticity. Searching for animals commenced from between seven to twenty-four days after initial camera set up in spring-summer and between six to thirty-one days after initial camera set up in autumn. Catching geckos was carried out in teams of 2-4 people. During spring-summer one attempt was made to catch geckos at night using eye-shine. However, no geckos were seen active outside their retreats during this search and geckos seemed to remain in their retreats. This may have been due to cool night-time temperatures (<15°C).

A highly effective method of capture involved carefully lifting loose slabs and other cover objects during the day to capture geckos living under superficial rock slabs. Care was taken to replace rocks in their exact position in an effort to avoid modifying the precise physical characteristics of the habitat (McDiarmid et al. 2011). Habitat modification could make the site undesirable for geckos. This could occur through increasing the size of the crevice and thus the amount of wind entering the retreat (McDiarmid et al. 2011). Geckos were returned to their retreats after the rocks were properly replaced. Common skinks Oligosoma nigriplantare polychroma and McCann’s skinks O. maccanni encountered under rocks were removed, the rocks returned and individuals returned to their retreat. At Macraes Flat, both skinks and geckos live in sympatry and were often found in the same retreats.

Rock turning as the main capture method, however, could not be applied to individuals inhabiting crevices in large rock tors. For these geckos, individuals were noosed, one by one. The noose used in this study consisted of hollow aluminium tubing through which catgut (a tough-fibrous cord) formed a noose. The noose was slipped over the head of the gecko and the catgut pulled firmly. Simultaneously, a probe was used to gently touch the tail of the gecko to promote the emergence of the gecko from the crevice. The noose was used primarily to stop the geckos from escaping during the capture process, rather than to pull the animal out of the crevice. This is because geckos are likely to use their lamellae on their toes to form a tight grip on the surface rock making it difficult to extract them. Bottle brushes (dish cleaners) were strategically
CHAPTER TWO

placed into the crevice to prevent the geckos retreating deeper. Using bottle brushes was an effective method; however, many geckos eluded capture. Immediately upon capture geckos were put in a cloth bag and placed in a shaded area (Whitaker 1994b).

*Gecko morphometrics, sex and reproductive status*

Once caught, the morphological measurements of geckos were taken, sex (of mature geckos) identified and reproductive status inferred. A range of 68-85 mm snout-vent length was used to classify geckos as mature adults (Rock *et al.* 2000). Any geckos captured that were below this measurement were regarded as sub-adults; these individuals were not included in later analyses. The snout-vent length, vent-tail length and tail regeneration length of captured geckos was measured using a ruler. The sex of adults was apparent from the presence (male) or absence (female) of a hemipenial sac at the base of the tail (Robb 1986). The presence of cloacal spurs as well as large femoral and preanal pores were also used to sex individuals (Whitaker 1994b). These pores are found on the abdomens of both males and females; however, in males these pores are enlarged and are found in greater quantities and can be considered a secondary sexual characteristic (McDiarmid *et al.* 2011).

Some of the sites chosen for monitoring consisted of up to 15 individuals per crevice. As every individual was not able to be captured at each site, more focus was directed towards capturing pregnant females. The reproductive status of females was inferred through palpation of the abdomen as either: negative, vitellogenic, early-mid pregnant, late pregnant, or postpartum. Hard spheres within a female’s abdominal cavity were identified as vitellogenic follicles (Cree and Guillette 1995). After ovulation, the initiation of early pregnancy was apparent when the ova became softer with an oval shape (Cree and Guillette 1995). Late pregnancy was distinguished from early pregnancy as the form and movements of the embryos could be felt through the female’s abdominal wall (Cree and Guillette 1995; Wilson and Cree 2003). In addition, often the jaw of the neonate can be felt through the female’s abdominal wall. Postpartum females were identified by an apparent lack of vitellogenic follicles or ova (Cree and Guillette 1995). Postpartum females were differentiated from negative females as the skin around the abdomen of postpartum females was loose (A. Cree
Palpation has been identified by multiple studies as a non-invasive method of determining reproductive condition and is both safe for the gecko and provides accurate information about female reproductive status (Cree and Guillette 1995; Wilson and Cree 2003; Cree and Hare 2010). Palpation however, is a skill that requires knowledge of reproductive status, embryo form and function and is developed over time. In this study however, there was little time to learn how to accurately infer status in the field (and no examples of each of the reproductive statuses for comparisons at any one point in time), leading to inconsistencies in inferring female reproductive status. Due to inexperience in palpation, not all females could be reliably placed into groups in respect to reproductive status. For females I was confident of the palpation in spring (4 October until 29 December 2012), females were divided into two groups: reproductive females (late vitellogenic, early-late pregnant) and non-reproductive females (including negative and postpartum females). However, in summer and autumn, when palpation was sometimes inaccurate, all reproductive and non-reproductive females were pooled.

Gecko identification

After measurements were taken and reproductive status inferred, the geckos’ natural markings were photographed from several angles. Natural markings have been used for long-term identification for a number of reptiles (Whitaker 1994b; Knox et al. 2012). Using natural markings as identification proved to be a valuable way of classifying individuals both within and between videos. This allowed me to determine which geckos were active at the initial period of filming before disturbance when the geckos were handled and also to identify recaptures. An additional identification method involved marking geckos with unique symbols using a non-toxic (xylene free) permanent silver marker (Pilot, Super Colour, Permanent Type Ink). This symbol lasted until the geckos’ next moult and was an easy way to identify geckos in photos. Animals that were close to shedding were noted; this was evident as individuals close to shedding appeared pale and the outer layer of skin was loose (Robb 1986).

In a previous study, it was inferred that shuttling thigmothermy occurs between retreats within close proximity, allowing a gecko to attain $T_{\text{sex}}$ in a thermally stratified habitat
(Rock and Cree 2008). Thus geckos from retreats within a 5 m radius of the retreat that was being photographed were also captured. This ensured that geckos within the immediate vicinity could be identified and monitored if they were to venture into the camera’s field of vision. After measurements were taken, geckos were released and encouraged back into their retreat site.

**Time-lapse photography image analysis**

The data from the time-lapse cameras were viewed using Microsoft Office Picture Manager (2006, Microsoft Corporation). Images from each day were watched twice consecutively. In the case of camera malfunction, each film was watched once only. Camera and site information including the camera number, site code, day of filming and date were recorded during data entry. If geckos were observed the time, animal code, behaviour and duration of behaviour were also documented (both start and end time for each behaviour). Calculating the number of frames for each behaviour provided a quantitative measure of the duration (in minutes) a gecko displayed the behaviour. Additional comments on the weather and geckos’ behaviour were noted.

**Basking behaviour in the Otago-Southland gecko**

The behaviours of Otago-Southland geckos observed using time-lapse photography were defined as either basking behaviours or in-retreat activity (see ‘List of abbreviations’ for definitions). In some cases, geckos were often shown to exhibit both basking and in-retreat activity. In this situation, basking behaviours took priority and in-retreat activity was only recorded when the gecko was not exhibiting any basking behaviours. This allowed me to more easily tease apart basking behaviours and in-retreat activity. As it is unknown whether in-retreat activity has any biological relevance in this study, the results for all analyses of in-retreat activity are provided in Appendix 3.

The definitions of each of the basking behaviours are as follows: head basking was defined as either complete (with both sides) or incomplete (only one side) exposure of the head to direct sunlight. Abdomen basking was defined as the exposure of one side
of the abdomen to direct sunlight. This behaviour was often exhibited by females that pushed one side of their abdomen into the sun, whilst the rest of their body remained in the shade of the retreat. The side of the abdomen exposed to sunlight was recorded. Whole-body basking, unlike abdomen basking required both sides of the abdomen to be exposed to the sun. ‘On-toes’ basking involved the gecko straightening its legs, lifting its abdomen off the substrate. Behaviours were not all mutually exclusive and often co-occurred; therefore, at any given time a gecko could exhibit up to three of these behaviours. Only whole-body and abdomen basking could not co-occur as they both measure the amount of radiation the trunk is exposed to. For photographs of these behaviours, see Results.

Environmental temperature

Throughout the filming period operative temperature ($T_e$) was monitored using i-button temperature loggers (DS1921G, Maxim Integrated Products, San Jose, CA, USA) inserted into copper models. In this study copper models of the same shape, size and heat capacity of an average Otago-Southland gecko were used to work out $T_e$ in a range of habitats. Measurements used to construct these models represent the average body measurements of female Otago-Southland geckos from a captive population (originating from Macraes Flat) at the Department of Zoology, University of Otago. Measurements of $T_e$ provide meaningful information about the thermal environments available to a lizard through examining the thermal profiles of a model.

Models were made from 24 mm diameter copper pipe. Models were cut into 110 mm long sections, slightly flattened and painted brown (Café Royale; Resene, Wellington, New Zealand) to mimic the size and colour of geckos. The distal (head) end of the model was crimped closed. The same model design has been validated for McCann’s skink Oligosoma maccanni (Hare et al. 2009) and accurately simulates $T_b$. These models have also been calibrated against a freshly euthanised Otago-Southland gecko, where the temperature of the model ($T_e$) and gecko ($T_b$) were similar (A. Cree pers. comm.).
CHAPTER TWO

Temperature loggers were set to a precision of 0.5°C and recorded at a frequency of one temperature reading every ten minutes. Initially, loggers were set to record temperature at one minute intervals; however, this level of accuracy was unnecessary as the changes in temperature were minimal over such a short period. Temperature loggers were wrapped in Parafilm “M” (Pechiney Plastic Packaging, Chicago, IL. 60631) to make them waterproof (see Appendix 1 for evidence that parafilm did not affect $T_a$). Plastic disks were used to suspend loggers within the model to ensure the logger recorded internal air temperature rather than model surface temperature. Loggers were inserted 40 mm into the model through the open (tail) end. The model end was then sealed using an initial layer of electric tape, followed by a layer of duct tape.

The models were positioned to mimic two retreat types and two basking behaviours that can be used by geckos: 1) a retreat site in a deep crevice (n=4), 2) in a retreat site under a loose rock slab (n=4), 3) the surface of a sun-exposed rock (n=4) and 4) elevated above the rock to imitate the ‘on-toes’ basking behaviour (n=4). Four models (one of each model type) were grouped into a set. Each set represented the variation in temperature available to geckos that behaviourally thermoregulate during the day. Within a set, loggers were placed on the same rock outcrop and kept within a maximum distance of 5 m. For the first model type, models were wedged c. 100 mm into north/northwest facing deep crevices. For the second model type, models were placed under superficial rock slabs. For the models in retreats, care was taken to ensure that retreats were suitable for Otago-Southland geckos. This was determined by previous occupancy of geckos inferred through the presence of fecal matter and shed skin. These models were positioned to contact the upper and lower rock surface. The third and fourth types of model were attached to the surface of the rock using a combination of super glue and duct tape. Care was taken to minimise the use of duct tape on the model surface. As the fourth model was designed specifically to mimic the ‘on-toes’ behaviour, each model had four appendages representing the legs of a gecko (Fig. 2.3). The front legs were attached 25 mm from the crimped section at the top of the copper model (this section represents the head of a gecko), whereas the hind legs were attached 80 mm from the top. A hollow copper tubing (6.25 mm diameter) was used to construct 15 mm long appendages. The base of the tube was crushed and bent to form a foot (5×5 mm, W×L); this surface was later used to attach the model onto the rock.
Figure 2.3. ‘On-toes’ copper model showing the crimped head end of the model and open, un-sealed tail end. Models were constructed using measurements of a captive population of the Otago-Southland gecko at Otago University.

Copper models were put in the field on the 26 October 2012. Data from these models were collected and models replaced to their original position eight times before the final collection on 25 April 2013 when models were brought in from the field. The position of copper models in this study did not change; models remained at the same site over both spring-summer and autumn.

Habitat may account for some variation in temperature at each of the model sets. As each set of models (with one of each of the four model types) was located in the same area, to some extent it controlled for site variation within a model set. However, this could not be controlled for across model groups, as they were located in different regions. Care was taken to ensure that models were placed at northwest facing sites; however, there may have been some variation in the time when the sun first hits the models (or crevices within which they were placed).
Statistical analyses

The incidence of basking behaviour in the Otago-Southland gecko

Fisher’s Exact Tests were used to compare the incidence of basking (and in-retreat activity, see Appendix 3) between sexes (all females and males) in spring-summer and autumn and reproductive conditions (reproductive and non-reproductive females) in spring (4 October until 29 December 2012). As the main aim of this analysis was to identify whether differences existed between female and male basking, geckos from both (deep crevice and superficial rock) retreats were pooled. The effect of reproductive condition, comparing basking incidence of reproductive and non-reproductive females was also made for a subset of the spring data, where palpations were most accurate. Reproductive females included pregnant and vitellogenic females; while, non-reproductive females included females that were categorised as negative for their palpation. These comparisons were conducted using GraphPad (http://graphpad.com/quickcalcs/contingency1.cfm). Only P-values will be reported for this section as confidence intervals and odds ratios cannot be calculate for tests including zero values.

Effect of retreat type on basking behaviour

Linear models were used to determine whether retreat type influenced the basking behaviour of female Otago-Southland geckos (males were excluded from all analyses hereafter, as the proportion of males observed basking was low). For this analysis, time of day was pooled. Data were standardized to account for variations in the number of filming days, as well as the number of geckos at each site. This was calculated by adding each of the separate female behaviours to create a total length of behaviour (for all individuals) for each retreat type, then divided the total by the number of individuals, then by the total number of frames. The resulting number is an average duration of a gecko basking in a particular behaviour on one day (duration (minutes/day)). This value was then log transformed to make the data follow a normal distribution and fit the assumption of homogeneity. An additional set of statistical models examined the average duration of basking behaviour over the two seasons. For
this analysis, all behaviours were pooled to create an average basking duration for each habitat type.

*Effect of time of day on basking behaviour at different retreat types*

An additional set of linear models were used to discern the effects of time of day on basking behaviour at deep crevice and superficial rock retreats. The response variables appeared to have quadratic effects; therefore, linear models accounting for quadratic effects were used to determine how basking behaviour changed over a diel cycle. For this analysis, time was analysed as hours past sunrise (i.e. if sunrise is at 0630 h, the first time period would be from 0630-0729 h, the second time period would be from 0730-0829 h and so on until the last full hour of filming). Retreat type was included as a factor in the model. Similarly to the retreat analysis, behaviours were standardised for the number of individuals and filming days and log transformed. Results are reported as duration (minutes/hour). In addition, fine-scale differences between basking behaviours at the two retreat types were examined at individual hourly time periods. Two-way t-tests were used to determine if there was a difference between the average basking duration of individuals at the two retreat types for each time period.

*Temperature of copper models*

For temperatures of copper models, temperature data were analysed using linear models with quadratic terms. Temperature data were first divided into three bi-monthly periods, November-December 2012, January-February 2013 and March-April 2013. Data were then divided into basking days – days where geckos were seen actively thermoregulating outside their retreat and non-basking days – days were either no activity was observed, or only in-retreat activity was observed using time-lapse footage. Temperature data were examined from 0600 to 1300 h, in coordination with the timing of time-lapse photography. This period was chosen as it represents the heating phase of the day – the time in which the sun is first exposed to rocks that have just experienced low night-time temperatures. The copper models were the experimental unit for all statistical analyses. Statistical model estimates and the Akaike information criterion (AIC) were used to determine if the statistical models predictions matched the data’s
distribution. All statistical models were shown to accurately describe trends in the data. A subset of the statistical model estimates and AIC for days where geckos were seen basking in November-December 2012 is provided in Appendix 2 to demonstrate the model fitting procedure. The rate of heating was also calculated between 0600-0900 h to determine which type of copper model had the fastest heating rate in the early morning. The rate was calculated by dividing the change in temperature by the change in time.

For time-lapse photography, both the number of filming days and the number of geckos at each camera varied. To ensure that there was no pseudo-replication, precautions were taken and both the number of geckos at each camera and the number of days each site was monitored was controlled for in each analysis. Pseudo-replication of data were controlled for by taking averages across different individuals located at each camera and treating cameras (rather than geckos) as my experimental units for all analyses.

For statistical analyses all data were log transformed, but are shown as non-transformed values in figures. In addition, for both Effect of retreat type on basking behaviour and Effect of time of day on basking behaviour, results are shown in a similar manner to Avery (1978); results do not show the basking behaviour of an individual lizard, but averages across a population of lizards. Many individuals showed dramatically higher or lower durations of basking from this average value. Statistical analyses were preformed for in-retreat activity, results for these analyses are provided in Appendix 3. All analyses were conducted in the statistical program R 2.15.1 for Windows (CRAN, Auckland, New Zealand), unless stated otherwise.
Results

*General observations of basking behaviour in the Otago-Southland gecko*

Time-lapse photography revealed substantial evidence of diurnal basking in the Otago-Southland gecko. Over spring-summer and autumn, a total of 196 filming days, yielding 564,480 photographs were examined. Out of 202 geckos caught in the vicinity of the camera or identified by footage (including: 84 females, 26 males, 58 unknown sex and 34 juveniles), 68 different individuals were observed basking on film (including: 44 females, 4 males, 18 unknown sex and 2 juveniles); but only one gecko was ever directly observed basking by eye (L. Gibson *pers. obs.*).

Females (both reproductive and non-reproductive) and males were observed basking in spring-summer and in autumn. No juveniles were seen basking in spring-summer or autumn and only a few juveniles exhibited in-retreat activity; therefore, juveniles were excluded from subsequent analyses. Using photo identification (for known geckos) and the presence/absence of secondary sexual characteristics (for unknown geckos), I was able to calculate the sex ratio of all geckos seen on camera or captured. The sex ratio was 3:1 (females n=42: males n=14) in spring-summer and 3.13:1 (females n=25: males n=8) in autumn.

Geckos often switched between behaviours rapidly. The majority of basking bouts only lasted a few frames, followed by brief periods of in-retreat activity. Head basking was the most frequently observed behaviour for both females and males (Fig. 2.4 A). Head basking only lasted a few minutes and was usually observed before complete emergence. In spring-summer some males were observed remaining in their retreats for prolonged periods (2-47 minutes, with an average of seven minutes). These males were typically found at deep crevice retreats with many other geckos and appeared to be ‘scanning’. Scanning males moved their heads from side to side, watching from the safety of their retreat. Scanning may be a form of mate guarding, or could be a form of anti-predator behaviour (Plasman *et al.* 2007). This behaviour was not evident in females.
Figure 2.4. Time-lapse photographs of the basking behaviours of a female Otago-Southland gecko at Macraes Flat, Eastern Otago. The four different basking behaviours are: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ basking. Natural markings identified that these photos are all of the same female. The head of the gecko is indicated by a white arrow.

Some females also exhibited prolonged periods of whole-body basking (Fig. 2.4 B). This involved complete emergence from the retreat, with both sides of the abdomen exposed to the sun. In some cases, females remained in the same – whole-body – basking position for bouts exceeding an hour. Females that exhibited abdomen basking often swapped between basking each side of their abdomen for a few minutes at a time (Fig. 2.4 C). ‘On-toes’ basking often lasted for only a few frames at a time (Fig. 2.4 D). Females were often observed switching between flat whole-body basking (while their abdomen was flat on the substrate), into an elevated ‘on-toes’, whole-body basking posture. A shift in body weight from a flat basking position, to an abdomen raise, marked ‘on-toes’ basking. This study revealed a range of ‘on-toes’ behaviours. Some geckos exhibited ‘on-toes’ behaviour with partial, mid, or even complete straightening of their legs. In addition, ‘on-toes’ behaviour could also be exhibited in different
regions of the body. Some geckos were shown to exhibit ‘on-toes’ basking only in their fore limbs or hind limbs, raising the gecko’s shoulder or pelvic region above the substrate. All these variants of the ‘on-toes’ behaviour have been pooled in subsequent analyses.

While basking, geckos showed strong site fidelity and remained in close proximity to their retreats. Emergence from a retreat (deep crevice or superficial rock) was rarely greater than the snout-vent length of the gecko (Fig. 2.4 B). Often, geckos would only partially expose their bodies to radiation, while sheltered in their retreat (Fig. 2.4 C). Abdomen basking may be particularly important in areas of high predation risk as it allows geckos to achieve an elevated $T_b$ whilst remaining partially within a retreat. Many geckos exhibited more than one behaviour at a time. For example, females could exhibit both abdomen and ‘on-toes’ basking simultaneously (Fig. 2.4 D).

Throughout each day’s filming period, geckos were observed moving within retreats, as well as shuttling between retreats. Within the northwest facing deep crevices monitored, geckos were observed shuttling up to 1.27 m down the length of the crevice. In the early morning, when the sun penetrated into crevices, geckos basked within their retreats. However, later in the day, geckos ventured further out of their retreats to exploit the afternoon sun. Geckos also angled their bodies (in a similar posture to ‘on-toes’ basking), elevating one side of their abdomen off the substrate, through stretching both a fore limb and a hind limb on one side. Geckos also shuttled between retreats in close proximity to one another, especially between retreats with multiple rocks or crevices. For example, one female that was monitored in spring-summer consistently changed basking locations during the day. This female would bask at a superficial rock that provided early morning sun (the rear rock in Fig 2.5 A). Once the sun hit the front superficial rock, she moved to this rock where she would consistently bask for the remainder of the filming period (the front rock in Fig. 2.5 B).
Figure 2.5. Time-lapse photography of the daily movements of a female Otago-Southland gecko during spring-summer at Macraes Flat. Photograph A was taken at 9:04 am, whereas photograph B was taken at 12:10 pm on 13 November 2012. In photograph A the female is located under the ledge of the rear rock, while in photograph B the female is basking at the front superficial rock. Natural markings were used to confirm that photo A and B were of the same female. The head of the gecko is indicated by a white arrow.

In spring-summer two out of the three males observed basking had experienced tail loss, or caudal autotomy. One of the males had recently autotomized its tail and had a regeneration length of only 3 mm, while the other male had almost recovered from its last autotomy, with a regeneration length of 63 mm. The third male from spring-summer and the sole male from autumn observed basking had complete tails – where no breaks or regeneration were visible.
The incidence of basking behaviours in the Otago-Southland gecko

In spring-summer and autumn, the incidence of basking was higher for females (reproductive and non-reproductive combined) than for males (Fig. 2.6). In spring-summer females were significantly more likely than males to exhibit head ($P<0.01$; Fig. 2.6 A), whole-body ($P<0.01$; Fig. 2.6 B), abdomen ($P<0.01$; Fig. 2.6 C) or ‘on-toes’ ($P<0.05$; Fig. 2.6 D) basking. A less dramatic trend was evident in autumn. In autumn, the incidence of head basking was higher for females compared to males ($P<0.05$; Fig. 2.6 A). However, no males were seen in whole-body, abdomen or ‘on-toes’ basking positions in autumn. No differences between the incidence of whole-body ($P>0.05$; Fig. 2.6 B), abdomen ($P>0.05$; Fig. 2.6 C) or ‘on-toes’ ($P>0.05$; Fig. 2.6 D) basking were evident between females and males.
Figure 2.6. The incidence of basking behaviours of female and male Otago-Southland geckos in spring-summer and autumn. Each graph represents a separate basking behaviour: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ basking. ‘Percentage of geckos’ is the number of geckos that exhibited a behaviour (marked as present or absent) divided by the total number of geckos observed within a 5 m radius of each camera’s study area (this includes geckos that were caught, as well as those seen solely by time-lapse photography). Sample sizes are as follows for spring-summer, females n=42, males n=14; while in autumn females n=25, males n=8. Retreat types and reproductive conditions for females have been pooled. One asterisk (*) indicates statistical significance at $P<0.05$, whereas two asterisks (**) indicates significance at $P<0.01$. 

Percentage of geckos

<table>
<thead>
<tr>
<th>Season</th>
<th>A) Head</th>
<th>B) Whole-body</th>
<th>C) Abdomen</th>
<th>D) ‘On-toes’</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring-summer</td>
<td><img src="url" alt="Graph A) Head" /></td>
<td><img src="url" alt="Graph B) Whole-body" /></td>
<td><img src="url" alt="Graph C) Abdomen" /></td>
<td><img src="url" alt="Graph D) ‘On-toes’" /></td>
</tr>
<tr>
<td>Autumn</td>
<td><img src="url" alt="Graph A) Head" /></td>
<td><img src="url" alt="Graph B) Whole-body" /></td>
<td><img src="url" alt="Graph C) Abdomen" /></td>
<td><img src="url" alt="Graph D) ‘On-toes’" /></td>
</tr>
</tbody>
</table>
Basking behaviours of each sex were also compared between the two seasons. It was evident that a significantly higher percentage of females in spring-summer exhibited whole-body basking compared to autumn ($P<0.05$; Fig. 2.6 $B$). All other comparisons between seasons, however, were non-significant ($P>0.05$).

*The incidence of basking behaviour among reproductive and non-reproductive females in the Otago-Southland gecko*

Comparisons of the incidence of basking behaviour in a subset of data during spring, where palpations were considered most reliable/accurate, revealed that there were no significant differences between the behaviours of reproductive and non-reproductive females ($P>0.05$; Fig. 2.7). Therefore, reproductive and non-reproductive females have been pooled in the following analyses.
Figure 2.7. The incidence of basking behaviour of reproductive and non-reproductive female Otago-Southland geckos in spring (October-December 2012). Sample sizes are as follows, reproductive females n=13 and non-reproductive females n=8. Note that the sum of reproductive and non-reproductive females is not equal to the total sample size of females in spring-summer (Fig. 2.6). Only females of known reproductive condition (females that were caught and palpated) were included in this analysis. Retreat types for this analysis have been pooled. There were no significant differences between the basking behaviours of reproductive and non-reproductive females ($P>0.05$).

**Effect of retreat type on basking behaviour**

For both seasons, it was evident that retreat type did not have a strong effect on the behaviour of female Otago-Southland geckos when time of day (0600-1400 h) was pooled. The majority of comparisons made revealed no significant differences overall, between the basking behaviour of females from the two retreat types, in either season (Table 2.1).

In spring-summer, there were no differences between basking duration and retreat type for head ($t_{10}=-1.430$, $P>0.05$), whole-body ($t_{10}=-0.594$, $P>0.05$), abdomen ($t_{10}=-0.980$, $P>0.05$) or ‘on-toes’ basking ($t_{10}=0.114$, $P>0.05$; Fig. 2.8 A).
Figure 2.8. Average duration of basking behaviour of female Otago-Southland geckos photographed by time-lapse cameras at superficial rock (n=6) and deep crevice (n=6) retreats in A) spring-summer and B) autumn. Duration (mean ± 1 SE) of behaviour is shown in minutes out of a total of 480 minutes per filming day. Duration was standardized for both the number of lizards and number of photographs taken at each camera. There were no significant differences between the duration of basking behaviour between retreat types in spring-summer or autumn (P>0.05).

In autumn, no significant differences in the duration of female behaviour were detected for basking behaviour between the two retreat types (Fig 2.8 B). A trend was detected for abdomen basking, where the basking duration of geckos tended to be longer at superficial rock retreats, compared to deep crevice retreats (t_{10}=2.152, P=0.057). However, this was not statistically significant.

I also tested to see if on average there was a difference between the duration of all basking behaviours and retreat type (Fig. 2.9). In spring-summer there was no significant difference between basking duration at the two retreat types (t_{47}=-1.632, P>0.05). In autumn, there was a significant difference between the average basking duration between deep crevice and superficial rock retreats (t_{47}=2.456, P<0.05).
Females in autumn, unlike in spring-summer, basked for longer durations on average at superficial rock retreats (Fig. 2.9).

Figure 2.9. Average duration of basking (across all behaviours) of female Otago-Southland geckos photographed by time-lapse cameras at superficial rock (n=6) and deep crevice (n=6) retreats in spring-summer and autumn. Average Duration (mean ± 1 SE) of behaviour is shown in minutes out of a total of 480 minutes per filming day. Duration was standardized for both the number of lizards and number of photographs taken at each camera. One asterisk (*) indicates statistical significance at P<0.05.
Table 2.1. Probabilities for the effect of retreat type on duration of basking behaviour of female Otago-Southland geckos in spring-summer and autumn. The degrees of freedom ($df$), $t$-value ($t$) and $P$-values ($P$) are provided. The behaviours exhibited at each retreat type are head, whole-body, abdomen and ‘on-toes’ basking. ‘All behaviours’ compares the average duration (across all behaviours) between retreats. One asterisk (*) indicates statistical significance at $P<0.05$.

<table>
<thead>
<tr>
<th></th>
<th>Spring-summer df</th>
<th></th>
<th></th>
<th>Autumn df</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$t$</td>
<td>$P$</td>
<td></td>
<td>$t$</td>
<td>$P$</td>
<td></td>
</tr>
<tr>
<td><strong>Head</strong></td>
<td>10</td>
<td>-1.430</td>
<td>0.183</td>
<td>10</td>
<td>1.320</td>
<td>0.216</td>
</tr>
<tr>
<td><strong>Whole-body</strong></td>
<td>10</td>
<td>-0.594</td>
<td>0.566</td>
<td>10</td>
<td>1.302</td>
<td>0.222</td>
</tr>
<tr>
<td><strong>Abdomen</strong></td>
<td>10</td>
<td>-0.980</td>
<td>0.350</td>
<td>10</td>
<td>2.152</td>
<td>0.057</td>
</tr>
<tr>
<td><strong>‘On-toes’</strong></td>
<td>10</td>
<td>0.114</td>
<td>0.912</td>
<td>10</td>
<td>1.923</td>
<td>0.083</td>
</tr>
<tr>
<td><strong>All behaviours</strong></td>
<td>47</td>
<td>-1.632</td>
<td>0.109</td>
<td>47</td>
<td>2.456</td>
<td>0.018*</td>
</tr>
</tbody>
</table>

Effect of time of day on basking behaviour at different retreat types

In spring-summer the basking behaviours of females over the filming period were significantly longer at deep crevice retreats overall, compared to superficial rock retreats, for head ($t_{66}=2.781, P<0.01$; Fig. 2.10 A), whole-body ($t_{66}=2.451, P<0.05$; Fig. 2.10 B) and abdomen ($t_{66}=2.487, P<0.05$; Fig. 2.10 C) basking. There were no significant differences between retreat types for ‘on-toes’ basking over time ($t_{66}=0.837, P>0.05$; Fig. 2.10 D).
Figure 2.10. Effect of time of day on basking behaviour of female Otago-Southland geckos from deep crevice and superficial rock retreats in spring-summer (October 2012 – February 2013). Each graph represents a separate basking behaviour: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ basking. Dark lines with diamond icons (♦) represent the average basking duration at deep crevice retreats (cameras n=6), while light grey lines with square icons (■) represent superficial rock retreats (cameras n=6). Means are ± 1 SE. One asterisk (*) indicates statistical significance at \( P<0.05 \) for comparisons between retreat types at individual time periods.

There was a significant increase in basking duration over time for geckos in deep crevices for head (\( t_{66}=3.948, P<0.001 \); Fig. 2.10 A), whole-body (\( t_{66}=3.489, P<0.001 \); Fig. 2.10 B) and abdomen basking (\( t_{66}=2.416, P<0.05 \); Fig. 2.10 C). However, there were no significant changes in duration for ‘on-toes’ basking over time for females in deep crevice retreats (\( t_{66}=0.516, P>0.05 \); Fig. 2.10 D). There were no significant changes in the basking duration of female geckos over time for any behaviour at superficial rock retreats (\( t_{66}<2, P>0.05 \)). In addition, basking duration at deep crevice...
CHAPTER TWO

retreats for head and whole-body basking had significant negative quadratic effects ($t_{66} \geq -2.311, P \leq 0.05$). In the early morning, head and whole-body basking duration increased, with a peak in average basking duration four hours past sunrise, followed by a decrease in basking duration in the early afternoon. Abdomen basking at deep crevice retreats appeared to show a quadratic effect; however, this was not quite significant ($t_{66} = -1.959, P = 0.054$). No quadratic effects were evident for ‘on-toes’ basking at deep crevice retreats ($t_{66} = -0.330, P > 0.05$) or any basking behaviour at superficial rock retreats ($t_{66} < 2, P > 0.05$).

Behavioural results were separated and analysed in hourly time periods (Table 2.2; Fig. 2.10). In spring-summer one hour after sunrise, head basking at superficial rock retreats was significantly longer than at deep crevice retreats; while five hours after sunrise head basking at deep crevice retreats was significantly longer in duration. The same trend was evident for both whole-body and abdomen basking, where basking was significantly longer at superficial retreats in the early morning (whole-body basking – two hours past sunrise and abdomen basking – one hour past sunrise), yet later in the afternoon, basking at deep crevice retreats was significantly longer (abdomen basking – five hours past sunrise). There appeared to be a longer duration of ‘on-toes’ basking at superficial rock retreats two hours after sunrise; however, this was not significantly different from the basking duration at deep crevice retreats.
Table 2.2. Significance of retreat type on average basking duration in relation to time of day. Time intervals are shown in hours past sunrise. Significant differences ($P<0.05$) are denoted by an asterisk (*), with probabilities shown to three decimal places. Dashed cells (-) do not have a $P$-value as behaviours were not seen at this time period.

<table>
<thead>
<tr>
<th></th>
<th>Spring-summer</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hours past sunrise</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td><strong>Head</strong></td>
<td></td>
<td>0.045*</td>
<td>0.323</td>
<td>0.425</td>
<td>0.082</td>
<td>0.026*</td>
</tr>
<tr>
<td><strong>Whole-body</strong></td>
<td></td>
<td>0.143</td>
<td>0.027*</td>
<td>0.784</td>
<td>0.061</td>
<td>0.275</td>
</tr>
<tr>
<td><strong>Abdomen</strong></td>
<td></td>
<td>0.036*</td>
<td>0.373</td>
<td>0.700</td>
<td>0.309</td>
<td>0.019*</td>
</tr>
<tr>
<td>‘On-toes’</td>
<td></td>
<td>0.247</td>
<td>0.057</td>
<td>0.300</td>
<td>0.216</td>
<td>0.624</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Autumn</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Hours past sunrise</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
</tr>
<tr>
<td><strong>Head</strong></td>
<td></td>
<td>0.428</td>
<td>0.224</td>
<td>0.061</td>
<td>0.109</td>
<td>0.203</td>
</tr>
<tr>
<td><strong>Whole-body</strong></td>
<td></td>
<td>0.341</td>
<td>0.341</td>
<td>0.164</td>
<td>0.495</td>
<td>0.615</td>
</tr>
<tr>
<td><strong>Abdomen</strong></td>
<td></td>
<td>0.397</td>
<td>0.158</td>
<td>0.087</td>
<td>0.075</td>
<td>0.371</td>
</tr>
<tr>
<td>‘On-toes’</td>
<td></td>
<td>0.341</td>
<td>0.095</td>
<td>0.178</td>
<td>0.341</td>
<td>0.247</td>
</tr>
</tbody>
</table>

During autumn, basking was less frequent (Fig. 2.11). For basking behaviours in autumn there were no significant differences between the duration of behaviours at the two retreat types over the filming period for all comparisons ($t_{66}<2$, $P>0.05$; Fig. 2.11). ‘On-toes’ basking at deep crevice retreats was the only behaviour that decreased significantly over time ($t_{66}=2.184$, $P<0.05$; Fig. 2.11 $D$). In addition, this was the only behaviour that appeared to have a negative quadratic effect close to statistical significance ($t_{66}=-1.950$, $P=0.055$). There were no other significant differences in basking over time for head, whole-body or abdomen basking, at deep crevice or superficial rock retreats ($t_{66}<2$, $P>0.05$). In autumn there were no significant differences between basking duration and retreat type for individual time periods (Table 2.2).
Figure 2.11. Effect of time of day on basking behaviour of female Otago-Southland geckos from deep crevice and superficial rock retreats in autumn (February – April 2013). Each graph represents a separate basking behaviour: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ basking. Dark lines with diamond icons (♦) represent the average basking duration at deep crevice retreats (cameras n=6), while light grey lines with square icons (■) represent superficial rock retreats (cameras n=6). Means are ± 1 SE. There were no significant differences in basking duration between deep crevice and superficial rock retreats at individual time periods (P>0.05).

**Temperatures of copper models**

Within copper model types, models followed a similar pattern irrespective of time period (Fig. 2.12). The models in retreats (superficial rock and deep crevice) and those in basking positions (flat and ‘on-toes’) followed two distinctive thermal profiles. Basking models started the day with significantly lower temperatures than retreat models and increased rapidly over time, consistently reaching higher temperatures than
retreat models ($t_{16}>2, \ P<0.05$). The temperatures of the retreat models did not change significantly over time and showed only a small increase in temperature throughout the day ($t_{16}<2, \ P>0.05$).

Figure 2.12. Copper model temperature profiles of four different positions available to geckos in the field for basking (A, C, E) and non-basking days (B, D, F) for three bi-monthly periods. Each data point represents an average temperature over days and model replicates. Means are ± 1 SE for n=4 models per position. Error bars have been offset for clarity.
There was a consistent trend over the three bimonthly periods for both basking and non-basking days. The flat and ‘on-toes’ basking models reached significantly higher temperatures compared to the deep crevice and superficial rock retreat models for all comparisons ($t_{116} \geq 2.180$, $P \leq 0.05$).

I also examined the heating profiles of each model type by looking for linear and quadratic changes in model temperature over time (Table 2.3). For basking and non-basking days in November-December, there were significant increases in model temperature over time for flat and ‘on-toes’ basking models ($t_{116} \geq 6.630$, $P < 0.001$; Fig. 2.12). In addition, both basking models also showed a positive quadratic effect over time ($t_{116} \geq 4.679$, $P < 0.001$). However, neither the deep crevice nor the superficial rock retreat models, showed a significant change in temperature over time as either a linear or quadratic effect ($t_{116} < 2$, $P > 0.05$). For both basking and non-basking days in January-February, the temperature of flat and ‘on-toes’ basking models increased significantly over time ($t_{116} \geq 3.538$, $P < 0.001$; Fig. 2.12). There were no significant quadratic effects for any model type ($t_{116} < 2$, $P > 0.05$). For basking days in March-April, both basking models tended to increase in temperature over time, however this was not statistically significant ($t_{116} < 2$, $P > 0.05$; Fig. 2.12). The superficial rock retreat model was the only model to show a significant change in temperature over time as a positive quadratic effect on both basking and non-basking days ($t_{116} \geq 2.358$, $P < 0.05$).
Table 2.3. Statistical probabilities for the significance of changes in temperature of copper models in basking positions (flat or ‘on-toes’) and in-retreats (in deep crevices or under superficial rocks) over the heating phase (0600-1400 h) of the day. Data were first divided into three bi-monthly periods: November-December 2012, January-February 2013 and March-April 2013, then into basking and non-basking days. Statistical results for the linear and quadratic response of temperature to copper model type are shown for each model position. Linear responses to temperature were observed as a steady increase or decrease in temperature over time. Quadratic responses to temperature were observed as a bell shaped curve, where temperature increased, levelled off and then decreased. One asterisk (*) indicates statistical significance ($P<0.05$). $P$-values are shown to three decimal places.

<table>
<thead>
<tr>
<th>Period</th>
<th>Model type</th>
<th>Basking days</th>
<th>Non-basking days</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Linear</td>
<td>Quadratic</td>
</tr>
<tr>
<td>November-December</td>
<td>Flat basking</td>
<td>&lt;0.001*</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td>2012</td>
<td>‘On-toes’ basking</td>
<td>&lt;0.001*</td>
<td>&lt;0.001*</td>
</tr>
<tr>
<td></td>
<td>Deep crevice retreat</td>
<td>0.697</td>
<td>0.613</td>
</tr>
<tr>
<td></td>
<td>Superficial rock</td>
<td>0.248</td>
<td>0.819</td>
</tr>
<tr>
<td></td>
<td>retreat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>January-February</td>
<td>Flat basking</td>
<td>&lt;0.001*</td>
<td>0.124</td>
</tr>
<tr>
<td>2013</td>
<td>‘On-toes’ basking</td>
<td>&lt;0.001*</td>
<td>0.068</td>
</tr>
<tr>
<td></td>
<td>Deep crevice retreat</td>
<td>0.526</td>
<td>0.231</td>
</tr>
<tr>
<td></td>
<td>Superficial rock</td>
<td>0.792</td>
<td>0.283</td>
</tr>
<tr>
<td></td>
<td>retreat</td>
<td></td>
<td></td>
</tr>
<tr>
<td>March-April 2013</td>
<td>Flat basking</td>
<td>0.243</td>
<td>0.418</td>
</tr>
<tr>
<td></td>
<td>‘On-toes’ basking</td>
<td>0.182</td>
<td>0.637</td>
</tr>
<tr>
<td></td>
<td>Deep crevice retreat</td>
<td>0.322</td>
<td>0.136</td>
</tr>
<tr>
<td></td>
<td>Superficial rock</td>
<td>0.139</td>
<td>0.013*</td>
</tr>
<tr>
<td></td>
<td>retreat</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The heating rate for each model was calculated between 0600-0900 h (Table 2.4). The flat basking model showed the fastest heating rate out of all model types. The deep crevice model showed the slowest heating rate for both basking and non-basking days.
For all comparisons, the heating rate of the flat basking model was significantly faster than the heating rates of the deep crevice ($t_{116}=4.637, P<0.01$) and superficial rock models ($t_{116}=4.061, P<0.01$). The ‘on-toes’ model also heated significantly faster than the deep crevice ($t_{116}=4.477, P<0.01$) and superficial rock retreat models ($t_{116}=3.901, P<0.01$). However, there was no significant difference between the heating rates of the flat and ‘on-toes’ basking model ($t_{116}=0.160, P>0.05$), or between the deep crevice and superficial rock retreat models ($t_{116}=0.576, P>0.05$).

Table 2.4. Rate of temperature increase / hour for four types of copper models from 0600 to 0900 h. Rates were calculated for three time periods of the year and for basking and non-basking days. Means are ± 1 SE for n=4 models per position.
Discussion

*Basking behaviours in the Otago-Southland gecko*

Time-lapse photography revealed that the Otago-Southland gecko does indeed bask. In addition, time-lapse cameras uncovered considerable variation in the basking behaviours exhibited by Otago-Southland geckos. The single sighting of a gecko basking in the field by a researcher reinforces the reclusive nature of this gecko. Time-lapse photography proved to be an invaluable method of studying diurnal behaviour. The main thermoregulatory mechanisms identified in this study are sporadic periods of direct basking, postural adjustments and retreat type.

My hypothesis that females will have a higher incidence of basking than males in both spring-summer and autumn, was supported. The incidence of basking for females (pooling reproductive and non-reproductive females) was higher than that for males in both seasons. The fact that a higher incidence of females basked suggests that females may require an elevated $T_b$ compared to the $T_b$ of males in the field. In a previous study the $T_{sel}$ of pregnant female Otago-Southland geckos was up to 8°C higher than the $T_{sel}$ of non-pregnant conspecifics (Rock et al. 2000). Therefore, females (both reproductive and non-reproductive) may bask overtly to achieve a higher $T_{sel}$ in the field. Males are only occasionally observed basking and may have lower thermal requirements.

My hypothesis that reproductive females, but not non-reproductive females and males will exhibit ‘on-toes’ basking in both spring-summer and autumn, was not supported. Both reproductive and non-reproductive females had a similar incidence of ‘on-toes’ basking. In addition, in spring-summer two males that had recently autotomized tails were also observed basking ‘on-toes’.

In the Otago-Southland gecko, thermoregulation appears to be the driving force for the postural adjustments observed in the field. Postural adjustments in reptiles can be used to display to individuals of the same or different species (Brattstrom 1974; Gans et al. 1984; Gillingham et al. 1995), or they can be used as a thermoregulatory mechanism (Kearney 2001; Rock et al. 2002). It is unclear whether ‘on-toes’ basking in this study had a social aspect.
This study revealed a range of ‘on-toes’ behaviours. In the laboratory pregnant females bask ‘on-toes’, with their dorsal surface exposed to the heat lamps (Rock and Cree 2003). When completely emerged, ‘on-toes’ basking minimises heat loss through conduction with the substrate, while maximizing heat gain through solar radiation. Unlike flat basking, where the abdomen is in contact with the substrate, ‘on-toes’ basking allows geckos to thermoregulate irrespective of substrate temperature. The type and duration of ‘on-toes’ basking however, appears to differ between geckos in the laboratory and the field. In the laboratory, some pregnant females have been observed basking ‘on-toes’ with complete limb extension (A. Cree pers. comm.; Fig. 1.2). However, no geckos were observed with complete limb extension in the field. In the field some females showed a variant of the ‘on-toes’ behaviour with only the back legs raised. This resembles what has been previously noted as a birthing posture (A. Cree pers. comm.). Furthermore, females would switch between flat basking and ‘on-toes’ basking, thus, ‘on-toes’ basking typically only lasted a few frames in the field; whereas it can last for up to 60 out of 75 filming minutes in certain laboratory situations (A. Cree pers. comm.). The ‘on-toes’ behaviour exhibited in the field may differ to those exhibited in the laboratory as Otago-Southland geckos are not exposed to convective heat loss in the form of wind (Pianka and Vitt 2003). Therefore, it may not be as beneficial for females in the field to raise their abdomen as high off the substrate, compared to females in the laboratory. Females in the field may gain similar thermoregulatory advantages from an ‘on-toes’ basking posture with a lesser raise, compared to laboratory females. These differences in postural adjustments between females in the laboratory and the field, may relate to the different costs and benefits of basking. For example, elevating the abdomen off the substrate may increase the risk of predation and/or be energetically expensive, thus females in the field may not expose themselves as much, or elevate their abdomen as high as females in the laboratory.

The effects of predation pressure on basking behaviour in the Otago-Southland gecko are unknown. Predators were infrequently observed during the six months of fieldwork; however, there were sightings of feral cats at the study site (L. Gibson pers. comm.). Potential predators of Otago-Southland geckos at Macraes Flat include raptors (Australasian harriers Circus approximans, New Zealand falcons Falco novaesslandiae), mustelids (ferrets Mustela furo, stoats M. erminea and weasels M.
nivalis), rodents (Kiore Rattus exulans, the Norway rat R. norvegicus, ship rat R. rattus and house mouse Mus musculus), as well as feral cats (Felis catus), hedgehogs (Erinaceus europaeus) and skylarks (Alauda arvensis). The high proportion of potential predators at Macraes Flat may influence gecko emergence and basking behaviour.

Geckos exhibited ‘on-toes’ postures in their retreats. In spring-summer both sexes were shown to exhibit ‘on-toes’ in-retreat activity, whereas in autumn, only females exhibited ‘on-toes’ in-retreat activity (see Appendix 3). In a previous study, the mean temperature of top rocks was almost always higher than the mean temperature of bottom rocks, which ranged from 15-24°C and from 13-17°C, respectively (Rock et al. 2002). While in a retreat, geckos can press the dorsal surface of the abdomen up against rocks above, reducing conduction through the ventral surface to the cool substrate below. Rock et al. (2002) noted that pregnant females were able to maintain higher $T_b$ than non-pregnant conspecifics experiencing the temperature of the bottom rock substrate (Rock et al. 2002). This suggests that compared to other reproductive conditions, pregnant females expose only a small proportion of their bodies to the substrate below, thus are less affected by substrate temperature (Rock et al. 2002). This suggest that ‘on-toes’ in-retreat activity may be important for not only exposing their dorsal surface to warm rocks, but also removing their ventral surface from cool rocks. As this behaviour was seen predominantly in females (with one male exhibiting ‘on-toes’ in-retreat activity in spring-summer), this behaviour appears to be female biased.

My hypothesis that reproductive females will have a higher incidence of basking compared to non-reproductive females, was not supported. There were no differences between the basking behaviours of reproductive and non-reproductive females in spring, as both reproductive and non-reproductive females showed similar basking behaviours. This suggests that the behaviour of reproductive and non-reproductive females may not be as different as previous studies have thought.

Previous studies have documented substantial overlap in $T_b$ between reproductive conditions (Rock and Cree 2008). Non-reproductive females may select temperatures that are intermediate to those of reproductive females and males. In the viviparous skink Bassiana duperreyi, non-pregnant females have a higher $T_{sel}$ on a laboratory thermal gradient compared to males, whereas, the $T_{sel}$ of non-pregnant females more
closely resembles the $T_{set}$ of pregnant females (Shine 2006). In a more recent study, field $T_b$ of the Otago-Southland gecko was studied using radio telemetry at hourly periods for five days in late summer – early autumn (Rock and Cree 2008). Pregnant females had higher $T_b$ compared to males, yet there were no differences between pregnant and non-pregnant females or between non-pregnant females and males (Rock and Cree 2008).

Similarities in basking behaviour between reproductive and non-reproductive females may be due to similar thermal requirements. Both reproductive and non-reproductive females require basking, yet this may be for different physiological reasons. Each major stage in the reproductive cycle (including the transitional period between reproductive cycles) has an argument for high energy requirements. During vitellogenesis, energy is required to yolk large vitellogenic follicles (Rock et al. 2000), that are high in fats and nutrients (Avery 1974). For postpartum females, energy is required to gain back the energy used on the last set of offspring and prepare for the next reproductive cycle (Bleu et al. 2012). Due to these explanations, I propose that it is equally important for non-reproductive females to bask and this is the main reason why reproductive and non-reproductive females were pooled.

My hypothesis that a higher incidence of basking will be observed in spring-summer compared to autumn, for both females and males, was not supported. There was a higher incidence of whole-body basking for females in spring-summer compared to autumn. However, this trend was not evident for any other behaviour for females or males. Even though these differences in basking incidence were not significant, there tended to be a higher incidence of basking in spring-summer. A higher incidence of basking in spring-summer could be due to changes in the environment with the onset of cooler months in autumn. As both sexes basked less in autumn, a reduction in basking could also be due to seasonal changes in behaviour. A previous study suggested that in spring-summer, after a long winter torpor, geckos may become heat-seeking (Rock et al. 2000). In autumn, geckos may become less active preparing for winter torpor.
CHAPTER TWO

**Effect of retreat type on basking behaviour**

My hypothesis that the duration of basking will be longer for females inhabiting deep crevice retreats than those from superficial rock retreats in both spring-summer and autumn, was not supported. When time of day was pooled, microhabitat did not affect basking behaviour. Instead, females from both deep crevice and superficial rock retreats displayed similar durations of basking behaviours. The basking duration of female geckos was then analysed in hourly periods (in *Effect of time of day on basking behaviour*). Once separated into hours past sunrise, it was evident that the basking duration was longer for females at deep crevice retreats for head, whole-body and abdomen, basking compared to superficial rock retreats in spring-summer. However, there were no differences between basking duration and retreat types for ‘on-toes’ basking in spring-summer, or for any behaviour in autumn.

The thermal environment and subsequently the ability of a gecko to reach $T_{\text{sel}}$ may differ between deep crevice and superficial rock retreats and gecko may select retreats for their thermal benefits and thermoregulate accordingly. Females were predicted to emerge and to bask for longer durations at deep crevice retreats, due to limited opportunity to reach $T_{\text{sel}}$ within deep crevices; while, females inhabiting superficial rock retreats were predicted to remain in their retreats for longer durations, as they may be able to achieve $T_{\text{sel}}$ more readily. Subsequently, retreat type may be particularly important for geckos to avoid reaching critical highs and overheating. In spring-summer, flat basking copper models exposed to direct sunlight reached afternoon temperatures exceeding 40°C (*pers. obs.*). Such temperatures would considerably surpass the mean maximum $T_{\text{sel}}$ of 28°C of the Otago-Southland gecko under laboratory conditions (Rock *et al.* 2000). A previous study on seasonal patterns of retreat-site selection in the marbled gecko *Christinus marmoratus*, suggested that geckos may not remain in one retreat type year round and shift from rocks in spring, to deep crevices in summer (Kearney 2002). The absence of seasonal retreat-type selection could result in freezing over winter, or overheating in summer. It is probable that Otago-Southland geckos move between retreat types to cope with season changes; however, as it was not in the scope or time-frame of this study, long-term habitat use was not examined here.
We may not see any difference in the basking behaviours of gecko in autumn, as the Otago-Southland gecko may be able to thermoregulate irrespective of retreat type. In a previous study on retreat type selection, the thick-tailed gecko *Nephrurus milii* showed a strong preference for narrow warm retreats that enhanced thermoregulatory opportunity (Shah et al. 2004). There was, however, no evidence of *N. milii* selecting thinner rocks in the laboratory (Shah et al. 2004). While rock thickness may be an important factor for thermoregulation in the field, this result suggests that geckos of this species are able to thermoregulate effectively in a variety of retreats (Shah et al. 2004). This relationship between retreat type and thermoregulatory opportunity for the Otago-Southland gecko, like *N. milii*, may not be as clear cut as previously thought. Collectively, these results may mean that retreat type either has little influence on thermoregulation, or has unexpected influences on thermoregulation.

*Effect of time of day on basking behaviour at different retreat types*

When time was included in the retreat analysis, the true trends of basking behaviour at deep crevice and superficial rock retreats became clear. My hypothesis that all basking behaviours (including the ‘on-toes’ behaviour), would be most commonly seen in the early morning and would decrease throughout the day until early afternoon, was not supported. The first set of linear models revealed that there were no differences between behaviour at the two retreat types over time. However, visualising the data revealed that the behaviour at these two retreat types did change over time; however, this change was not linear. Using both linear and quadratic terms provided a more detailed analysis of the change in basking duration over time. The negative quadratic effect observed for head and whole-body basking in spring-summer suggests that there is an optimal basking duration in-between two suboptimal zones. For example, short basking durations in the early morning may be a result of cool night-time temperatures. While geckos forage at night-time temperatures as low as 10-13°C (Werner and Whitaker 1978), activity in the early morning may be limited by these cool temperatures. A few hours of sunshine in the early morning may enable geckos to reach $T_{set}$ and sustain activity throughout the morning. Four hours after sunrise basking durations were highest. After this peak, there was a rapid drop-off in basking duration.
This rapid decrease in basking duration may be a mechanism for geckos to avoid overheating during the warmest period of the day (early afternoon). A previous study noted a similar triphasic diel pattern of $T_b$ for the Otago-Southland gecko between 0630-1930 h (Rock and Cree 2008); this may directly relate to the pattern of basking behaviour observed in this study.

*Temperature of copper models*

Temperature loggers revealed that a wide range of $T_e$ were available to lizards in basking positions and in retreat sites. My hypothesis that copper models in deep crevice and under superficial rock retreats will experience little thermal variability, with warm early morning temperatures and only a small increase in temperature throughout the heating phase, was supported. The models in deep crevices showed the highest early morning temperatures and the lowest afternoon temperature in all comparisons. The models in superficial rock retreats were slightly cooler in the early morning compared to models in deep crevices and reached higher temperatures than models in deep crevices in the early afternoon. In addition, models in retreats had a slower heating rate from 0600-0900 h and had less thermal variability compared to the models in basking positions.

Operative temperature ($T_o$) data obtained from the copper models demonstrated that deep crevice and superficial rock retreats have slightly different thermal profiles during the heating phase. Deep crevices were thermally buffered; while, superficial rocks showed large temperature fluctuations over the course of a day (Appendix 4). At superficial rock retreats geckos may require longer durations of basking due to cool night-time temperature. While at deep crevice retreats geckos may be active in their retreats for longer durations, as deep crevices retain heat.

Geckos may use a variety of retreats for different thermal advantages on a scale as short as a day (Rock *et al.* 2002). Superficial rock retreats provide greater opportunities for thermoregulation during the day and geckos can reach a higher $T_b$ without emerging from their retreat. Although deep crevices are cool during the day and heat slowly, they offer an important night-time retreat. These data suggest that it may be beneficial for
geckos to retreat into deep crevices during the night as they provide a thermal buffer from environmental extremes (Pianka and Vitt 2003), while during the day, geckos can bask and shuttle between retreats with different thermal qualities to achieve $T_{\text{sel}}$ (Rock and Cree 2008). Shuttling between areas with the greatest thermoregulatory opportunity would maximise the amount of heat a lizard can achieve over a diel cycle. This strategy of utilising different retreats for different thermoregulatory benefits may be a reason why the Otago-Southland gecko can remain active at cool temperatures and therefore, inhabit a temperate environment such as Macraes Flat.

My hypothesis that copper models in the ‘on-toes’ and flat basking positions will experience the greatest thermal variability, with lower temperatures in the early morning and higher temperatures in the early afternoon, than models in retreats, was supported. In November-December and in January-February, the models in flat and ‘on-toes’ basking positions showed the lowest early-morning temperatures – with the models in flat basking positions commencing the heating phase with the coolest early morning temperatures. In March-April, temperature responded in a similar way over time; however, no statistical trend was evident. The models in basking positions achieved the highest early-afternoon temperatures, compared to models in retreats.

Using a combination of $T_{\text{sel}}$ and $T_e$ measurements, we can infer the optimal basking times for reptiles – i.e. when we would expect geckos to bask. In the Otago-Southland gecko, using both $T_e$ and the observations from Effect of time of day on basking behaviour, this optimal time appears to be from 1200-1300 h. During this time, geckos in flat basking positions should be able to reach a $T_{\text{sel}}$ of up to 28°C (Rock et al. 2000; Rock et al. 2002). Models in ‘on-toes’ basking positions in November-December, just fall short of reaching 28°C, yet in January-February and March-April, models in ‘on-toes’ positions reach a maximum temperature of 28°C.

My hypothesis that copper models in ‘on-toes’ positions would achieve warmer temperatures in the early morning while the rocks are cool, and cooler temperatures in the early afternoon once the rocks have warmed, compared to models in flat basking positions, was not supported. In the early morning models in flat and ‘on-toes’ basking positions achieved similar temperatures, while in the early afternoon, models in flat basking positions tended to be warmer. In most comparisons, there were no differences
between the temperatures of the two models in basking positions in the early afternoon. However, on basking days in January-February and March-April and on non-basking days in March-April, models in flat basking positions reached higher temperatures than models in ‘on-toes’ positions.

The ‘on-toes’ basking behaviour was predicted to be beneficial to reproductive females as it permits thermoregulation in the early morning, without conforming to the temperature of the substrate (such as in flat basking). The lack of a tangible difference in model heating rates in the field was particularly interesting, as these models target different heating routes. Models in ‘on-toes’ positions heat by solar radiation and gain only a small amount of heat through conduction. In contrast, models in flat basking positions gain heat by solar radiation, as well as conduction. For models in flat basking positions conduction has a large contribution to $T_c$ and once the substrate has heated models in flat basking positions consistently achieved higher afternoon temperatures than any other model type. A similar relationship between $T_b$ and degree of substrate contact, is evident in the zebra-tailed lizard *Callisaurus draconides*; lizards in prostate (flat basking) positions had the highest heating rate, whereas lizards in the elevated (‘on-toes’) position had the lowest heating rate (Muth 1977). This similarity between copper models and thermoregulatory behaviour in lizards, implies that the flat basking models achieve higher temperatures, yet lizards still bask ‘on-toes’; the purpose of ‘on-toes’ basking may, therefore, be not as predicted – to gain heat rapidly in the morning – and may have other behavioural or physiological significance.

*A new activity pattern for the Otago-Southland gecko?*

Given the evidence provided by this thesis, it is no longer appropriate to label the Otago-Southland gecko as solely ‘nocturnal’, as previous studies have (Cree *et al.* 2003; Wilson and Cree 2003). However, some studies have reached a consensus that the Otago-Southland gecko is not solely nocturnal and basks overtly in the laboratory (Rock and Cree 2003; Preest *et al.* 2005) and at least occasionally in the field (Rock and Cree 2008; Besson *et al.* 2009). Recent studies have tried to avoid imprecisely labelling this species by classifying it as primarily or partially nocturnal (Rock and Cree 2008; Cree and Hare 2010).
CHAPTER TWO

This study provides clear evidence that the Otago-Southland gecko is active diurnally. Geckos are active both within their retreats and emerge from their retreats to bask overtly; thus, I propose the use of diurno-nocturnal to best describe the activity pattern of the Otago-Southland gecko.

Recommendations for future research

The foremost limitation of this research was the sample size. In spring-summer and autumn more females were caught or observed basking compared to males. There are two potential reasons for this: 1) the population is female biased (fewer males) or 2) the population ratio is equal yet males are cryptic and difficult to catch. Care was taken to try and capture every gecko within the cameras vicinity, however many geckos in this study were not captured and therefore could not be sexed or their reproductive status inferred. In addition, in spring the sample size of reproductive and non-reproductive females was limited by the accuracy of palpation. For future research, a larger sample size may permit more accurate comparisons between the basking behaviour of females in different reproductive conditions. Future laboratory studies examining intraspecific differences in basking behaviour may provide exciting opportunities for future research and could control for the uneven sex ratio observed in the field.

Could time-lapse photography be used to monitoring other species?

Time-lapse photography proved to be an invaluable method for studying diurnal behaviour in the Otago-Southland gecko. The application of this technology extends far beyond the scope of my study species and has the potential to study the ecology and life history of many free-living reptiles. Behavioural studies on cryptic species such as the tuatara Sphenodon punctatus and the harlequin gecko Takutuku rakiurae, provide exciting opportunities for future research. As both S. punctatus (Gillingham and Miller 1991; Gillingham et al. 1995) and T. rakiurae (McFarlane 2007; Lindsey and Morris 2011) show diurnal and nocturnal activity, much of these species ecology and life history is unclear. In addition, little is known about the prolonged reproductive cycle of T. rakiurae, in which females produce offspring every two to three years (triennial).
CHAPTER TWO

Time-lapse photography may bring us one step closer to understanding how reptiles in temperate climates can achieve successful pregnancies. In addition, future research on other Woodworthia species (previous members of the H. maculatus species complex) located throughout New Zealand may provide valuable insight into the effects of climate on basking behaviour. It would be of interest to determine if differences in climatic conditions affect the basking behaviour of common geckos from the north island compared to geckos from the south island.

What are the thermal advantages of basking in the field?

This study revealed that Otago-Southland geckos bask overtly and exhibit a range of basking behaviours. The ‘on-toes’ basking behaviour was of particular interest in this study. Temperature data from models in ‘on-toes’ and flat basking positions suggested that there were no differences between model temperatures or heating rates. However, as this study did not measure gecko $T_b$, the thermal benefits for geckos in these basking behaviours are unknown. The use of infra-red photography in unison to time-lapse photography could allow us to compare the thermal benefits of ‘on-toes’ basking, to other basking behaviours in the field. In addition, as all reproductive conditions and sexes exhibited ‘on-toes’ basking, the physiological mechanism(s) driving ‘on-toes’ basking are currently unclear. Field studies measuring the $T_b$ of geckos in both ‘on-toes’ and flat basking positions, may identify the thermoregulatory (and possibly physiological) advantages underlying this behaviour.

What physiological mechanisms drive males with autotomized tails to bask?

The subject of male basking poses many questions and provides exciting opportunities to examine the effects of induced caudal autotomy (tail loss) in a controlled environment. It would be beneficial to determine if all males with recent autotomies basked. If so, it would also be of interest to determine if males follow a similar basking cycle to females (both pregnant and non-pregnant) and whether they are able to achieve similar $T_b$ as reported for pregnant females (Rock et al. 2000). Future research experimentally manipulating the effects of tail loss may provide rewarding results
(Bateman and Fleming 2009) and aid in our understanding of how autotomy affects basking behaviour.

*Are there any differences between diurnal and nocturnal activity?*

As the thermal profiles of the four copper model types were only examined in respect to the timing of time-lapse photography, there is still much to be learnt about the thermal advantages and disadvantages of basking positions and retreat types. As many reptiles exhibit diurno-nocturnal activity patterns, the focus of studies needs to shift from primarily examining diurnal activity to a combination of diurnal and nocturnal activity. It would be informative for researchers to distinguish between the energetic costs of diurnal and nocturnal activity and determine if any activities are confined to specific periods. For example, to our knowledge foraging in the Otago-Southland gecko is confined to night time activity, yet locomotion and emergence occurs both during the day and the night.

**Conclusion**

This chapter provides evidence that the Otago-Southland gecko is active diurnally and should be henceforth referred to as diurno-nocturnal. In the field, geckos exhibited sporadic periods of direct basking, postural adjustments and variation in basking duration between retreat types. Research delving into the $T_b$ of geckos in these behaviours in the field is needed to determine the thermoregulatory advantages of these three aspects of diurnal thermoregulation. In conclusion, this chapter has made headway for research on the diurnal behaviour of a reclusive gecko; these techniques can be use to examine the behaviour of other cryptic species in future studies.
Chapter Three

Challenges associated with the definition of activity patterns in lepidosaurian reptiles: a review using New Zealand species as examples

Introduction

Some lepidosaurian reptiles (squamate and rhynchocephalian reptiles) rely on external heat sources to achieve body temperatures ($T_b$) that are optimal for physiological performance (Davenport 1992; Seebacher and Franklin 2005). As there is considerable variation in environmental temperature over a diel cycle (2400 h), daily fluctuations in $T_b$ (Sheeba et al. 1999) are positively correlated with activity (Bennett 1982); therefore, reptile $T_b$ influences the timing of activity. Activity patterns – also known as activity cycles (Pianka and Vitt 2003) – are a form of circadian rhythm and are used to define reptile activity over a diel cycle (McDonald 1976; Underwood 1992). These patterns remain stable while maintained in a constant – aperiodic – environment (Sheeba et al. 1999), suggesting that they are driven by endogenous (internal) factors (Underwood 1992).

In previous studies, the activity of reptiles has been predominantly described as ‘diurnal’ or ‘nocturnal’, where activity is restricted to the photophase or the scotophase, respectively (Hare 2005). However, many species do not fit these strict criteria (Werner and Whitaker 1978; Rock and Cree 2008). Additional terms including crepuscular, diurno-nocturnal and cathemeral have also been used to describe more ambiguous activity patterns. Yet, there is little consensus over the use of these terms in herpetology.

Despite the challenges associated with labelling reptiles by activity pattern, it is important to be able to categorise reptile activity patterns. Knowledge of activity patterns is particularly important as: 1) the activity patterns of reptiles have several implications related to the time of day an animal is studied (Terezow et al. 2008). For
example, researchers should focus on studying the behaviour of an animal during their activity period(s). For example, as tuatara *Sphenodon punctatus* exhibit both diurnal and nocturnal activity, previous studies examining the behaviour, $T_b$ and activity pattern of tuatara, have been performed over 2400 h (Saint Girons *et al.* 1980; Barwick 1982; Terezow *et al.* 2008). 2) Activity patterns can have implications for conservation management and captive management procedures (Gillingham and Miller 1991; Goetz and Thomas 1994). Behavioural patterns of activity should be taken into account before any form of conservation management is carried out. For example, as territorial behaviour can be classified as a type of activity (Vitt *et al.* 2003), it is important to know if reptiles are territorial and if so, to determine how many can be safely housed together. In addition, some lepidosaurs only mate when conditions are appropriate, as is reflected by a lack of mating for some lepidosaurs held in captivity (Gillingham and Miller 1991). 3) Knowledge of activity patterns may allow us to predict how reptiles will respond to dramatic changes in climate (Meiri *et al.* 2013). The conservation of some species may be affected by climate change. For example, nocturnal lizards are less affected by changes in $T_b$ than diurnal lizards, as nocturnal lizards have greater metabolic stability and lower thermal sensitivity (Hare 2005). Consequently, nocturnal lizards may be affected by processes such as climate change in different ways than diurnal reptiles and thus may require different approaches to management.

This review examines the existing literature on activity patterns of lepidosaurian reptiles. First, I define activity and activity patterns. I then review definitions that have been used to describe lepidosaurian reptile activity patterns since Cowles and Bogert’s (1944) seminal paper on the thermal biology of desert reptiles, which marked the start of modern-day herpetology. I then address some of the terms currently used to describe activity patterns. I identify some of the problems associated with the labels currently used in herpetology, including behavioural differences during activity and intraspecific differences in activity between sexes, reproductive conditions and age classes. I then consider the activity patterns of New Zealand species and look specifically at three species commonly labelled as nocturnal and provide suggestions on the most suitable label for each. As the literature on activity patterns in New Zealand lepidosaurs is limited, I review a wider scope of studies to evaluate how researchers may be able to
use technological advances to study reptile activity patterns in the future. Finally, I conclude this review with some recommendations for future research.

How are activity and inactivity defined?

In the past, ‘activity’ has been defined as any form of behaviour exhibited by a reptile outside its retreat (Huey 1982). Types of activity commonly studied in reptiles include thermoregulatory behaviour (Bustard 1967; Werner and Goldblatt 1978), movement (Frankenberg 1978), retreat emergence (Walls 1983) and foraging behaviour (Bustard 1967). These forms of activity entail costs such as increased predation risk, intraspecific encounters and water and energy expenditure; whereas, benefits associated with activity include increased chances of finding mates, access to food and opportunities for thermoregulation (Huey 1982). Activity is favoured when the benefits of activity outweigh the costs (Gans and Pough 1982). For example, a diurnal heliotherm will thermoregulate during the day when the benefits of basking are high and will return to a retreat when the costs of sustained activity during the night outweigh the benefits (Gans and Pough 1982).

As reptiles cannot maintain constant activity over a diel cycle, they often experience periods of inactivity, intended for sleep and torpor (Pianka and Vitt 2003). To establish patterns of reptile activity we need to identify signs of inactivity, such as reduced metabolic rate and physiological depression (Zug 1993). In the past, inactivity has been classified by observations alone (Frankenberg 1978); however, activity cannot be accurately defined without comparisons between metabolic rate during resting and activity (Bennett 1982).

Previous studies have mainly studied reptile activity by examining one aspect of their behaviour or physiology (Frankenberg 1978; Werner and Goldblatt 1978; Arad et al. 1989). However, more recent studies have reached a consensus that activity can have a wide variety of different contexts (Zug 1993; Pianka and Vitt 2003). To distinguish between periods of activity and inactivity researchers need to take a quantitative approach to examine reptile behaviour and ecology in both laboratory and field based studies (Bennett 1982).
Activity patterns in lepidosaurian reptiles: two ends of a spectrum

As ectotherms, lepidosaurs exhibit daily fluctuations in their physiology and behaviour (Pianka and Vitt 2003). These fluctuations are driven by endogenous (internal) factors (Underwood 1992). Endogenous rhythms arise through the temporal organisation of biological processes into a ‘biological clock’ (Underwood 1992). Activity patterns are a form of endogenous rhythm (Underwood 1992), that can be studied over a diel cycle. The activity patterns of a reptile is constrained by time and is dependent on an animal’s response to temperature and photoperiod (Pianka and Vitt 2003). As activity patterns are closely linked to \( T_b \) (Zug et al. 2001), changes in temperature modify the time window within which reptiles can be active (Pianka and Vitt 2003). This response permits physiological and behavioural adjustments, in anticipation of environmental change (Sheeba et al. 1999). Activity patterns are also dependent on a variety of ecological factors (Adolph and Porter 1993). Intrinsic factors that affect activity include age (juveniles and adults), diet and reproductive condition (e.g. pregnant versus non-pregnant females), whereas extrinsic factors include environmental factors such as prey availability (Llewelyn et al. 2005). Collectively, these factors influence the timing of activity over a diel cycle (Llewelyn et al. 2005).

A brief history of the definitions used to describe the activity patterns of lepidosaurs

One of the most influential studies on reptile thermoregulation paved the way for future studies examining reptile physiology and behaviour (Cowles and Bogert 1944). Cowles and Bogert (1944) described the ‘normal activity range’ (defined as a mean \( T_b \) predicted to represent a physiologically optimal temperature) of desert reptiles through measuring the \( T_b \) of 18 species of desert squamates. Reptiles were described as diurnal or nocturnal; however, the activity of some desert snakes was described as both nocturnal and crepuscular (active during the twilight) (Cowles and Bogert 1944). Following this study, many researchers described reptile activity in terms of circadian rhythms (McDonald 1976) and activity times (Gans and Pough 1982) as either diurnal or nocturnal. Spellerberg (1982) described reptile activity as diurnal or nocturnal; however, he implied that many animals stray away from these strict labels and coined some species as ‘mainly nocturnal’ (active during twilight and night). A study by
Pianka (1973) standardized the times of activity for diurnal species as ‘time since sunrise’ and for nocturnal species as ‘time since sunset’. Pianka (1973) suggested that these broad categories corrected for (seasonal) difference in activity pattern over time. In recent volumes of the *Biology of the Reptilia* series, lepidosaur activity patterns (referred to as time of activity and activity rhythms) were described as either diurnal or nocturnal (Huey 1982; Underwood 1992). In the first edition of *Herpetology: an introductory biology of amphibians and reptiles*, the activity cycles of reptiles were described as diurnal, nocturnal, or crepuscular (Zug 1993). However, in later issues, the term crepuscular is used sparingly and is only used to describe the nocturnal and crepuscular tendencies of sand boas (Boidae) (Zug *et al.* 2001), night lizards (Xantusiidae) and rosy boas (Boidae) as nocturnal and crepuscular foragers (Vitt and Caldwell 2013). A recent work acknowledged that variation in reptile activity patterns does exist and that not all species are diurnal, nocturnal or crepuscular, but can be a combination of these (Pianka and Vitt 2003).

In the scientific literature on reptiles, the term diurno-nocturnal has rarely been used. To the best of my knowledge, only a handful of studies dating back to 1978 have used this term to describe reptile activity during both the day and the night (Frankenberg 1978; Werner and Whitaker 1978). The term cathemeral – random or sporadic periods of activity during both the day and night – has been used even less frequently than diurno-nocturnal to describe reptile activity patterns. Since the initial proposal of the term cathemeral in 1979, it has been primarily used to describe the activity of primates (Tattersall 1987); however, it has recently been applied to reptiles to describe activity during both the day and the night (Meiri *et al.* 2012; Meiri *et al.* 2013). The categories diurnal, nocturnal and crepuscular have remained relatively consistent over the last 69 years since Cowles and Bogert’s (1944) influential paper. The term diurno-nocturnal has been applied to several species, however, this term has been infrequently used to describe reptile activity patterns in recent studies. Conversely, cathemeral has – to my knowledge – only been used in the context of reptiles twice, in large-scale studies.
Definitions and examples of current labels used to describe the activity patterns of lepidosaurs

Reptiles experience peaks in activity during periods where environmental temperature is optimal for physiological performance (Pianka and Vitt 2003). These peaks are typically either unimodal – where activity peaks at one point in time over a diel cycle, bimodal – where activity peaks twice, or they can be multimodal – with several peaks in activity over a diel cycle (Foà et al. 1994). Activity distributions are commonly split into diurnal and nocturnal unimodal distributions, crepuscular bimodal distributions and diurno-nocturnal and cathemeral multimodal distributions (Fig. 3.1). For example, Kluge’s dwarf gecko *Lygodactylus klugei* is a diurnal heliotherm that basks overtly during the day (Vitt 1986). As a result of day-time activity, heliotherms maintain high day-time $T_b$ (Adolph and Porter 1993; Belliure and Carrascal 2002), yet they are exposed to suboptimal night-time temperatures. On the other end of the continuum, the leopard gecko *Eublepharis macularius* is a nocturnal thigmotherm, that is restricted to night-time activity and remain within retreats during the day (Autumn and De Nardo 1995; Belliure and Carrascal 2002). Within the genus *Sphaerodactylus* the activity patterns of many species are described as crepuscular. For example, the gray gecko *Sphaerodactylus cinereus* (Dunson and Bramham 1981) and the lesser Antillean dwarf gecko complex, *Sphaerodactylus fantasticus* (Thorpe et al. 2008), exhibit a crepuscular activity pattern. These geckos are commonly active in the twilight – during the rising of the sun at dawn and the setting of the sun at dusk (Dunson and Bramham 1981).
CHAPTER THREE

Figure 3.1. Hypothetical diel activity of lepidosaurs illustrating five different activity patterns. Shaded bars indicate the timing of activity over 2400 h.

The classification of diurnal, nocturnal and crepuscular activity, however, does not encompass the true complexity of activity patterns in lepidosaurs. Some reptiles labelled as nocturnal, including *E. macularius*, select for higher temperatures than are available during their activity period. Many studies provide evidence that ‘nocturnal’ reptiles actively thermoregulate during the day to reach higher $T_b$ than is available in their activity period (Cowles and Bogert 1944; Autumn and De Nardo 1995; Kearney and Predavec 2000). As a result of thermoregulatory activity during the day, some ‘nocturnal’ lepidosaurs have been described as diurno-nocturnal (Werner and Whitaker 1978) or cathemeral (Meiri *et al.* 2013). The differences between diurno-nocturnal and cathemeral activity, are more ambiguous and subjective compared to the differences between diurnal, nocturnal and crepuscular activity. The term diurno-nocturnal suggests that lizards are active both during the day and the night and has been used sparingly to describe reptiles in historical studies. For example, movement in the Moorish wall gecko *Tarentola mauritanica* is described as diurno-nocturnal (Frankenberg 1978); whereas, the thermoregulatory behaviour – examined through measurements of selected body temperature ($T_{sel}$, preferred body temperature in a laboratory thermal gradient) – of the fan-fingered gecko *Ptyodactylus hasselquistii guttatus* has been described as diurno-nocturnal, where geckos thermoregulate during both the day and night (Werner
and Goldblatt 1978; Arad et al. 1989). The term cathemeral has been used to describe the activity pattern of primates exhibiting relatively equal periods of activity during the day and night (Tattersall 1987). Cathemeral has only been recently applied to reptiles (Meiri et al. 2012; Meiri et al. 2013). For example, some studies have labelled some of the species in the family Helodermatidae as cathemeral (Hall 2008; Hall 2009), as a result of both diurnal and nocturnal activity (Pianka and Vitt 2003).

Activity patterns in New Zealand lepidosaurs

New Zealand lepidosaurs exhibit a range of activity patterns; these range from diurnal heliotherms and nocturnal thigmotherms, to species with combinations of diurnal and nocturnal behaviour. Within the family Diplodactylidae, *Naultinus* geckos are diurnal heliotherms; whereas geckos in the genera *Dactylocnemis, Toropuku, Mokopirirakau, Tukutuku, Hoplodactylus* and *Woodworthia*, are commonly considered as nocturnal thigmotherms (Nielsen et al. 2011). Within the family Scincidae, skinks in the genus *Oligosoma* are diurnal heliotherms (Hare et al. 2007a). The sole representative of the family Sphenodontia, the tuatara *S. punctatus* has been commonly regarded as nocturnal (Sharell 1966; Goetz and Thomas 1994). However, some studies have referred to the activity pattern of *S. punctatus* as diurno-nocturnal (Werner and Whitaker 1978; Besson and Cree 2011).

New Zealand lepidosaurs are susceptible to challenges associated with defining activity patterns. As New Zealand is a temperate climate, there is little opportunity for thermoregulation during the night; therefore, the ‘nocturnal’ status given to many reptiles, poses many questions about day-time behaviour. The Otago-Southland gecko *Woodworthia* “Otago/Southland”, harlequin gecko *Tukutuku rakiurae* and tuatara *S. punctatus* are three species that are commonly labelled as ‘nocturnal’, yet all three have been observed to some degree to be active during the day, basking in the sun.

Previous studies have labelled the Otago-Southland gecko as either nocturnal (Rock et al. 2002; Wilson and Cree 2003) or primarily nocturnal (Cree 1994; Rock et al. 2000; Gaby et al. 2011). One study labelled the *Hoplodactylus maculatus* species complex, including the Otago-Southland gecko as diurno-nocturnal (Werner and Whitaker 1978).
This gecko is active nocturnally and often emerges from its retreat to feed on nocturnal insects – similarly to other species in the genus Woodworthia (Gill and Whitaker 1996; Lindsey and Morris 2011). While, many studies have focused on diel patterns in Tb between sexes and reproductive conditions (Rock et al. 2000; Rock et al. 2002; Rock and Cree 2008), the diurnal behaviour of this gecko has received little attention. This thesis provides quantitative evidence that it is no longer appropriate to label the Otago-Southland gecko as solely nocturnal (Chapter 2). As Otago-Southland geckos are active diurnally and emerge from their retreats to bask during the day, I therefore suggest that this species shows a diurno-nocturnal activity pattern.

Some information is available on the activity pattern of the harlequin gecko T. rakiurae (previously Hoplodactylus rakiurae; Nielsen et al. 2011). The harlequin gecko was discovered in 1969 (Gill and Whitaker 1996), but not formally described until 1981 (Thomas 1981) due to its cryptic nature and restriction to the southern regions of Stewart Island (Whitaker 1994a; McFarlane 2007). The activity pattern of the harlequin gecko is currently unknown and the few studies describing activity patterns of the harlequin gecko have labelled this species as nocturnal (Gill and Whitaker 1996; Hitchmough et al. 2010). However, this gecko frequently basks in the sun during the day (Hitchmough et al. 2010) and has been observed foraging during the day and the night (Whitaker 1994a; Lindsey and Morris 2011). Similarly to the Otago-Southland gecko, the harlequin gecko may require diurnal basking to achieve optimal Tb and may also be better described as having a diurno-nocturnal status. The use of the term diurno-nocturnal to describe activity pattern has been supported by two herpetologists who have worked with harlequin geckos in the field (M. Tocher pers. comm.; L. Moran pers. comm.).

The tuatara S. punctatus is New Zealand’s most iconic species and the only living representative of the rhynchocephalian reptiles (Bogert 1953). This species was formally described in 1842 (Gray 1842) and has received much scientific attention in recent times (Terezow et al. 2008; Besson and Cree 2010; Hay et al. 2010). Previous studies have labelled the tuatara as nocturnal and noted both diurnal and nocturnal activity (Sharell 1966; Saint Girons et al. 1980; Goetz and Thomas 1994; Gill and Whitaker 1996). Tuatara commonly sun bask during the day (Barwick 1982; Mello et
al. 2013), but also emerge during the night (Gill and Whitaker 1996; Terezow et al. 2008). However, only a handful of studies have acknowledged these sightings and labelled *S. punctatus* as diurno-nocturnal (Werner and Whitaker 1978; Besson and Cree 2011).

**Why is defining reptiles as solely diurnal or nocturnal uninformative? New Zealand lepidosaurs as an example**

Previous studies have often classified activity pattern in a binary way (Jaksić et al. 1982; Vitt and Vangilder 1983; Vitt 1986; Autumn and De Nardo 1995), that can be attributed to differences in the way a reptile responds to photoperiods (Pianka and Vitt 2003). Some examples of ‘strictly diurnal’ or ‘strictly nocturnal’ activity do exist. For example, the Marlborough green gecko *Naultinus manukanus* is strictly diurnal, with no evidence of nocturnal activity (Hare et al. 2007b). The activity pattern of the Marlborough green gecko was defined using an extensive data set of mark-recapture and population surveys, captive rearing of juveniles and radio telemetry, from over the last 25 years (Hare et al. 2007b).

Current labels of reptile activity pattern, however, are restrictive (Hare 2005) and fail to incorporate the complexity of ectotherm activity. Many species do not fit the criteria of strictly diurnal or strictly nocturnal and the majority of species show a combination of diurnal and nocturnal activity. The classification of activity pattern is, in fact, a continuum between nocturnal and diurnal (Vitt et al. 2003). Similarly, heliothermy and thigmothermy are also extremes at each end of the spectrum of reptile thermoregulation (Pough et al. 2001) and reptiles may use any combination of these two mechanisms to thermoregulate (Autumn and De Nardo 1995; López et al. 1998; Rock and Cree 2008). Some reptiles labelled as nocturnal are active during the day and thermoregulate through both heliothermic and thigmothermic means. For example, members of the *Hoplodactylus maculatus* species complex (including the Otago-Southland gecko), have been previously labelled as nocturnal, yet they bask during the day (Werner and Whitaker 1978). In addition, some reptiles labelled as diurnal are also active at night. This includes two species of skink, *Oligosoma striatum* and *Oligosoma zelandicum*, which are active when temperature permits activity, irrespective of time of day (Neilson
These two species are currently labelled as diurnal (Neilson et al. 2004); however, strictly speaking this label cannot encompass the true behavioural complexity of these species (Hare 2005).

The use of diurnal and nocturnal to describe species activity may be used as a general guideline to provide information about the different routes of heat exchange. For example, researchers commonly associate the thermoregulatory mode of heliothermy with diurnal species – as they bask overtly (Huey 1982) and thigmothermy with nocturnal species – as they are secretive and remain in their retreats during the day (Garrick 2008). However, to be categorised as completely nocturnal (or diurnal), activity should not occur outside of the defined activity period.

Using current definitions for activity patterns, thermoregulation by nocturnal reptiles during the day is not defined as activity. However, many reptiles have been shown to be actively thermoregulating while they were predicted to be inactive (Kearney 2001; Rock and Cree 2008) and some nocturnal reptiles thermoregulate during the day while in their retreats through microhabitat choice and postural adjustments (Werner and Whitaker 1978; Huey 1982; Kearney and Predavec 2000; Kearney 2001; Rock and Cree 2008), yet they are commonly defined as inactive. One common misconception is to assume that inactive reptiles are thermally passive, with little to no control over $T_b$ (Huey 1982). Yet reptiles that appear to be inactive may be actively thermoregulating.

In addition, what is the thermoregulatory mode of a species that is not completely diurnal, or completely nocturnal? Does this mean that every species that is not strictly diurnal or nocturnal is diurno-nocturnal, or cathemeral? To accurately describe reptile activity we may need to modify the way we think about thermoregulation and activity patterns. In many cases, I suggest that diurnal and nocturnal are inappropriate labels that lead to inaccurate assumptions about thermoregulatory mode. Either, a consensus for the definition of activity patterns needs to be reached, or a new method of classification that accurately describes activity pattern is needed. A reclassification of activity patterns may allow us to define specific activities and provide us with more meaningful information about reptile life-history.
Through describing the various behaviours in which an animal is active during different periods, we may be able to better understand the flexible nature of activity patterns in reptiles. A more informative way to describe activity patterns may be through describing different activities. For example, a species may be active both diurnally and nocturnally, however, the way in which it is active – and the behaviours it exhibits during these times – may differ (Pianka and Vitt 2003). For example, to my knowledge foraging is confined to night-time activity in the purportedly nocturnal Otago-Southland gecko (Lindsey and Morris 2011). In contrast to a previous study that stated that individuals of the Otago-Southland gecko were dormant in their retreats during the day (Spencer and Grimmond 1994), my research revealed that geckos are diurnally active in their retreats and exhibit discreet periods of basking (pers. obs.). Subsequently, the Otago-Southland gecko may be a nocturnal forager, yet it thermoregulates diurnally.

*Are activity patterns the same for all individuals within a species? New Zealand lepidosaurs as examples*

A new method of describing activity patterns to examine intraspecific differences in behaviour would allow us to better understand how reptiles change in response to their environment. In the past, the activity patterns of individuals within a species were said to be the same (Robb 1986); however, this may not be the case for many lepidosaurs, as previous studies have acknowledged intraspecific differences in activity pattern between sexes (Rock et al. 2000; Sun et al. 2001; Rock et al. 2002), reproductive conditions (Rock et al. 2000) and age classes (Zug 1993; Sun et al. 2001; Webb and Whiting 2005). In this section I will use the Otago-Southland gecko and tuatara as examples to demonstrate intraspecific differences in activity (the harlequin gecko will not be included in this section due to insufficient data).

A difference may exist between the activity patterns of males and females. My research suggests that for the Otago-Southland gecko different sexes exhibit different activity patterns and may carry out different behaviours at certain times of day (see Chapter 2). Time-lapse cameras were used to examine emergence and show footage of males active at the mouths of crevices, in full shade, whilst females at the same site actively basked.
Thus, during the day, both females and males may be active, yet the way they are active differs. Female Otago-Southland geckos had a higher incidence of basking, therefore they may sit closer to the diurnal end of the diurnal-nocturnal spectrum, compared to males. This underlies the idea that differences exist not only between populations of the same species, but also between sexes within a population (Rock et al. 2000).

Differences between male and female activity have also been noted for the courtship displays of tuatara. Male tuatara exhibit extensive series of courtship displays in which they elevate the trunk off the substrate into a ‘press up’ position, inflating spines on the dorsal crest and colour darkening around the shoulders and eyes in an attempt to attract females (Gillingham et al. 1995). Males then approach females in a flamboyant gait known as the ‘stolzer Gang’; receptive females proceed to mating following male displays, while non-receptive females retreat (Gillingham et al. 1995). In this situation male tuatara exhibit extensive displays and longer periods of activity, compared to females.

In addition, many viviparous species undergo behavioural changes during pregnancy that may affect activity pattern. For example, pregnant female Otago-Southland geckos had a $T_{sel}$ of up to 8°C higher than that of non-pregnant females and males (Rock et al. 2000). My research identified no differences in basking behaviour between different reproductive conditions (reproductive and non-reproductive females). However, a previous study on the Otago-Southland gecko compared field $T_b$ of pregnant females, non-pregnant females and males and found that pregnant females had a higher thermoregulatory precision (higher thermoregulatory effectiveness), compared to males (Rock et al. 2002). Yet, there were no differences between the thermoregulatory precision of pregnant and non-pregnant females (Rock et al. 2002). In this situation, differences in thermoregulatory precision were related to differences in sex, rather than reproductive condition.

It is also possible that within a species there are marked differences between the activity patterns of adults and juveniles. This difference may be a result of intraspecific competition and/or to avoid cannibalism of juveniles by adults (McIntyre and Robertson 1997). It is often very difficult to study juvenile activity and behaviour due to the cryptic nature and low detectability of juveniles (Shine et al. 2002). As juveniles
heat faster than adults – a result of small body size – they may spend less time thermoregulating (Sun et al. 2001) and be observed less often. In addition, juveniles are often relatively sedentary (Pike and Grosse 2006) and remain in habitats where they are less vulnerable to predation (Pike et al. 2008). In my field study of the Otago-Southland gecko, juveniles were seldom seen active during the day, whereas both adult females and males were active in their retreat and basked overtly (pers. obs.). One study suggested that differences in adult and juvenile detection are also evident in the tuatara, in which juveniles are less active during the night and more difficult to detect compared to adults (Walls 1983). However, a recent study on the activity patterns of juvenile tuatara showed a peak in oxygen consumption from late afternoon to midnight, similar to that of adults, suggesting that there are no differences in activity period and that lower detectability may be a result of cryptic behaviour of juveniles (Birchard et al. 2006).

The development of a system, grouping reptiles by sex, reproductive condition and/or age class, may be a critical concept to analyse activity patterns in the future. Therefore, a new method to classify the basking, foraging and thermoregulatory activity of pregnant, non-pregnant females, males and juveniles is required. Currently, activity patterns are used to describe all individuals within a species. However, describing the activity patterns of females and males together may be misleading. Without the inclusion of sex, reproductive condition and age as intraspecific behavioural differences in activity, researchers may make inappropriate assumptions of reptile activity. These differences need to be taken into account when examining reptile behaviour and may bring us one step closer to understanding intraspecific differences in reptile activity.

Meta-analyses and activity patterns, the Otago-Southland gecko as an example

‘Nocturnal’ and ‘diurnal’ are imprecise terms that are commonly misused when undertaking research on a large-scale – commonly in meta-analyses. In two recent meta-analyses the Otago-Southland gecko was classified as nocturnal (Meiri et al. 2013; Tingley et al. 2013). Tingley et al. (2013) used only ‘diurnal’ and ‘nocturnal’ to describe activity patterns; whereas Meiri et al. (2013) used three different classifications for activity: ‘diurnal’, ‘nocturnal’ and ‘cathemeral’. In this context,
reptiles with cathemeral activity patterns were those that were active for sporadic/random periods during both the day and the night (Meiri et al. 2013). The term cathemeral is used so widely, that it could potentially be used for every animal that does not fit the status of strictly diurnal or strictly nocturnal. While the inclusion of this term provides some insight into the time of day a species is active, it does not provide us with meaningful information about how long the species is active, or the activities that are performed at different times. The use of fewer categories to explain a diverse range of reptile activity patterns may be simpler in the short term; however, imprecise labelling may cause unexpected consequences further down the track and may in turn affect the reliability of the results.

A new method that can quantify the degree of diurnal and nocturnal activity and move beyond simplistic categorisation of reptiles into activity patterns is of the utmost importance. To gain insight into large scale trends in activity patterns, a consensus needs to be reached about a broader range of the terms appropriate to describe reptilian activity.

*How can we determine the activity time of different behaviours?*

Time-lapse cameras, temperature loggers and radio telemetry are some methods available to herpetologists that could be used to examine reptile activity patterns (Kucera and Barrett 2011). Time-lapse cameras provide us with an effective way of determining reptile behaviour; whereas radio telemetry with temperature-sensitive transmitters and temperature loggers can provide valuable information about reptile $T_b$. In addition, temperature loggers can also be used to study operative temperature ($T_o$). As $T_b$ often correlates with activity, in synergy these methods may enable us to explore various activity patterns in reptiles.

Over the last few decades studies have incorporated the use of automatic, photographic recording devices in studies monitoring wildlife (Temple 1972; Montalbano et al. 1985; Kucera and Barrett 2011). Recent technological advances have led to an increasing use of automatic cameras to study animal behaviour (Cutler and Swann 1999; Kucera and Barrett 2011). The use of automatic triggering or video recording software has great
potential for studying reptile behaviour in the field (Cutler and Swann 1999), particularly for species with cryptic behaviour (Kucera and Barrett 2011). A recent study used video recorders to analyse burrow use and heliothermic basking behaviour in the endangered Slater’s skink *Liopholis slateri* (Fenner et al. 2012). Time-lapse cameras have also been used to study activity patterns of one-week old, laboratory reared hatchlings of the Eastern three-lined skink *Bassiana duperreyi* (Shine 1995), prey behavioural response of western timber rattlesnakes *Crotalus horridus* (Clark 2005) and predation behaviour of *C. horridus* (Clark 2006).

Time-lapse photography has the potential to replace traditional procedures, such as physical surveys (Cutler and Swann 1999) and enables researchers to gather continuous observations with minimal disturbance (Kucera and Barrett 2011). In addition, this method is extremely flexible, allowing researchers to conduct multiple analyses simultaneously. Time-lapse cameras, however, do not provide any information about the *Tb* of an animal and the most effective and non-invasive method for monitoring *Tb* has been a topic of intensive investigation (Goodman et al. 2009).

Many studies on behaviour and physiology have used temperature loggers to record *Te* and *Tb* of lepidosaurian reptiles (Shine and Kearney 2001; Angilletta and Krochmal 2003). Previous studies have used temperature loggers inserted into copper models to simulate the thermal profiles lepidosaurs experience in the field (Adolph 1990; Bauwens et al. 1996; Hare et al. 2009). Thermochron temperature loggers have also been used to measure skin (surface) temperature of elapid snakes (Elapidae) (Llewelyn et al. 2005). Llewelyn et al. (2005) reduced the size and weight of the logger by removing the metal casing from temperature loggers and encased loggers in rubber, supposedly a measure taken to decrease any deleterious effects on locomotion or behaviour. In addition, in a recent study temperature loggers were surgically implanted into pregnant and non-pregnant female children’s phythons *Antaresia children* to determine how reproductive status influenced *Tb* (Lourdais et al. 2008). Lourdais et al. (2008) found that pregnant females maintained a higher and less variable *Tb* compared to non-pregnant females.

Radio telemetry with temperature-sensitive transmitters can effectively provide *Tb* measurements for small-bodied lepidosaurs. In the Otago-Southland gecko
temperature-sensitive transmitters that were ≤10% of the gecko’s body weight have been surgically implanted, with no discernible negative effects on T_{sel} (Rock and Cree 2008). Transmitters recorded variation in T_b for pregnant females, non-pregnant females and males over a diel cycle for five consecutive days. Pregnant females had higher T_b than males, yet there were no differences between the T_b of non-pregnant females compared to pregnant females or males (Rock and Cree 2008). High day-time T_b suggested that Otago-Southland geckos actively thermoregulate during the day, while in a retreat. However, transmitter implantation is an invasive procedure and for pregnant geckos, to fit the transmitter into the abdominal cavity geckos were surgically modified and the developing neonate from the right ovary removed (Rock and Cree 2008). Rock and Cree (2008) reported one case of a female aborting the remaining embryo – which may have been a result of transplantation procedure, yet they stated that other pregnant females showed no deleterious signs of transmitter transplantation.

A recent long-term study on west Indian rock iguanas (Cyclura sp.), examined the effects of implantation, ingestion and a range of external attachments of radio transmitters on signal strength, animal health, behaviour and disturbance (Goodman et al. 2009). All methods provided adequate signal strength, however the amount of data attained for each technique differed. Implantation provided long-term data, yet this method was invasive and expensive. Ingestion provided short-term data as the transmitter passed through the digestive tract. External attachments with breakaway mechanisms were less reliable in the long-term, however, they were less invasive and cost effective compared to implantation and ingestion techniques (Goodman et al. 2009).

*The use of multiple approaches in studies of lepidosaurs behaviour and activity patterns*

The way we study reptile ecology and behaviour is changing. Recent technological advances have allowed researchers to fit temperature loggers, single-stage very high frequency (VHF) transmitters and Global Positioning Satellite (GPS) technology to large-bodied (≥261 mm) reptiles as vest-style backpacks (Price-Rees and Shine 2011). This technology has been used to track long-term movements and habitat use of two
species of bluetongue lizards *Tiliqua multifasciata* and *T. scincoides intermedia* (Price-Rees and Shine 2011; Price-Rees *et al.* 2013) and has the potential to be used to examine a range of measures of reptile performance (*T* <sub>b</sub>, movement, prey capture, territorial and courtship displays; Pianka and Vitt 2003). The applications of these technological innovations are, however, limited by animal body size, device longevity and expense and animal life history traits such as retreat type (Rock and Cree 2008). The weight and size of attachments that an animal can carry is limited by body size. Bluetongue lizards are large-bodied reptiles with a snout-vent length of up to 370 mm once sexually mature (Price-Rees and Shine 2011). In a recent study on bluetongue lizards the VHF, GPS and temperature loggers vest attachments accounted for between 1.7 and 6.4% of the lizards’ mass and had no apparent effects on behaviour (Price-Rees and Shine 2011). However, such substantial attachments cannot be fitted to small-bodied species (Knapp and Abarca 2009). Large attachments also tend to have a longer battery life and as a result, while data sets may be extensive for large-bodied species such as the bluetongue lizard (Price-Rees *et al.* 2013), data sets for small-bodied species are less extensive. The life history and retreat type of a reptile also has implications for the type and size of the attachments. For example, the use of large external attachments, such as GPS devices are restricted by obstructions in satellite coverage (Glasby and Yarnell 2013); therefore, this technology may only be suitable for ground-dwelling species and not for burrowing species (Price-Rees and Shine 2011). Some studies have used external attachments employing breakaway mechanisms that allowed animals to escape from their attachments if they became stuck (Warner *et al.* 2006; Goodman *et al.* 2009). This precaution is particularly important when dealing with burrow and crevice-dwelling species that can get into confined spaces.

Currently, the use of these techniques to study reptile ecology and behaviour is limited. Species-specific life-history characteristics determine which of these techniques could be most successfully used to examine the activity patterns, ecology and behaviour of reptiles. Technological advances reducing both the size, as well as expense of GPS devices, temperature logger and radio telemetry (both transmitters with temperature-sensitive transmitters – to measure reptile *T*<sub>b</sub> and those without – to measure movement and homing behaviour) attachments will allow more research to examine the ecology and behaviour of small-bodied reptiles and lead to a fruitful area of future research.
Conclusions and future research

This review addressed some of the challenges associated with defining the activity patterns of lepidosaurs. There has been some confusion related to the definition of activity. The word ‘activity’ can be used in a variety of contexts to describe locomotion, emergence, thermoregulation, territorial and courtship behaviour. However, when using this term, it is vital that researchers explicitly state the context of activity. For example, in my research activity was classified by retreat emergence and heliothermic basking (Chapter 2). Furthermore, activity is energetically costly, therefore, surveys and casual observations of reptile behaviour are not enough to accurately describe activity patterns. I suggest the use of physiological measures to distinguish between active and inactive states. Through analysis of oxygen consumption as an index of metabolic rate (Hare et al. 2010) we may be able to resolve some misconceptions about reptile activity.

As many reptiles labelled as ‘nocturnal’ thermoregulate diurnally, a consensus needs to be reached over whether thigmothermic thermoregulation should be defined as activity. I propose that thigmothermy is a passive process and should not be considered as activity. Heliothermy on the other hand, involves emergence from a retreat and should be considered as a form of activity. In addition, as many studies have revealed that reptiles undertake different activities during different times of the day, it is in the interest of researchers to quantify the temporal organisation of reptile behaviour. There is evidence that some species may be active outside their activity period; however, activity may not be obvious due to the location, or type of activity.

I found that the categories diurnal, nocturnal and crepuscular have remained relatively consistent since Cowles and Bogert’s (1944) influential paper on reptile thermal biology. However, there has been little consensus over the use of diurno-nocturnal and cathemeral. In scientific literature, cathemeral and diurno-nocturnal have been used to describe lepidosaurs with both diurnal and nocturnal activity. Due to the historical context of cathemerals and previous application to primates, I suggest this term should not be applied to reptile activity. I propose the use of diurno-nocturnal, henceforth, to describe lepidosaurs that are active both diurnally and nocturnally.
I provided a broad overview of the activity patterns of New Zealand lepidosaurs and used three examples to demonstrate that classifying many reptiles in a binary way – as either diurnal or nocturnal – can be uninformative and may lead to inappropriate assumptions of activity. Furthermore, many species exhibit intraspecific variation in activity. In this review, the Otago-Southland gecko and tuatara were used as examples to demonstrate that the activity patterns of lepidosaurs are dependent on a variety of factors including sex, reproductive condition and age class. Intraspecific differences in activity pattern need to be quantified on a species-specific basis. I suggest that additional precautions need to be taken when categorising lepidosaurs into activity patterns. Furthermore, the Otago-Southland gecko was used as an example to demonstrate how species can be imprecisely categorized in large-scale studies such as meta-analyses.

This review has provided evidence that a rich assemblage of different tools are available to herpetologists to study activity. This provides exciting opportunities for future research and will continue to develop our understanding of reptile activity and the many factors that influence activity. I suggest the use of multiple approaches to research lepidosaurs activity. The type, size and weight of attachments need to be species specific and cater for differences in life-history traits. Furthermore, technological advances are reducing the size of attachments and increasing battery life; therefore, more research can be directed towards small-bodied reptiles.

Overall, the problems identified in this review have global application. New Zealand reptiles have been predominantly used as examples; however, these problems with activity patterns have global significance and have been identified for other reptiles worldwide. Future research on reptile activity patterns should aim to use universal terms that can be used to describe a broader range of reptile activity patterns. To do this we need to move away from the binary descriptions currently used and give more attention to detail to create more specific descriptions of activity.
REFERENCES


Appendix 1

The effects of Parafilm on temperature logger temperature records

Introduction

Temperature loggers have transformed the way researchers study thermoregulation in amphibians and reptiles (Roznik and Alford 2012). Thermochron i-button temperature loggers are the most commonly used logger in the field of herpetology (Angilletta and Krochmal 2003). These loggers can be surgically implanted into animals to study body temperature ($T_b$) or they can be used to study operative temperature ($T_e$) in different microhabitats (Angilletta and Krochmal 2003). Temperature loggers provide accurate and reliable estimates for studies of $T_e$ in the field (Angilletta and Krochmal 2003). However, temperature loggers are not waterproof (Roznik and Alford 2012). In field research, equipment malfunction is a costly problem (Roznik and Alford 2012). To avoid the loss of data in the field, scientists can take additional precautions to protect or ‘weatherproof’ equipment (Roznik and Alford 2012).

A recent study aimed to determine if covering temperature loggers in a clear plastic dip (Plasti Dip, Plasti Dip International, Blaine, MN, USA) could be used to waterproof temperature loggers (Roznik and Alford 2012). However, the waterproof coating altered recorded temperatures by 0-1.3°C (Roznik and Alford 2012). While this difference is small, it may have dramatic consequences when studying differences in microhabitat temperature, or thermoregulatory precision in reptiles.

Parafilm is an invaluable method of making equipment water resistant and even waterproof. It has been employed in many scientific studies primarily for this reason (Kennett et al. 1993; Weisrock and Janzen 1999; Oort et al. 2004; Gür 2012). A previous study used Parafilm covered loggers to examine free-range activity of reindeer Rangifer tarandus (Oort et al. 2004). In this study, temperature loggers were in contact with the deer’s skin, so additional measures were taken to make the loggers water and damage proof through embedding the logger in silicone and encasing it in a metal case (Oort et al. 2004). A more recent study demonstrated that in Wistar albino rats Rattus norvegicus, the application of Parafilm on temperature loggers did not compromise
temperature logger function (Gür 2012). In Gür (2012), temperature loggers were
designed for implantation in five male rats weighing >300 g. Parafilm was applied
around the temperature logger to protect the logger from body fluids while inside the
animal. Parafilm was also used to protect the logger from an additional wax coating,
this coating of paraffin-elvax compound was required to prevent tissue reactions (Gür
2012). Wax coated loggers accounted for between 3-5% of the animals total body
weight (14.65 ± 0.94 g) and had no discernible affects on the rodents daily fluctuations
in $T_b$ or activity pattern (Gür 2012).

Macraes Flat is an unpredictable and variable environment (Hare et al. 2008), that
shows extreme fluctuations on a daily as well as season cycle (Rock and Cree 2008).
As this study is based at Macraes Flat, all equipment needed to be tested to make sure it
could withstand the conditions. This preliminary study was used determine if Parafilm
could be used as a medium to waterproof the temperature loggers within the copper
models. For this method to be used, I first needed to establish whether covering
temperature loggers with Parafilm would affect the temperatures recorded by the
loggers. I hypothesised that Parafilm would have no effect on the temperatures recorded
by the temperature loggers. If the Parafilm covering doesn’t affect the temperatures
recorded, Parafilm could be an easy solution to waterproofing temperature loggers in
the field. If Parafilm does affect the temperatures recorded, the next step would be to
see how it affects temperature, then determine if temperature can be standardised to
account for this.

Methods

Before the initiation of the first field season, a preliminary test was undertaken in a
controlled laboratory thermal regime to examine the effects of Parafilm on the
temperatures recorded by i-button temperature loggers (DS1921G, Maxim Integrated
Products, San Jose, CA, USA). The non-Parafilm (control) and Parafilm (treatment)
groups had four and five replicates, respectively. For the Parafilm group, $20 \times 20$ mm
sections of Parafilm were used. Each section was stretched up to twice its original
length. Parafilm was applied long-ways around the outer edge of the logger. Pressure
was applied to the top and bottom sections to join the ends and completely cover the logger. Control loggers did not have the Parafilm cover. Models were set to record temperature at 10 minute intervals (this time interval was used for all following analyses) over two days.

Statistical analyses

A linear model was used to examine the relationship between average temperatures recorded by control and Parafilm covered loggers. This analysis was conducted in the statistical program R 2.15.1 for Windows (CRAN, Auckland, New Zealand).

Results and Discussion

There was a significant positive relationship between the temperatures recorded by the Parafilm covered loggers and control loggers ($P<0.0001$). The Parafilm covering on the temperature loggers therefore, did not affect recorded temperature ($R^2=0.99$; Fig. A.1.1).
Figure A.1. The positive correlation between the temperature recorded by Parafilm (n=5) and non-Parafilm covered i-button temperature loggers (n=4). The linear regression equation was $y = -0.00454 + 1.004132 (R^2=0.99)$.

The strong correlation between Parafilm and non-Parafilm covered loggers meant that I could put the Parafilm on the temperature loggers with confidence that it had no effect on the temperatures recorded by the temperature loggers under the laboratory thermal gradient (fluctuating between 4 and 22 °C) (Fig. A.1.2).

I assumed that in the field, the same result would be evident. In the field, temperature loggers inserted into copper models recorded temperatures exceeding those tested under laboratory conditions. The direct basking model that was exposed to direct sunlight, experienced highs between 30-40°C. However, this temperature range is unlikely to affect the temperatures recorded by the temperature loggers. Further tests should examine the effects of Parafilm on temperature records over a wider range of temperatures. This would allow us to determine if Parafilm covered loggers act the same as non-Parafilm covered loggers under extreme temperatures.
Figure A.1.2. Thermal profiles of Parafilm and non-Parafilm covered i-button temperature loggers under a laboratory thermal regime. Dashed lines represent the control group with no parafilm cover $n=4$; while dotted lines represent the treatment group $n=5$. Temperatures were recorded in ten minute intervals. There was a significant positive correlation between control and Parafilm covered temperature loggers ($P<0.0001$).
Appendix 2

Environmental temperature and copper models

Statistical analyses

A subset of data for basking days in spring-summer is shown here to demonstrate how statistical models were fitted using Akaike information criterion (AIC) and statistical model estimates. Copper model temperatures were plotted in hourly periods from 0600-1300 h. Each of the four copper model types had four replicates.

The fit of the statistical model was first assessed using AIC. This assesses the fit of the statistical model in relation to model complexity (i.e. the number of parameters). The statistical model with the lowest AIC value is the most likely model, given the data. Akaike information criterion calculated the fit of four different statistical models to the data. The difference in AIC (ΔAIC) was calculated by subtracting the AIC of each statistical model from the statistical model with the best AIC (Burnham and Anderson 2002). The AIC weights ($w_i$) were for each model were calculated using standard equations from Burnham and Anderson (2002):

$$w_i = \frac{\exp[-\frac{1}{2} \Delta_i]}{\sum_{t=1}^{m} \exp[-\frac{1}{2} \Delta_t]}$$

The relative likelihood ($\exp[-\frac{1}{2} \Delta_i]$) was calculated by multiplying the exponential by negative half of the difference in AIC. This was then divided by the sum of the relative likelihoods ($\sum_{t=1}^{m} \exp[-\frac{1}{2} \Delta_t]$) for all statistical models to create the AIC model weights ($w_i$). The AIC model weight is the probability that a given model is the most likely and best represents the data (Burnham and Anderson 2002).
Statistical model estimates for the model with the smallest AIC value were then used to evaluate the fit of the statistical model to the data. Curves were created using a standard quadratic equation:

\[ f(x) = a + bx_t + cx_t^2 \]

In this equation \( f(x) \) is the response variable, temperature. The temperature of a copper model is equal to the initial model temperature at time zero \((a)\), the slope of the linear effect \((b)\) multiplied by the time \((x_t)\) and the quadratic effect \((c)\) multiplied by time \((x_t)\).

Throughout statistical analyses AIC and model estimates was used to evaluate the fit of statistical models against the data. All AIC calculations were conducted in the statistical program R 2-15-1 for Windows (CRAN, Auckland, New Zealand).

**Results and Discussion**

Statistical model D had the smallest AIC value (-149.325) and the greatest model weight \((w_i = 0.999; \text{Table A.2.1})\). Together, these values suggest that statistical model D had the best balance between model fit and model complexity and is the most likely model given the data. While statistical model D had more parameters than the other models, it is the best explanation of the change in temperature over time.
Table A.2.1. Statistical model selection and Akaike information criterion (AIC) of four statistical models for copper model temperature data for days with basking opportunity in November-December 2012. The format of this table is based on a table in Burnham and Anderson (2002). The number of parameters (K) and R squared value (R²) of each model are provided. ‘Model formulas’ indicate which parameters were included in the model, a is the initial temperature at time zero, bx_i is the linear effect of time, while cx_i is the quadratic effect of time. For each model AIC was calculated. The model with the best AIC was used to calculate the difference in AIC between the other (less-likely) models (Δ AIC). Together, these were used to calculate Akaike weights (w_i(AIC)).

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>Model formula</th>
<th>R²</th>
<th>AIC</th>
<th>Δ AIC</th>
<th>Relative likelihood</th>
<th>w_i(AIC)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>2</td>
<td>a</td>
<td>0.712</td>
<td>-118.095</td>
<td>31.23</td>
<td>1.65383E-07</td>
<td>1.65383E-07</td>
</tr>
<tr>
<td>B</td>
<td>2</td>
<td>a + bx_i</td>
<td>0.887</td>
<td>-121.106</td>
<td>28.219</td>
<td>7.45284E-07</td>
<td>7.45283E-07</td>
</tr>
<tr>
<td>C</td>
<td>2</td>
<td>a + cx_i^2</td>
<td>0.892</td>
<td>-121.519</td>
<td>27.806</td>
<td>9.16229E-07</td>
<td>9.16227E-07</td>
</tr>
<tr>
<td>D</td>
<td>3</td>
<td>a + bx_i + cx_i^2</td>
<td>0.917</td>
<td>-149.325</td>
<td>0</td>
<td>1</td>
<td>0.999998173</td>
</tr>
</tbody>
</table>

After model D was identified as the most likely model given the data, statistical model estimates from model D were used to plot curves against copper model temperature for hourly periods from 0600 to 1300 h. It was evident that statistical model predictions matched the temperature data for each type of copper model (Fig. A.2.1). Curves accurately described the distribution of the data and identified quadratic and linear effects for each copper model type.
Figure A.2.1. Fitted lines from quadratic models of copper model temperature for models in basking positions (flat and ‘on-toes’) and models in retreats (deep crevice and superficial rock) for days geckos were seen basking in November-December 2012. The statistical model estimates from model D were used to calculate the curves. Each colour represents a different copper model type; the flat basking model is black, the ‘on-toes’ basking model is green, the deep crevice retreat model is red and the superficial rock model is blue. Each copper model type had four replicates.
Appendix 3

The incidence of in-retreat activity in the Otago-Southland gecko

Compared to females, only a small percentage of males were seen in the shade of their retreat (Fig. A.3.1). In spring-summer there was a significantly higher incidence of female in-retreat activity than males for head ($P<0.01$; Fig. A.3.1 A), whole-body ($P<0.01$; Fig. A.3.1 B) and abdomen ($P<0.05$; Fig. A.3.1 C) activity. However, there was no difference between the percentage of females and males that exhibited ‘on-toes’ in-retreat activity in spring-summer ($P>0.05$; Fig. A.3.1 D). In autumn, females also exhibited a higher incidence of abdomen in-retreat activity compared to males ($P<0.05$; Fig. A.3.1 C); however, the incidence of in-retreat activity in females compared to males that exhibited head ($P>0.05$; Fig. A.3.1 A), whole-body ($P>0.05$; Fig. A.3.1 B) and ‘on-toes’ ($P>0.05$; Fig. A.3.1 D) activity did not differ. In autumn, the sole male whose head was seen in the shade of a retreat, appeared to be scanning. No males were seen exhibiting whole-body, abdomen or ‘on-toes’ in-retreat activity in autumn.
Figure A.3.1. The incidence of in-retreat activity of female and male Otago-Southland geckos in spring-summer and autumn. Each graph represents a separate in-retreat activity: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ activity. ‘Percentage of geckos’ is the number of geckos that exhibited a behaviour (marked as present or absent) divided by the total number of geckos observed within a 5 m radius of each camera’s study area (this includes geckos that were caught, as well as those only seen by time-lapse photography). Sample sizes are as follows for spring-summer, females n=42, males n=14; while in autumn females n=25, males n=8. Retreat types and reproductive conditions for females have been pooled. One asterisk (*) indicates statistical significance at $P<0.05$, whereas two asterisks (**) indicate significance at $P<0.01$. 
It was also evident that a significantly higher incidence of females in spring-summer exhibited head ($P<0.05$; Fig. A.3.1 A) and whole-body ($P<0.05$; Fig. A.3.1 B) in-retreat activity, compared with females in autumn. No other significant differences were found for the incidence of in-retreat activity for either sex between spring-summer and autumn ($P>0.05$; Fig. A.3.1).

The incidence in-retreat activity among reproductive and non-reproductive females in the Otago-Southland gecko

The incidence of in-retreat activity in spring revealed that there were no significant differences between the behaviours of reproductive and non-reproductive females ($P>0.05$; Fig. A.3.2).

Figure A.3.2. The incidence of in-retreat activity of reproductive and non-reproductive female Otago-Southland geckos in spring (October-December 2012). Sample sizes: reproductive females n=13, non-reproductive females n=8. Only females of known reproductive condition (females that were caught and palpated) were included in this analysis. Retreat types for this analysis have been pooled. There were no significant differences between the in-retreat activity of reproductive and non-reproductive females ($P>0.05$).
Effect of retreat type on in-retreat activity

In spring-summer, the duration of head in-retreat activity for females tended to be longer at deep crevice retreats, however this was not significant ($t_{10}=-2.029$, $P>0.05$; Fig. A.3.3 A). There were no significant differences between in-retreat activity and retreat type for whole-body, abdomen, or ‘on-toes’ activity ($t_{10}≤-1.762$, $P>0.05$). In autumn, there were no significant differences in the duration of in-retreat activity between the two retreat types for all comparisons ($t_{10}≤-1.756$, $P>0.05$; Table A.3.1).

A) Spring-summer

![Graph showing duration of in-retreat activity for different parts of the body across different retreat types in spring-summer.]

B) Autumn

![Graph showing duration of in-retreat activity for different parts of the body across different retreat types in autumn.]

Figure A.3.3. Duration of in-retreat activity of female Otago-Southland geckos at superficial rock (n=6) and deep crevice (n=6) retreats in A) spring-summer and B) autumn. Average Duration (mean ± 1 SE) of behaviour is shown in minutes out of a total of 480 minutes per filming day. Duration was standardized for both the number of lizards and number of photographs taken at each camera. There were no significant differences between the duration of in-retreat activity for any behaviour between retreat types ($P>0.05$).
There was, however, a significant difference between average in-retreat activity across all behaviours in spring-summer ($t_{47}=-2.643$, $P<0.05$; Table A.3.1). Female geckos at deep crevice retreats exhibited in-retreat activity, on average, for longer durations than females from superficial rocks (Fig. A.3.4). In autumn, there tended to be longer durations of in-retreat activity for geckos at deep crevice retreats; however, this comparison was not quite significant ($t_{47}=-1.950$, $P=0.057$).

![Figure A.3.4. Average duration of in-retreat activity (across all behaviours) of female Otago-Southland geckos at superficial rock ($n=6$) and deep crevice ($n=6$) retreats in spring-summer and autumn. Duration (mean ± 1 SE) of behaviour is shown in minutes out of a total of 480 minutes per filming day. Duration was standardized for both the number of lizards and number of photographs taken at each camera. One asterisk (*) indicates statistical significance at $P<0.05$.](image-url)
Table A.3.1. Probabilities for the effect of retreat type on duration of in-retreat activity of female Otago-Southland gecko in spring-summer and autumn. ‘All behaviours’ compares the average duration (across all behaviours) between retreat types. One asterisk (*) indicates statistical significance at \( P<0.05 \).

<table>
<thead>
<tr>
<th></th>
<th>Spring-summer</th>
<th></th>
<th></th>
<th>Autumn</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( df )</td>
<td>( t )</td>
<td>( P )</td>
<td>( df )</td>
<td>( t )</td>
</tr>
<tr>
<td><strong>Head</strong></td>
<td>10</td>
<td>-2.029</td>
<td>0.070</td>
<td>10</td>
<td>-1.703</td>
</tr>
<tr>
<td><strong>Whole-body</strong></td>
<td>10</td>
<td>-1.587</td>
<td>0.144</td>
<td>10</td>
<td>1.756</td>
</tr>
<tr>
<td><strong>Abdomen</strong></td>
<td>10</td>
<td>-1.762</td>
<td>0.109</td>
<td>10</td>
<td>-1.220</td>
</tr>
<tr>
<td>‘On-toes’</td>
<td>10</td>
<td>-0.844</td>
<td>0.419</td>
<td>10</td>
<td>-0.676</td>
</tr>
<tr>
<td><strong>All behaviours</strong></td>
<td>47</td>
<td>-2.643</td>
<td>0.018*</td>
<td>47</td>
<td>-1.950</td>
</tr>
</tbody>
</table>

Effect of time of day on in-retreat activity at different retreat types

For in-retreat activity in spring-summer there were no significant differences between the duration of behaviours at the two retreat types over the filming period for head, abdomen or ‘on-toes’ activity (\( t_{66}<2, P>0.05 \); Fig. A.3.5). At deep crevice retreats the duration of whole-body activity decreased significantly over time (\( t_{66}=-2.246, P<0.05 \)) and was significantly longer than that at superficial rock retreats (\( t_{66}=-2.394, P<0.05 \); Fig. A.3.5 B). The duration of ‘on-toes’ activity increased significantly over the day at deep crevice retreats (\( t_{66}=2.184, P<0.05 \)) and showed some evidence of a quadratic effect; however, this was not statistically significant (\( t_{66}=-1.950, P=0.055 \); Fig. A.3.5 D).
Figure A.3.5. Effect of time of day on in-retreat activity of female Otago-Southland geckos from deep crevice and superficial rock retreats in spring-summer (October 2012 – February 2013). Each graph represents a separate in-retreat activity: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ activity. Dark lines with diamond icons (♦) represent the average basking duration at deep crevice retreats (cameras n=6), while light grey lines with square icons (■) represent superficial rock retreats (cameras n=6). Means are ± 1 SE. One asterisk (*) indicates statistical significance at $P<0.05$ for comparisons between retreat types at individual time periods.

In-retreat activity in spring-summer, however, did not show strong differences between the two retreat types (Table A.3.2). For head in-retreat activity, activity was significantly longer at deep crevice retreats at four hours past sunrise (Fig. A.3.5 A). No statistically significant differences were found for any of the other in-retreat behaviours. However, a slight yet non-significant trend was found five hours past sunrise for whole-body activity – where activity tended to be longer at deep crevice retreats and two hours past sunrise for ‘on-toes’ in-retreat activity – where activity
tended to be longer at superficial rock retreats. No significant changes in activity over time were evident for either retreat type for head and abdomen activity (Table A.3.2).

Table A.3.2. Significance of retreat type on in-retreat activity in relation to time of day. Time intervals are shown in hours past sunrise. One asterisk (*) indicates statistical significance at P<0.05. Probabilities are shown to three decimal places. Dashed cells (-) do not have a P-value as behaviours were not seen at this time period.

<table>
<thead>
<tr>
<th></th>
<th>Hours past sunrise</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
<td>5</td>
<td>6</td>
</tr>
<tr>
<td><strong>Spring-summer</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>0.238</td>
<td>0.154</td>
<td>0.122</td>
<td>0.032*</td>
<td>0.063</td>
<td>0.371</td>
</tr>
<tr>
<td>Whole-body</td>
<td>0.164</td>
<td>0.341</td>
<td>0.306</td>
<td>0.158</td>
<td>0.075</td>
<td>0.357</td>
</tr>
<tr>
<td>Abdomen</td>
<td>0.148</td>
<td>0.445</td>
<td>0.283</td>
<td>0.293</td>
<td>0.110</td>
<td>0.501</td>
</tr>
<tr>
<td>‘On-toes’</td>
<td>0.341</td>
<td>0.062</td>
<td>0.662</td>
<td>0.460</td>
<td>0.410</td>
<td>0.597</td>
</tr>
<tr>
<td><strong>Autumn</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head</td>
<td>0.341</td>
<td>0.619</td>
<td>0.656</td>
<td>0.588</td>
<td>0.939</td>
<td>0.207</td>
</tr>
<tr>
<td>Whole-body</td>
<td>-</td>
<td>-</td>
<td>0.341</td>
<td>-</td>
<td>0.341</td>
<td>0.341</td>
</tr>
<tr>
<td>Abdomen</td>
<td>0.341</td>
<td>0.335</td>
<td>0.317</td>
<td>0.553</td>
<td>0.924</td>
<td>0.552</td>
</tr>
<tr>
<td>‘On-toes’</td>
<td>-</td>
<td>0.341</td>
<td>0.372</td>
<td>0.341</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

In autumn there were no differences in female in-retreat activity between retreat types overall (t_{66}<2, P>0.05; Fig. A.3.6). In addition, there were no significant changes in duration of in-retreat activity over time for deep crevice or superficial rock retreats (t_{66}<2, P>0.05). For females at superficial rock retreats, head basking appeared to show a quadratic effect, however this was not significant (t_{66}=-1.844, P=0.070). No other form of in-retreat activity at either deep crevice or superficial rock retreats showed evidence of a quadratic effect over time (t_{66}<2, P>0.05; Fig. A.3.6).
Figure A.3.6. Effect of time of day on in-retreat activity of female Otago-Southland geckos from deep crevice and superficial rock retreats in autumn (February – April 2013). Each graph represents a separate basking behaviour: A) head, B) whole-body, C) abdomen and D) ‘on-toes’ activity. Dark lines with diamond icons (♦) represent the average basking duration at deep crevice retreats (cameras n=6), while light grey lines with square icons (■) represent superficial rock retreats (cameras n=6). Means are ± 1 SE. There were no significant differences in basking duration between deep crevice and superficial rock retreats at individual time periods (P>0.05).

No significant differences were found for individual time periods between the two retreat types for in-retreat activity in autumn (Table A.3.2). Head, abdomen and ‘on-toes’ in-retreat activity appeared to show a peak at three hours past sunrise at deep crevice retreats, however, this was non-significant.
Appendix 4

Thermal profiles of copper models in basking and in retreat positions over a diel cycle

Figure A.4.1. The thermal profiles of copper models in (flat and ‘on-toes’) basking positions and models in (deep crevice and under superficial rock) retreats for basking days in November-December 2012. Means are ± 1 SE for n=4 models per position (averaged across days). Error bars have been offset for clarity.