

# Can Snow Skinks Survive Climate Change?

*The potential for behaviour, physiology and competition to mitigate and enhance climate change impacts on snow skink life history, distribution and persistence.*



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A thesis submitted in fulfilment of the requirements for  
the degree of Doctor of Philosophy

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I would like to dedicate my thesis to God, to the snow skinks and to my son William. God, thank you for starting me on the research path and helping me see it finished. To the lizards, may you live long and prosper in your cold mountain homes and warm seaside retreats. Dear William, I've loved every day with you. I look forward to exploring the world with you and seeing what our future brings.

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# SYNOPSIS



## Abstract

Shifting climates are affecting a diverse range of species, with many taxa predicted to become extinct. A great proportion of reptile species are at risk of extinction within the 21st century due to climate change, yet species-specific impacts of climate change are difficult to predict. This is partly due to inter-specific variance in the physiological and behavioural traits which mediate environmental temperature effects at the organismal level. A Tasmanian lizard genus, *Niveoscincus*, provides an excellent example of this, as variation in altitudinal distribution between species has led to divergent adaptations to local thermal conditions. In this thesis, I provide a systematic assessment of traits likely to mediate climate change effects on widespread lowland and range-restricted highland members of the *Niveoscincus* genus.

Variation in thermal niche width underlies extinction risk from climate change, yet basal physiological data is often unavailable and there is little understanding of the way physiology varies within and between species. I determined the critical thermal limits and evaporative water loss rates of a widespread lowland species of snow skink, *N. metallicus*, and two highland species of snow skink, *N. microlepidotus* and *N. greeni*, in a laboratory setting. I found that the widespread lowland species had significantly higher critical thermal minimum and maximum temperatures, and significantly lower evaporative water loss rates than either of the highland species. I then examined the potential for these critical thermal limits to mediate climate effects on the activity periods from 2010 – 2100. Projections indicate that both widespread lowland and highland snow skink species will experience an increase in their available activity period during the 21<sup>st</sup> century under predicted climate change.

Behavioural plasticity is at the forefront of organisms' potential to respond to novel environments yet our understanding of the extent of behavioural plasticity possessed by species is limited. I examined the potential for behavioural responses to changes in basking opportunity by a high and low altitude population of two widespread lowland species, *N. ocellatus* and *N. metallicus*, and two highland species of snow skink, *N. microlepidotus* and *N. greeni*, in a laboratory setting. All of the populations and species showed reductions in the time spent basking in response to increased basking opportunity. The widespread lowland species, but not the highland species, showed reductions in body temperature when exposed to increased basking opportunity. These plastic behavioural and body temperature responses to the thermal environment have the potential to mediate climate change effects on these species.

Annually reproducing widespread lowland *Niveoscincus* species interact with biennially reproducing highland *Niveoscincus* species in narrow zones ~1100 m above sea level. Warming temperatures projected under climate change may enable widespread lowland species to invade higher altitude areas. Consequently, the reduced reproductive rate of highland species may act as an evolutionary trap under climate change, as widespread lowland species outnumber and outcompete highland species at increasingly high altitude areas. Using a spatially-explicit individual-based model I simulated an interacting population of the widespread lowland, *N. ocellatus*, and the highland, *N. microlepidotus*, snow skink species on Mount Wellington, Tasmania. Higher temperatures were projected to increase the abundance and upper range boundary of *N. ocellatus*. The increase in competition for territory is predicted to drive *N. microlepidotus* into a long acting extinction vortex.

Intra- and inter-specific differences in behaviour, physiology and phenology, along with climate-mediated variation in life history traits, are likely to impact the responses of species to climate change. However, the majority of species distribution models do not explicitly incorporate these factors, potentially resulting in erroneous predictions. I incorporated a wide range of biological trait data into a process-based model, NicheMapR, to test the effects of projected climate change on the life history, activity and distribution of *N. ocellatus* and *N. microlepidotus*. These models predicted climate change would result in a number of fitness benefits for both of these species, including increased reproductive output and frequency. When simulated across an altitudinal transect the models predicted the widespread lowland species would be able to colonise higher altitude sites under projected climate change.

This thesis represents a comparative examination of the potential for climate change to impact the life history, persistence and distribution of several reptile species. My results suggest that climate change impacts are likely to be population and species-specific, according to climatic and biological processes operating at local scales. This study highlights the potential for climate change to have a number of beneficial effects on the fitness of temperate reptile taxa. However, the downstream effects of climate change for species' abundance, range margins and long term persistence depend on climatic effects on, and responses of, neighbouring competitors. My findings support the call for studies of climate change impacts to take a process-based approach and suggest metamodels provide a promising avenue for future research into the prediction of the responses of species to climate.

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# CHAPTER ONE



## General Introduction

*“Isn't it funny how day by day nothing changes, but when you look back, everything is different...” C. S. Lewis.*

We live in a changing world. In 1981, Hansen *et al.* (1981) predicted that the signal of human-induced climate change would soon emerge from natural climate variability. The signal is now apparent. Over the last one hundred years the concentration of greenhouse gases in the atmosphere has sharply increased, driving a rise in the mean global surface temperature of almost 1°C (Box 1, Meehl *et al.* 2007; Field *et al.* 2014a). Recent decades have witnessed climatic changes on all continents and across the oceans (Field *et al.* 2014a). The last century has heralded greater warming of winter months than any other season, coupled with minimum temperatures increasing more than maximum temperatures (e.g. sites examined in Ashcroft, Chisholm & French 2009). Since the 1950s the frequency of extreme events such as heat waves, storms and wild fires has increased (Meehl *et al.* 2007; Westerling & Bryant 2008; Krawchuk, Cumming & Flannigan 2009; Field *et al.* 2014a). The rate of warming since 1976 has been greater than at any other time during the last 1,000 years (Figure 1, Change 2001).

Without additional mitigating measures to curb the current rate of greenhouse gas emissions, mean global temperature is predicted to rise above the average temperatures recorded from 1850–1900 to a median level of 3.7 – 4.8°C by 2100 (Figure 1, Field *et al.* 2014a). When climate uncertainty is considered, the range widens to 2.5 – 7.8°C (Field *et al.* 2014a). Greater warming is being recorded (and is projected to continue to occur) in higher latitudes and altitudes (Qin *et al.* 2009; Ohmura 2012). Hot and arid climates are anticipated to expand globally, producing new environmental states with no current analogue (Pederson *et al.* 2010; Garcia *et al.* 2014). Forecasts under the higher-emissions scenarios (which Earth's climate is currently tracking) exceed the natural variability observed over the historical record (Figure 1). Evidence of historical periods of climate change and associated effects on natural systems are signposts of the sensitivity of natural systems to changes in climate (Nogués-Bravo *et al.* 2010). Consideration of the late Quaternary, in which climatic change drove large scale megafaunal extinctions, indicates that the rate and magnitude of climate change projected for the next century are without precedent, and will present many unique challenges to Earth's biota (Figure 1, Jackson & Overpeck 2000).

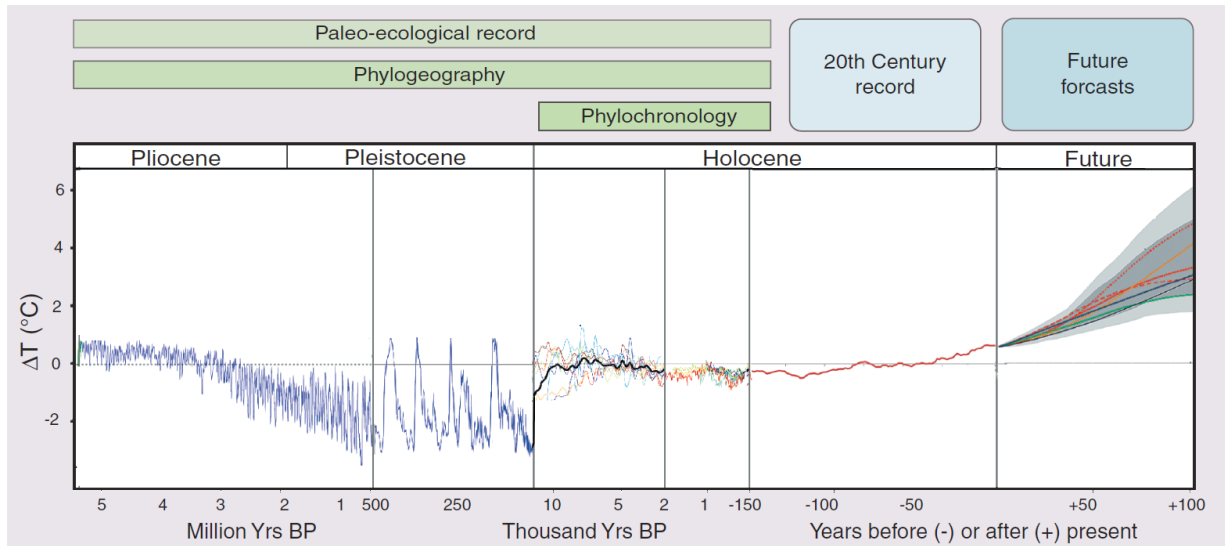


Figure 1. Historical and predicted future fluctuations in global mean temperature and scales of inference. This figure was produced using a modified paleoclimate record from [http://commons.wikimedia.org/wiki/File:All\\_palaeotemps.png](http://commons.wikimedia.org/wiki/File:All_palaeotemps.png) by Moritz and Agudo (2013). Data for the 20th-century record were obtained from [http://data.giss.nasa.gov/gistemp/graphs\\_v3/](http://data.giss.nasa.gov/gistemp/graphs_v3/), and forecasts of future change are adapted from Solomon (2007), figure SPM.  $\Delta T$ , change in temperature; Yrs BP, years before the present.

Thirty years after Hansen et al. (1981) predicted the emergence of a climate change signal, we have reached a similar threshold for the signal of climate change effects on biodiversity (reviewed by Parmesan & Yohe 2003; Root *et al.* 2003; Rosenzweig *et al.* 2008). Although still infrequent, extinctions are increasingly being attributed to the effects of climate change (Cahill *et al.* 2012). Applying model-averaging techniques to 131 multi-species studies of the effect of climate change on extinction risk, Urban (2015) project that up to one-sixth of species are threatened with extinction under a “business as usual” carbon emissions scenario. Furthermore, extinction risk is not only predicted to increase, but to accelerate as global temperatures continue to rise (Urban 2015). To minimise global biodiversity loss, significant decreases in global emissions must be combined with environmental management that is informed by realistic predictions of species’ vulnerabilities to climate change (Figure 2, Williams *et al.* 2008; Urban 2015). This requires a thorough understanding of the aspects of ecological and evolutionary biology which will increase or decrease species’ climate-induced extinction risk, followed by the identification of management responses which have the potential to minimise realised impacts on vulnerable species (Williams *et al.* 2008).

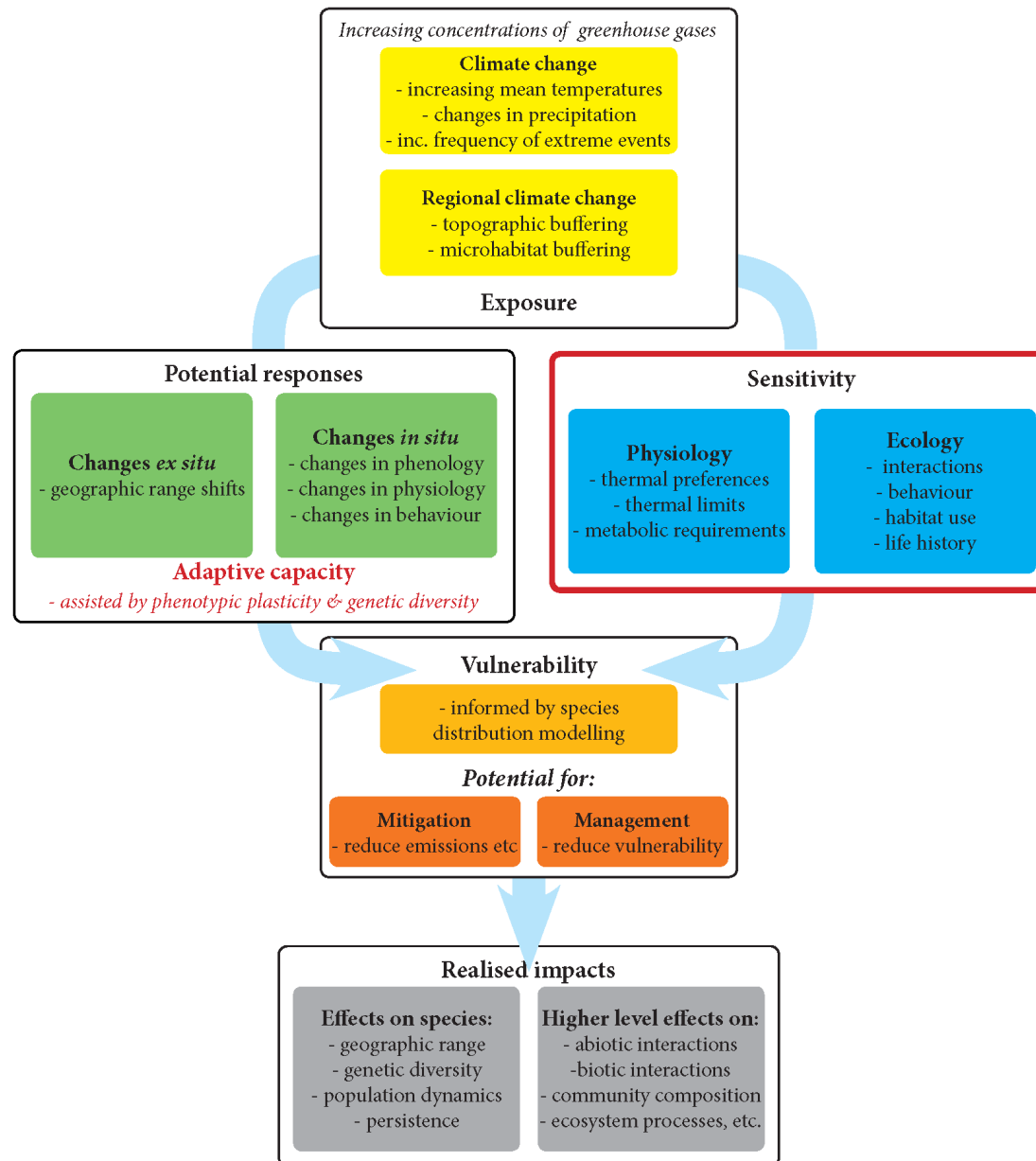


Figure 2. This general framework summarises the pathways of climate change effects on individual species and species' vulnerabilities to climate change (similar figures in Hughes 2000; Williams *et al.* 2008; Lavergne *et al.* 2010). Species' vulnerabilities to increasing atmospheric concentrations of greenhouse gases depend on a cumulative interchange between exposure, vulnerability and potential responses. Species distribution models assess species' vulnerabilities to inform policy decisions and enable strategic management. Together these processes may lead either to extinctions or further range changes and effect community structure and composition. The red text represents mechanisms often overlooked in forecasts of climate change effects (Section 1.2). The red box outlines mechanisms that render species vulnerable to climate change which are not often explicitly incorporated into models which predict the vulnerability of a species to climate change.

### 1.1 Pathways for climate change effects and the potential for species to respond

A growing number of studies have provided confirmation that the comparatively small contemporary changes in climate have resulted in changes in the distribution, physiology and phenology of a broad array of species (reviewed by Parmesan & Yohe 2003; Root *et al.* 2003; Parmesan 2006; Moritz *et al.* 2012). Identifying and predicting the ways in which climate change affects species and communities is an endeavour that was first championed by Hughes (2000) and is now a dominant frontier for environmental science (Figure 2).

Species' responses to climate change can be divided into two categories: responses *in situ* (which may or may not be adaptive e.g. Duputié *et al.* 2015) or responses *ex situ* (i.e. geographic range shifts, Figure 2). The most well documented examples of responses *in situ* are shifts in the timing of events (i.e. phenology), including migration, breeding and hibernation (Root *et al.* 2005; Miller-Rushing *et al.* 2010). For example, climate change results in the earlier onset of spring events (Parmesan & Yohe 2003) and later onset of autumn events (Ge, Wang & Dai 2015). Adaptation *in situ* is facilitated by two primary mechanisms: (i) phenotypic plasticity in the form of behavioural, morphological or physiological responses to accommodate change, and (ii) adaptive evolution via changes in gene frequencies produced by natural selection (e.g. Umina *et al.* 2005; Bradshaw & Holzapfel 2006; Beldade, Mateus & Keller 2011; Hoffmann & Sgrò 2011). Responses by individual species to climate change have 'second-tier' ramifications for interactions with other species as initially forecast by Hughes (2000), and knock-on effects for species abundance, population dynamics, geographic range and population persistence (e.g. Suttle, Thomsen & Power 2007; Miller-Rushing *et al.* 2010).

While adaptation *in situ* does occur (Huntley *et al.* 2006), the strongest signals of species' responses to historical periods of climate change (such as that of the late Quaternary, Figure 1) are shifts in geographic distribution (Davis & Shaw 2001; Huntley *et al.* 2010). Species are responding to anthropogenic climate change via changes in geographic distributions (Figure 2, Parmesan & Yohe 2003; Parmesan 2006; Chen *et al.* 2011). Global meta-analyses of terrestrial organisms have identified mean poleward range shifts of 16.9 km per decade and elevational increases of 11.0 m per decade (Chen *et al.* 2011), with latitudinal and elevational range shifts often an order of magnitude higher in marine systems (Burrows *et al.* 2011). However, responses to climate change vary widely between species, with geographic range



shifts occurring at highly variable rates and in different directions (Parmesan & Yohe 2003; Thomas *et al.* 2004; Chen *et al.* 2011; La Sorte & Jetz 2012; Sunday, Dulvy & Bates 2012). Within both terrestrial and marine environments up to 60% of species are not shifting as anticipated and are moving, for example, to higher latitudes, higher elevations, or greater depths (Parmesan & Yohe 2003; Thomas *et al.* 2004; Perry *et al.* 2005; Chen *et al.* 2011; La Sorte & Jetz 2012; Sunday, Dulvy & Bates 2012). Species which fail to adapt and / or shift in response to climate change experience reduced fitness and ultimately exhibit range contractions and population decline (e.g. Day & Kokko 2015).

### *1.2 Research gaps: central factors which determine a species vulnerability to climate change*

Three principal factors interact to determine a species' vulnerability to climate change (Figure 2). (1) Exposure to climate change. This equates to the magnitude of experienced changes in climatic means and extremes and is mediated by processes occurring at the regional level along with the potential for local topographic and microhabitat buffering. (2) Intrinsic sensitivity to climate change. This factor is the product of a diverse range of interacting biological traits. For example, a major component of the intrinsic sensitivity of a species to climate change is its thermal niche width (Huey *et al.* 2012; Munoz *et al.* 2014; Sunday *et al.* 2014). Thermal niche width broadly defines the range of temperatures which will be able to be tolerated in novel climates. Similarly, species interactions have the potential to enhance effects of climate change on species' distribution and persistence, particularly for range-restricted species (Davis *et al.* 1998a; Davis *et al.* 1998b). (3) The potential for a species to demonstrate adaptive plastic phenotypic or genetic responses to buffer climatic alterations *in situ* (Williams *et al.* 2008; Dawson *et al.* 2011; Bellard *et al.* 2012; Moritz *et al.* 2012).

While exposure is a principle consideration of the majority of existing species distribution models, species' sensitivities and potential to respond to climate change are only now gaining traction as important components of predictive models of species' responses to climate change (Lambers 2015; Urban 2015). Despite major reviews identifying the importance of a consideration of species' sensitivities and potential to respond in species distribution models (Davis *et al.* 1998a; Chown *et al.* 2010), these factors are often ignored or not explicitly incorporated into current models of climate change. Despite an increasing number of techniques capable of incorporating these factors, efforts are hampered by the lack of available data. Studies are required which (i) systematically collect multi-species and

population data on species' sensitivities and potential to respond to climate change, (ii) establish the potential for species interactions to alter species' potential to respond to climate change, and (iii) incorporate this data into process-based models of species' distributions under climate change. This data will provide a comprehensive and robust understanding of the potential impacts of projected climate change on biodiversity.

### *1.3 Forecasting climate change effects on species' distribution and persistence*

Distributional modelling can be utilised to identify both the species and areas at risk under projected climate change (Elith & Leathwick 2009). Realistic predictions of climate change effects on species are required to address societal commitments to the management of natural resources and conservation (Pereira *et al.* 2010; McMahon *et al.* 2011). Typically, predictions of species' responses to climate change at the individual species level take one of two approaches: (i) correlative statistical models or (ii) mechanistic process-based models (Kearney & Porter 2009). Correlative models typically apply a climate envelope approach to assess whether a species' realised niche continues to exist under novel environments.

Although widely used, correlative models are hampered by intrinsic limits and are subject to numerous criticisms concerning the validity of the approach (Pearson & Dawson 2003; Guisan & Thuiller 2005; Araujo & Guisan 2006; Heikkinen *et al.* 2006; Dormann 2007; Wiens *et al.* 2009). In particular, correlative models lack a mechanistic basis by definition, and there are concerns about extrapolation under no-analogue environments (Hof *et al.* 2011b).

Consequently, correlative statistical models are generally regarded as better suited to measure the extent of climate stress experienced due to exposure to climate change rather than predicting a species' vulnerability to climate change (Moritz *et al.* 2012).

In contrast to correlative models, mechanistic models explicitly incorporate the links describing an organisms fundamental niche (e.g. physiology and behaviour) with the environment it experiences to predict species' responses to climate change (Buckley 2008; Kearney & Porter 2009; Kearney, Shine & Porter 2009). This enables predictions to be made about species' responses to novel situations using a functional understanding of the processes underlying interactions between the organism and its local environment (e.g. Kearney 2012). At present, the use of mechanistic modelling methods is hindered for many species by a lack of demographic and physiological data, so that most assessments of climate change impacts rely on statistical rather than process-based approaches (Garcia *et al.* 2014).



#### 1.4 Reptiles as a group of conservation concern

As ectotherms, reptiles are a group of concern within the context of climate change. In a recent global analysis of extinction risk in reptiles by Böhm *et al.* (2013), nearly one in five reptile species were found to be threatened with extinction (with similar estimates elsewhere: Thomas *et al.* 2004; Bickford *et al.* 2010; Sinervo *et al.* 2010). A further one in five species were classified as Data Deficient (Böhm *et al.* 2013). Reptiles occupy important niches in community assemblies: they are grazers, predators, prey, seed dispersers and commensal species (Olsson & Shine 2000a; Böhm *et al.* 2013). Reptiles act as bio-indicators of environmental health (Lambert 1997; Crain & Guillette 1998; Read 1998) and often serve as an ideal study system to explore the biological and evolutionary processes driving speciation (Raxworthy *et al.* 2008a; Camargo, Sinervo & Sites 2010).

The high likelihood of large scale climate-driven reptile extinctions is attributed to their reliance on the environment for the mediation of biological processes and life history traits, including metabolism, growth, development, and embryogenesis (Bennett 1980). Reptiles also have typically narrow niches and narrow distributions (compared to other vertebrates, Anderson 1984; Anderson & Marcus 1992), which further renders them susceptible to impacts from changing temperatures. For example, basking is necessary for most reptiles to attain physiologically active body temperatures, however, death can result from activity in hot weather when the critical thermal maximum is exceeded (Sinervo *et al.* 2010, but see Kearney 2013). While reptiles can seek shade to avoid exceeding the thermal maxima, this limits time spent foraging, thereby constraining costly metabolic functions like growth, maintenance, and reproduction (Deutsch *et al.* 2008; Sinervo *et al.* 2010; Buckley, Hurlbert & Jetz 2012). These negative effects on reptile species' fitness are further compounded by rising temperatures increasing metabolic rates and thereby energy requirements (Dillon, Wang & Huey 2010).

#### 1.5 Snow skinks as a study genus

I used the genus *Niveoscincus* as model system to systematically examine the potential for climate change effects. *Niveoscincus* are a group of eight closely related scincid lizards, six of which are endemic to Tasmania (Figure 3). This genus is composed of widely distributed lowland species and range-restricted highland species (Figures 3 and 4). For my thesis, I selectively used two widespread lowland species, *N. ocellatus* and *N. metallicus*, and two highland species, *N. greeni* and *N. microlepidotus* (Figures 3 and 4). While widespread

lowland species occur from sea level to approximately 1150 m above sea level, highland species are confined to disjunct mountain top populations at altitudes exceeding 1100 m above sea level. In contrast to lowland regions, alpine environments tend to experience lower temperatures, higher levels of precipitation and greater climatic variability (Pen *et al.* 2010). Molecular analyses indicate that a ground-dwelling species similar to *N. metallicus* (Figure 4) gave rise to the modern lineages of *Niveoscincus* during the late Tertiary (1.5 – 7.5 million years ago, Hutchinson & Schwaner 1991; Melville & Swain 2000a). Despite remarkable similarities in reproductive life history (e.g. overwinter gestation discussed below) the two highland species, *N. greeni* and *N. microlepidotus*, are more closely related to other widespread lowland *Niveoscincus* species than to each other (Greer 1982; Melville & Swain 1998; Melville & Swain 2000a). Further phylogeographic studies of the two widespread lowland *Niveoscincus* species, *N. ocellatus* and *N. metallicus*, indicate that these species have formed distinct clades, with evidence of geographic subdivisions of populations and restricted gene flow (Cliff, Wapstra & Burrridge 2015; Kreger 2015) suggesting the potential for local adaptation.

While all *Niveoscincus* species are viviparous, widespread lowland and highland species have different reproductive strategies. The widespread lowland species show a typical annual reproductive cycle where females give birth in summer following a 3 – 4 month gestation (Jones & Swain 1996; Jones, Wapstra & Swain 1997; Wapstra *et al.* 1999; Hutchinson, Swain & Driessen 2001). Thermal constraints on annual reproduction in cold alpine sites appear to limit the upper altitudinal range margin of widespread lowland *Niveoscincus* species to areas where gestation can be completed within a single season (Wapstra *et al.* 1999; Swain & Jones 2000; Girling, Jones & Swain 2002a; Atkins *et al.* 2007). While highland females also ovulate in late spring, fully developed embryos are retained *in utero* through winter and born the following spring (Hutchinson, Robertson & Rawlinson 1989; Olsson & Shine 1998; Hutchinson, Swain & Driessen 2001). This results in an unusual biennial reproductive frequency not seen in other temperate Australian reptiles (Greer 1989). Pregnant *N. microlepidotus* exposed to warm laboratory conditions readily give birth to viable neonates in spring (Olsson & Shine 1998; Olsson & Shine 1999). Consequently, prolonged uterine retention appears to be an adaptation to increase offspring fitness in cold alpine environments, as survival of spring-born offspring is much higher than autumn-born offspring (Olsson & Shine 1998; Olsson & Shine 1999; Atkins, Swain & Jones 2007).

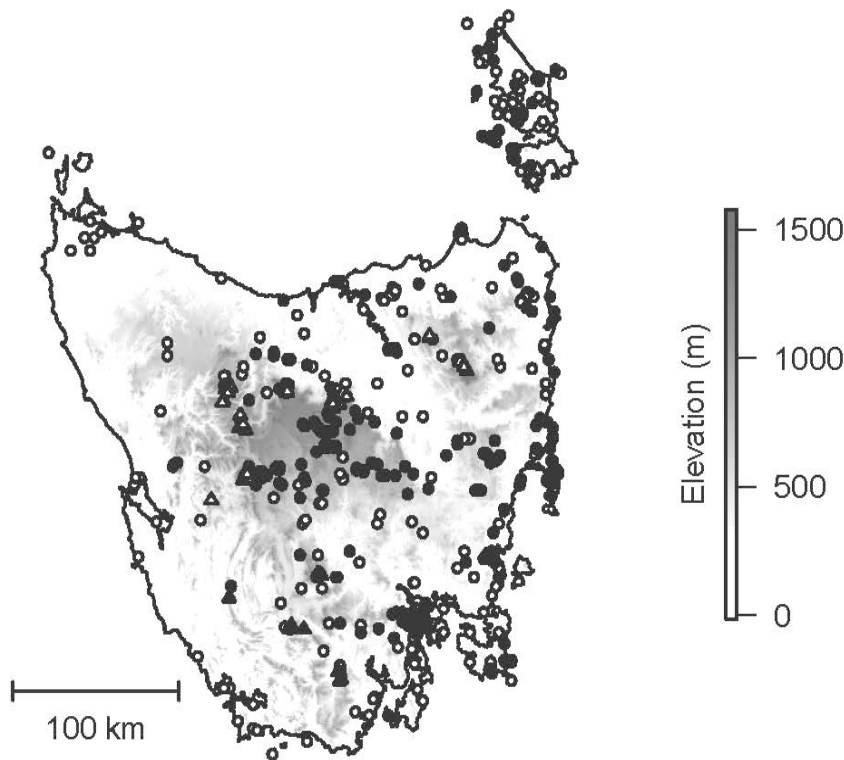


Figure 3: Occurrence of the four species of snow skink, *Niveoscincus*, from Natural Values Atlas records, used selectively in this thesis. The two widespread lowland species, *N. ocellatus* (open circles) and *N. metallicus* (closed circles), are widely distributed across Tasmania, inhabiting sites located at sea level to mid altitudes. The two highland species, *N. greeni* (white triangles) and *N. microlepidotus* (black triangles), are found at disjunct high altitude sites in the north and south of Tasmania respectively.

A number of key snow skink life history traits (such as body size, birth date, sex ratio and reproductive frequency) are strongly influenced by the thermal environment (Olsson & Shine 1999; Wapstra 2000; Cadby *et al.* 2010; Pen *et al.* 2010; Wapstra *et al.* 2010; Uller *et al.* 2011; Cadby, Jones & Wapstra 2014). There is also evidence of adaptation to local climates by populations of the widespread lowland species *N. ocellatus* (e.g. maternal basking behaviour, Cadby, Jones & Wapstra 2014; Yuni, Jones & Wapstra 2015). For example, female *N. ocellatus* from a low altitude population more finely tuned their basking behaviour in response to basking opportunity than female *N. ocellatus* from a high altitude population (Cadby, Jones & Wapstra 2014). This suggests geographic differences in basking behaviour in line with exposure to local climatic regimes. However, the growth of offspring produced by these females varied between treatments despite differences in maternal behaviour, further suggesting local adaptation to basking conditions (Uller *et al.* 2011; Cadby, Jones & Wapstra

2014). Climate change may act through these and other responses to the thermal environment to impact snow skink species' distribution and persistence under projected climate change. However, as with other ectotherms, snow skinks also possess a number of mechanisms (physiological and behavioural) which may alter species' responses to climate change (e.g. Kearney, Shine & Porter 2009; Yuni, Jones & Wapstra 2015). Thus the *Niveoscincus* genus allows for a powerful comparative approach to explore the potential for divergent localised adaptations to alter the effect of climate change on species' distribution and persistence.

### **Thesis aims and structure**

The overarching aim of this thesis was to examine multiple lines of evidence of the potential for *Niveoscincus* species to be impacted by, and respond to, climate change. To produce realistic forecasts of species' distribution and persistence under projected climate change it is imperative that we establish the potential for phenotypic traits, phenotypic plasticity and inter-specific interactions to mediate climate change effects, and incorporate these mechanisms into species distribution models. In this thesis I experimentally and theoretically establish the mechanisms likely to mediate the effect of changing thermal environments on the life history, distribution and persistence of several *Niveoscincus* species (Figure 4). I provide an examination of how physiology (Chapter 2), behaviour (Chapter 3), and inter-specific interactions (Chapter 4) mediate responses to variation in the thermal environment at the individual level, and explore the implications of species level responses for persistence and distribution under climate change (Chapter 5). By including species which inhabit different thermal environments I was able to explore the complex interactions between species' biology (e.g. thermal sensitivity), geography and vulnerability to climate change. Further information on the extent of physiological constraint (e.g. tolerance to changes in the thermal environment), level of innate behavioural plasticity (e.g. changes in basking behaviour in response to changes in the thermal environment), and the role of inter-specific interactions in mediating climate effects, will indicate the potential for climate change to impact widespread lowland and highland *Niveoscincus* species' distribution and persistence. My thesis provides a crucial step towards integrating the effects of processes operating at the individual and species levels, to produce realistic predictions of the consequences of climate change for populations' life history, distributions and persistence. These mechanistic based predictions constitute an important step forward in evaluating the ecological consequences of human induced climate change.



Figure 4: Images of the four lizard species investigated selectively through the course of this thesis. Top: the widespread lowland species, *Niveoscincus metallicus* (left) and *N. ocellatus* (right). Bottom: the highland species, *N. greeni* (left) and *N. microlepidotus* (right). Image credit: <http://mandycaldwell.co.nz>

## Chapter Summaries

1. *To examine inter-specific variation in thermal niche width and implications for activity period under projected climate change.*

A number of major reviews have identified physiology as playing an important role in mediating climate effects (Hughes 2000; Parmesan & Yohe 2003; Possingham, Hughes & Howden 2003; Root *et al.* 2003). Thermal tolerance, which shows a large magnitude of inter-specific variation (e. g. Brattstrom 1965), will determine the extent of climate change effects. Yet little research has been undertaken of the way thermal niche differs both within and between closely related species (Beldade, Mateus & Keller 2011). To what degree will differences in thermal niche drive differences in climate change effects on species' distributions and persistence? In the second chapter of this thesis, I investigated the critical thermal limits and evaporative water loss rates of a widespread lowland, *N. metallicus*, and two range-restricted highland, *N. microlepidotus* and *N. greeni*, snow skink species (Figures 3 and 4, Chapter 2). I predicted that the widespread lowland and highland snow skink species would differ in thermal tolerance due to fundamental differences in their thermal biology driven by adaptations to divergent environments (Melville & Swain 1998). Using this data, I forecast the effect of climate change on available activity time for each species.

2. *To determine the potential for plastic behavioural and selected body temperature responses to the thermal environment*

Behaviour is at the forefront of species' abilities to respond to novel environments produced under climate change (Huey & Tewksbury 2009). To respond effectively to rapidly changing environmental temperatures reptiles may have to rely largely on plastic behavioural responses over short time scales (Deutsch *et al.* 2008; Kearney, Shine & Porter 2009; Aubret & Shine 2010). In the absence of behavioural plasticity, populations may face demographic collapse and extinction under the current pace of climate change (Sinervo *et al.* 2010). Yet we have a limited understanding of the extent to which species will be able to exhibit behavioural plasticity in response to climate change. I undertook a laboratory study to (1) determine the extent of behavioural plasticity possessed by two widespread lowland species, *N. metallicus*, and *N. ocellatus*, and two highland species, *N. microlepidotus* and *N. greeni*, in response to changes in the thermal environment and (2) to establish the potential for physiological

plasticity to variation in thermal opportunity (Figures 3 and 4). I incorporated low and high altitude populations to determine the magnitude of inter-population variability in these traits.

3. *To explore the potential for inter-specific interactions to mediating species' distribution and persistence under projected climate change*

Changing climates can alter both the strength and nature of species interactions (Gilman *et al.* 2010; Van der Putten, Macel & Visser 2010) as a result of different sensitivities to environmental change (Chen *et al.* 2011), differences in dispersal rates (Angert *et al.* 2011; Urban, Zarnetske & Skelly 2013) and changes to relative performance (Huey *et al.* 2009). What will the role of biotic relationships be, when this factor has the potential to both exacerbate (Colwell, Dunn & Harris 2012) and mitigate (Pateman *et al.* 2012) climate change effects (Hof *et al.* 2011a; Lawler *et al.* 2013)? Understanding how altered thermal conditions influence biotic interactions will be crucial for determining the long term impacts of climate change on population viability and distribution, yet biotic interactions are often ignored in models of species' distributions under climate change (Davis *et al.* 1998a). I produced a spatially-explicit individual-based model of interacting populations of a widespread lowland species, *N. ocellatus* and an highland species, *N. microlepidotus*, of snow skink.

4. *To project the likely impacts of changing climates on the life history and distribution of a widespread lowland and highland Niveoscincus species.*

Realistic predictions of the effect of climate change on biodiversity are required to address societal commitments to the management of natural resources and conservation (Pereira *et al.* 2010; McMahon *et al.* 2011). Mechanistic models, which incorporate various interlinked variables influencing the environment experienced by the organism, can incorporate mechanisms by which species can respond to climate change (Kearney, Shine & Porter 2009). Inputs to mechanistic models include species-specific data on behavioural and physiological traits. I parameterised mechanistic models for a low and high altitude population of the widespread lowland species, *N. ocellatus*, and a population of the highland species, *N. microlepidotus*. Using these models, I produced an assessment of how projected climatic change is likely to affect the life history, activity and distribution of these temperate reptile species.



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# CHAPTER TWO



# Potential for thermal tolerance to mediate climate change effects on three members of a cool temperate lizard genus, *Niveoscincus*.

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## Abstract

Climatic changes are predicted to be greater in higher latitude and mountainous regions but species specific impacts are difficult to predict. This is partly due to inter-specific variance in the physiological traits which mediate environmental temperature effects at the organismal level. We examined variation in the critical thermal minimum ( $CT_{min}$ ), critical thermal maximum ( $CT_{max}$ ) and evaporative water loss rates (EWL) of a widespread lowland (*Niveoscincus ocellatus*) and two range restricted highland (*N. microlepidotus* and *N. greeni*) members of a cool temperate Tasmanian lizard genus. The widespread lowland species had significantly higher  $CT_{min}$  and  $CT_{max}$  and significantly lower EWL than both highland species. Implications of inter-specific variation in thermal tolerance for activity were examined under contemporary and future climate change scenarios. Instances of air temperatures below  $CT_{min}$  were predicted to decline in frequency for the widespread lowland and both highland species. Air temperatures of high altitude sites were not predicted to exceed the  $CT_{max}$  of either highland species throughout the 21<sup>st</sup> century. In contrast, the widespread lowland species is predicted to experience air temperatures in excess of  $CT_{max}$  on 1 or 2 days by three of six global circulation models from 2068 – 2096. To estimate climate change effects on activity we reran the thermal tolerance models using minimum and maximum temperatures selected for activity. A net gain in available activity time was predicted under climate change for all three species; while air temperatures were predicted to exceed maximum temperatures selected for activity with increasing frequency, the change was not as great as the predicted decline in air temperatures below minimum temperatures selected for activity. We

hypothesise that the major effect of rising air temperatures under climate change is an increase in available activity period for both the widespread lowland and highland species. The consequences of a greater available activity period will depend on the extent to which changes in climate alters other related factors, such as the nature and level of competition between the respective species.

**Keywords:** critical thermal limit; evaporative water loss; reptile; climate change; alpine species; squamate

## 1. Introduction

Climate change is expected to detrimentally affect a great diversity of species worldwide (Pereira *et al.* 2010; Dawson *et al.* 2011; Bellard *et al.* 2012). Lizards are particularly at risk from climate change because their physiological processes, including locomotion, metabolism, growth and reproduction, are strongly influenced by the thermal environment (Sinervo & Adolph 1989; Huey *et al.* 2009; Munoz *et al.* 2014). As a result, recent research has predicted significant declines in lizard biodiversity over the next century (Thomas *et al.* 2004; Sinervo *et al.* 2010). Such dire predictions highlight the need to understand the fundamental processes driving species vulnerabilities to changing climates (Williams *et al.* 2008). Physiology provides the underlying constraints on organismal distribution and abundance (Kearney & Porter 2009) and will mediate climate change impacts according to species' physiological sensitivity to temperature change (Deutsch *et al.* 2008; Foden *et al.* 2013). Despite this, our understanding of even basic physiological processes of many organisms is limited. Therefore, we are currently poorly equipped to integrate this information into forecasts of species survival and distribution under projected climate change.

Three physiological traits are likely to be particularly important for predicting the impacts of climate change on lizard survival and distribution. The first two traits are an individual's critical thermal minimum ( $CT_{min}$ ) and maximum ( $CT_{max}$ ) temperatures which define the thermal tolerance range within which an organism is able to continue activity necessary for survival (Kearney & Porter 2004; Kearney & Porter 2009). Climate change can have two important implications for thermal tolerance. First it can result in changes in thermal tolerance *per se*. Changes in  $CT_{min}$  are known to occur over relatively short timescales, suggesting a strong lability in this trait and an ability to respond to changing thermal conditions (~35

generations in the lizard *Anolis cristatellus*, Leal & Gunderson 2012). In contrast,  $CT_{max}$  is less variable between lizard species (van Berkum 1988; Sunday, Bates & Dulvy 2011; Araújo *et al.* 2013). Therefore, rising temperatures may be problematic if  $CT_{max}$  is relatively conserved, especially for range restricted species (Hoffmann, Chown & Clusella-Trullas 2013). Alternatively, species may show responses that allow them to circumvent reaching those physiological limits, for example, reducing exposure to lethal temperatures and desiccating conditions via plastic behavioural responses (Kearney, Shine & Porter 2009; Sunday *et al.* 2014). Specifically, warming temperatures may force individuals to spend more time in the shade or in burrows to avoid lethally high temperatures, restricting time for other important activities, such as foraging, territory defence or mating (Sinervo *et al.* 2010). When modelled against projected climate warming, thermal tolerances provide an indication of the frequency and degree to which organisms will need to modify their activity to avoid thermal extremes.

The third trait is evaporative water loss (EWL, Kearney & Porter 2004; Kearney *et al.* 2009). Evaporative water loss has the potential to play a key role in warming environments by decreasing the discretionary water balance available and increasing the risk of death by dehydration (García-Muñoz & Carretero 2013; Guillon *et al.* 2013). The main source of EWL for lizards is the skin (cutaneous EWL), with further EWL occurring via the respiratory passages and the eyes (Shoemaker & Nagy 1977; Mautz 1982b). Rates of cutaneous EWL have been found to differ between lizard species according to habitat aridity (Mautz 1982a). Lizard species occupying drier (xeric) environments are predicted to exhibit lower rates of EWL than species inhabiting wetter (mesic) areas due to selection pressure to retain water more effectively (Warburg 1965; Eynan & Dmi'el 1993; Osojnik *et al.* 2013). Phenotypic adaptations can lower EWL, for example, species in more arid environments generally possess larger and fewer scales than species in humid environments, which lowers the exposure of non-keratinised skin to reduce water loss (Alibardi 2003; Wegener, Gartner & Losos 2014). While the potential implications of high EWL under climate change for species survival and distribution are widely recognised, there is a large gap in our knowledge of how much this trait varies both within and between species (Osojnik *et al.* 2013).

Inter-specific variation in critical thermal limits and EWL is increasingly recognised as having the potential to alter species survival and distribution under climate change (Huey *et*

*al.* 2012; Munoz *et al.* 2014; Sunday *et al.* 2014). Advances in our understanding of the level of inter-specific variation in key physiological traits allows species specific forecasts of responses under warming climates (Sinervo *et al.* 2010; Huey *et al.* 2012; Hoffmann, Chown & Clusella-Trullas 2013). Our aim in this study was to quantify inter-specific differences in thermal tolerances ( $CT_{min}$  and  $CT_{max}$ ) and EWL among closely related members of a temperate skink genus, *Niveoscincus* (Hutchinson & Schwaner 1991; Melville & Swain 2000b). This genus is composed of widespread lowland species which inhabit a wide geographic range from warm lowland areas to cooler subalpine areas and highland species limited to small disjunct mountain top populations (Wapstra *et al.* 2001; Melville 2008). We determined  $CT_{min}$ ,  $CT_{max}$  and EWL of a low altitude population of a widespread lowland species, *N. ocellatus*, and two highland snow skink species, *N. microlepidotus* and *N. greeni*. The population of the widespread lowland species inhabits a coastal site and has historically been exposed to warmer, lower humidity conditions, while the highland species have been subject to colder, highly variable (both among seasons and years), more moist conditions. We hypothesized that (1) the widespread lowland species would possess higher  $CT_{min}$  than both highland snow skink species; (2) the widespread lowland species and both highland species would exhibit relatively similar  $CT_{max}$  and; (3) that the widespread lowland species would exhibit lower EWL than both highland snow skinks. We subsequently examined the implications of widespread lowland and highland species' thermal tolerances for activity under two climate change scenarios. We used existing data on minimum and maximum temperatures selected for activity by the widespread lowland species at highland and lowland sites to examine the change in opportunity for activity at each sample site from 1960 to 2100.

## 2. Methods

The *Niveoscincus* genus is composed of small to medium sized viviparous skinks and encompasses eight species in total, six of which are endemic to the Southern Hemisphere island of Tasmania. We studied one widespread lowland species, *N. ocellatus*, and two highland species, *N. microlepidotus* and *N. greeni*. These species vary in distributional range. *Niveoscincus ocellatus* is widely distributed throughout eastern and central Tasmania from sea level to 1200 m above sea level (Figure 1, Melville & Swain 2000b). In contrast *N. microlepidotus* occurs in disjunct high altitude sites in southwest and central west Tasmania while *N. greeni* inhabits disjunct alpine locations in north east and central Tasmania (both species generally above 1100 metres above sea level; Figure 1).



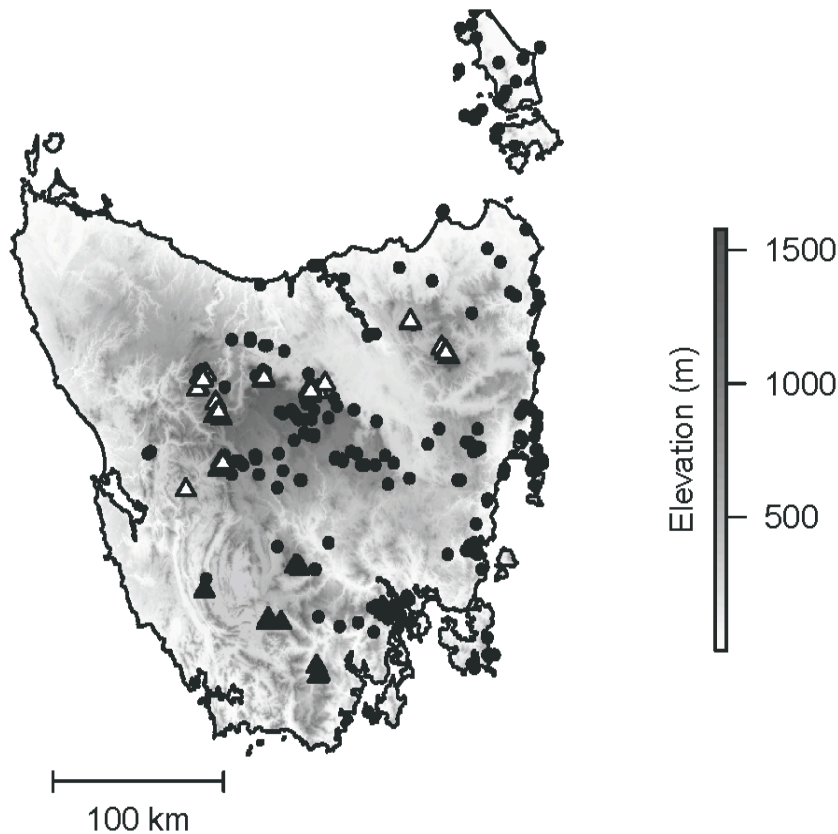


Figure 1: Distributions of the widespread lowland species, *N. ocellatus* (circles), and the highland species, *N. microlepidotus* (open triangles) and *N. greeni* (closed triangles).

### 2.1 Collection and husbandry of animals

*Niveoscincus ocellatus* was sampled from the warm lowland (50 metres above sea level) of its distribution in Orford (mean body mass  $4.87 \text{ g} \pm 0.27 \text{ s.e.}$ , mean snout-vent length (SVL)  $64.25 \text{ cm} \pm 1.05 \text{ s.e.}$ ,  $N = 12$ , captured December 5 2012, January 11, 29 and February 3 2013,  $-42.58^\circ$ ,  $147.85^\circ$ ). The first highland species, *N. microlepidotus*, was sampled from around 1200 meters above sea level on Mount Wellington (mean body mass  $4.06 \text{ g} \pm 0.15 \text{ s.e.}$ , mean SVL  $61.12 \text{ cm} \pm 1.11 \text{ s.e.}$ ,  $N = 17$ , captured January 20 and 28, 2013,  $-42.89^\circ$ ,  $147.23^\circ$ ). The second highland species, *N. greeni*, was sampled from Ben Lomond, an alpine site located 1560 – 1572 m above sea level (mean body mass  $4.79 \text{ g} \pm 0.18 \text{ s.e.}$ , mean SVL  $64.42 \text{ cm} \pm 0.71 \text{ s.e.}$ ,  $N = 19$ , captured January 6 2013,  $-41.53^\circ$ ,  $147.66^\circ$ ). We captured males to avoid the confounding effects of female reproductive cycles on physiology, which have been found to impact thermal traits including temperature preference profiles (Rodríguez-Díaz & Brana 2011). Capture took place within a two month period to avoid confounding seasonal effects on physiology (Seebacher & Franklin 2005; Andrews & Schwarzkopf 2012). Lizards were caught by “fishing” using a mealworm tied to a piece of cotton on the end of a

rod and lizards were held in cloth bags in the field before transfer to terraria for transport. Animals were transported to the Terrestrial Ecology Laboratories at the School of Biological Sciences at the University of Tasmania on the same day.

## 2.2 Critical Thermal Minimum, Critical Thermal Maximum and Evaporative Water Loss

Testing of  $CT_{min}$  and  $CT_{max}$  respectively occurred within the following mean days of capture for each species: *N. ocellatus*:  $13.50 \pm 4.82$  s.e. and  $13.92 \pm 4.87$  s.e. ( $N = 12$ ); *N. microlepidotus*:  $10.71 \pm 0.81$  s.e. and  $10.29 \pm 0.75$  s.e. ( $N = 17$ ); *N. greeni*:  $13.68 \pm 0.55$  s.e. and  $12.11 \pm 0.47$  s.e. ( $N = 19$ ). We employed the dynamic method to test  $CT_{min}$  and  $CT_{max}$  (Lutterschmidt & Hutchison 1997b). Specifically, the righting reflex was used to determine  $CT_{min}$  and the onset of spasms and loss of locomotor coordination used to establish  $CT_{max}$  (Lutterschmidt & Hutchison 1997a; Lutterschmidt & Hutchison 1997b). Once an observer is experienced these endpoints are readily identifiable and variance around the endpoints is typically low (Lutterschmidt & Hutchison 1997a). A single observer (A.J.C.) made all of the measurements and no adverse impacts on any animal were observed. Up to four animals at a time were placed in individual metal containers and these containers were placed inside a water bath. Thermocouples were used to monitor the temperature of the water bath and inside the holding container. In preliminary trials of  $CT_{min}$  and  $CT_{max}$  a thermocouple probe was inserted 1 cm into the cloaca to determine that the temperature of the animal matched the temperature of the metal holding container. As the temperature of the animal tracked the temperature of the container in preliminary trials a cloacal thermocouple was not used in subsequent tests as it restricts movements and hampered the identification of  $CT_{min}$  and  $CT_{max}$  endpoints. To determine  $CT_{min}$  the temperature in the water bath was decreased at a rate of  $0.64 \pm 0.01^{\circ}\text{C}$  s.e. per minute by adding ice until the temperature reached  $0^{\circ}\text{C}$ , and then transferring the container into a water bath of coolant and adding a predetermined volume of supercooled coolant at a steady rate. At each degree decrease below  $4^{\circ}\text{C}$  each animal was flipped on its dorsal surface to check for a righting response. To calculate  $CT_{max}$  the temperature of the water bath was increased from  $15^{\circ}\text{C}$  to  $45^{\circ}\text{C}$  at a rate of  $0.73 \pm 0.01^{\circ}\text{C}$  s.e. per minute using a water bath with a constant volume of water using a heating element. We chose these rates as slower heating rates have unpredictable effects on  $CT_{max}$  depending on the presence of positive effects of acclimation and the animals physical condition as longer heating rates require more energy (Rezende, Tejedo & Santos 2011). The order of testing each

critical thermal tolerance was varied so half the animals were tested for  $CT_{max}$  first and the other half of the sample were tested for  $CT_{min}$  first.

The EWL of animals were tested within  $13.0 \pm 5.48$  s.e. (*N. ocellatus*,  $N = 9$ ),  $7.65 \pm 0.485$  s.e. (*N. microlepidotus*,  $N = 17$ ) and  $4.32 \pm 0.265$  s.e. (*N. greeni*,  $N = 19$ ) mean days of capture. Evaporative water loss rates were determined using a closed circuit respirometry system maintained at  $15^{\circ}\text{C}$  to reflect mean maximum air temperatures experienced by highland populations (Pen *et al.* 2010). For consistency and due to the more benign measurement protocol, EWL was measured before  $CT_{min}$  and  $CT_{max}$ . Up to six animals were tested in each round within independent respiratory chambers. Completely dry air was alternately cycled through each chamber and passed through a corresponding syringe containing silica beads for five minutes in 35 minute intervals for 20 to 22 hours. A control syringe that was not connected to a chamber was used to measure baseline increases in weight of the syringes containing silica beads. Air flow was maintained within a range of 205 – 210 ml/min. The silica bead containing syringes were weighed two hours after the animals were introduced to the chamber and between 20 – 22 hours after the experiment began. Following placement in the respiratory chamber, a two hour stabilisation period was given to enable normalisation of metabolic rates. Silica beads were changed before each experiment and dried until the blue indicator returned to neutral prior to reuse. Data for three *N. ocellatus* were not included for EWL due to a misrun as a result of power failure midway through the test. Each animal chamber was cleaned and dried prior to the next experiment. The rate of mass specific evaporative water loss was calculated by dividing the change in mass of water by mass of the animal and the time of the trial ( $\text{mg g}^{-1} \text{h}^{-1}$ ). There were no adverse impacts in any of the trials, and all lizards were released at the location of their capture.

Data were analysed using IBM SPSS Statistics 20. We were interested in species differences in  $CT_{min}$ ,  $CT_{max}$  and EWL. Using Q-Q plots we established that  $CT_{min}$ ,  $CT_{max}$  and EWL adhered to assumptions of normality and homogeneity of variance. One way analyses of variance and Tukey's HSD test were performed to determine species differences in  $CT_{min}$ ,  $CT_{max}$  and EWL. Mass did not affect the critical thermal tolerance limits of any of the species ( $p > 0.05$  in all cases).

### 2.3 Climate Data and Impact Projections

We explored projected climatic changes at each sample site and possible implications of inter-specific differences in thermal tolerances for survival and activity. Fine scale climate projections of 0.1 degree resolution or better (approximately 10 km) were produced for Tasmania by Climate Futures for Tasmania (Corney *et al.* 2010). These projections were produced using dynamical downscaling and account for the complex processes influencing Tasmania's weather and climate (Corney *et al.* 2010). The Climate Futures for Tasmania data allows for location specific predictions to be made for a range of climate parameters for any day within the 21<sup>st</sup> century. Six general circulation models (GCM) were used to indicate the range of potential future climates (Corney *et al.* 2010). To bracket probable future climate change in the absence of mitigation policies, our projections were based on a high and low emissions scenario (A2 and B1 respectively, Le Quere *et al.* 2009; Peters *et al.* 2013).

We extracted data for predicted environmental evaporative water loss and daily minimum and maximum air temperatures and relative humidity using coordinates for each of our collection sites for the period 1960 – 2100 from the Climate Futures for Tasmania. To examine how physiological traits influence survival under climate change, we examined instances of predicted air temperatures which were outside each species thermal limits at their respective sample sites. These models tallied the number of days per year that daily minimum and daily maximum ambient air temperatures were below or above each species  $CT_{min}$  or  $CT_{max}$  respectively from 2010 – 2100. To provide an estimate of the effect of climate change on activity we reran the thermal tolerance models in R using known minimum and maximum body temperatures selected for activity ( $T_{sel}$ ) by the widespread lowland species (Yuni, Jones & Wapstra Submitted). The range of  $T_{sel}$  (15 – 30°C) that the widespread lowland species were recorded as active was derived from the same lowland population examined in this study over three seasons (Yuni, Jones & Wapstra Submitted). The average  $T_{sel}$  of a highland population of the widespread lowland species (10 – 25°C) over three seasons was used as a proxy for both highland species  $T_{sel}$  as there is no comparable data available for these species (Yuni, Jones & Wapstra Submitted). Modelling of the highland species via the comparable high altitude population of the lowland species data allows activity to be conservatively estimated. These species occur in sympatry over a narrow altitudinal range and have similar activity times at these areas (Melville & Swain 1997). We estimated the effect of climate change on the availability of daily maximum air temperatures within the range of the widespread lowland species  $T_{sel}$  over the next century at the lowland and highland sample

sites. Because these species are diurnally active we did not use minimum daily air temperatures in the  $T_{sel}$  models as low temperatures generally occur at night, outside of the normal activity period. We calculated the cumulative number of days on which the maximum predicted air temperatures remain within the minimum and maximum  $T_{sel}$  for the widespread lowland species (15 – 30°C) and the highland species proxy  $T_{sel}$  (10 – 25°C) for 2010 – 2020 and 2090 – 2100 under both the A2 and B1 scenarios of climate change. All climatic data analysis was carried out in R (R core team 2014).

### 3. Results

We found significant differences between species in all three of our physiological traits. First, we found significant species level differences in  $CT_{min}$  ( $F_{2, 47} = 25.911$ ,  $p < 0.001$ ). The widespread lowland species had a  $CT_{min}$  approximately 3.5°C higher than the highland species, *N. greeni* ( $p < 0.001$ , Figure 2a) and *N. microlepidotus* ( $p < 0.001$ , Figure 2a), while the  $CT_{min}$  of the highland species did not differ significantly from each other ( $p = 0.965$ , Figure 2a). Second,  $CT_{max}$  also differed significantly among species ( $F_{2, 47} = 4.799$ ,  $p = 0.01$ ). The widespread lowland species had a  $CT_{max}$  approximately 1.2°C degree higher than both highland species, *N. microlepidotus* ( $p = 0.023$ , Figure 2b) and *N. greeni* ( $p = 0.020$ , Figure 2b), while  $CT_{max}$  did not differ between the two highland species ( $p > 0.100$ , Figure 2b). Finally, there were significant differences among species in evaporative water loss rates ( $F_{2, 44} = 6.843$ ,  $p = 0.003$ ). The widespread lowland species had a significantly lower EWL than both highland species: *N. microlepidotus* ( $p = 0.006$ ) and *N. greeni* ( $p = 0.003$ , Figure 3). The highland species did not differ significantly from one another in EWL ( $p = 0.976$ , Figure 3). Differences in the thermal tolerances established for these species closely correspond to temperature and humidity patterns of respective sample sites (Figure 4).

We examined the potential consequences of inter-specific differences in thermal tolerance for activity and survival as a result of changes in air temperatures and humidity over the next 100 years. Under both the A2 and B1 scenarios of climate change the number of days with minimum air temperatures below the  $CT_{min}$  are predicted to decrease greatly over the next century at each study site (Figure 5). In contrast, we found little evidence of a change in the number of days with maximum air temperatures above  $CT_{max}$  (Figure 5). These results suggest that lizards will not need to decrease their activity to avoid fatally high temperatures.

In contrast to  $CT_{max}$ , the incidence of daily maximum air temperatures above the maximum  $T_{sel}$  across all sites increased, which will limit activity in the middle of the day on the hottest days (Figure 6). Increased incidences of temperatures above the maximum temperatures selected for activity were greater at the highland species sites than the widespread lowland species site (Figure 6). However, we also found a reduction in the incidence of air temperatures below the minimum  $T_{sel}$  at both the highland species' sites and the widespread lowland species sites. This reduction in daily maximum air temperatures below the minimum  $T_{sel}$  was greater than the increase in air temperatures above the maximum  $T_{sel}$  for all sites, resulting in an overall increase in the total number of days that are thermally suitable for activity (Figure 6). Specifically, under the A2 scenario of climate change the number of days in which the maximum predicted air temperature falls within  $T_{sel}$  for 2010 – 2020 and 2090 – 2100 respectively increased by 30% for the widespread lowland species (from 221 to 287 days) and by 24% (from 232 to 288 days) and 26% (from 242 to 306 days) for the two highland species, *N. microlepidotus* and *N. greeni*, respectively. Under the B1 scenario similar increases were observed for the periods 2010 – 2020 and 2090 – 2100, with the number of days in which the maximum predicted air temperature falls within  $T_{sel}$  rising by 14% for the widespread lowland species (from 222 to 253 days), by 10% for *N. microlepidotus* (from 235 to 259 days) and 13% for *N. greeni* (from 243 to 274 days).

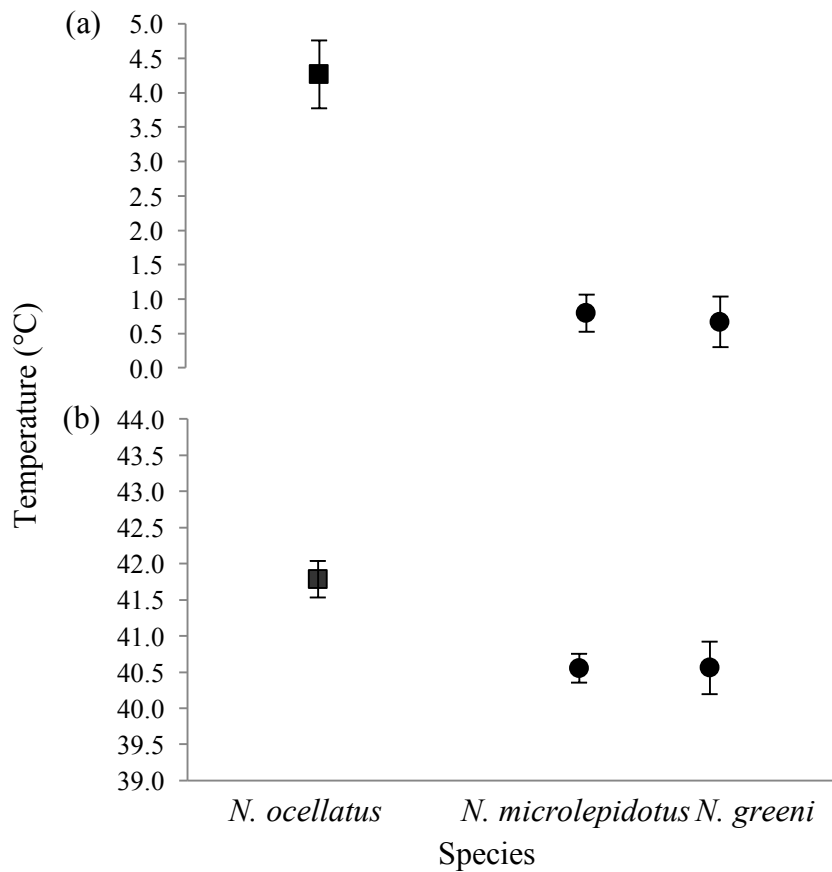


Figure 2. Mean  $\pm$  SE critical thermal tolerance (a) minimum (CT<sub>min</sub>) (b) and maximum (CT<sub>max</sub>) for a widespread lowland (*N. ocellatus*, N= 12) and two highland (*N. microlepidotus*, N = 17; *N. greeni*, N = 19) members of the snow skink genus *Niveoscincus*.

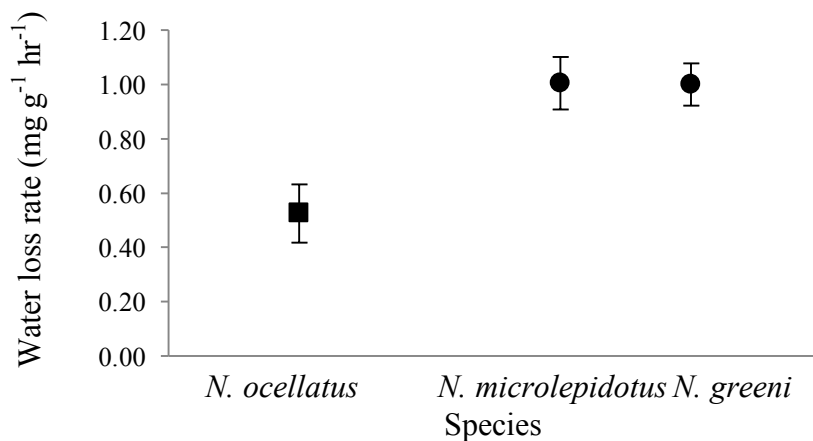


Figure 3. Mean  $\pm$  SE mass specific evaporative water loss rate of a widespread lowland (*N. ocellatus*, N = 9) and two highland (*N. microlepidotus*, N = 17; *N. greeni*, N = 19) members of the snow skink genus *Niveoscincus*.

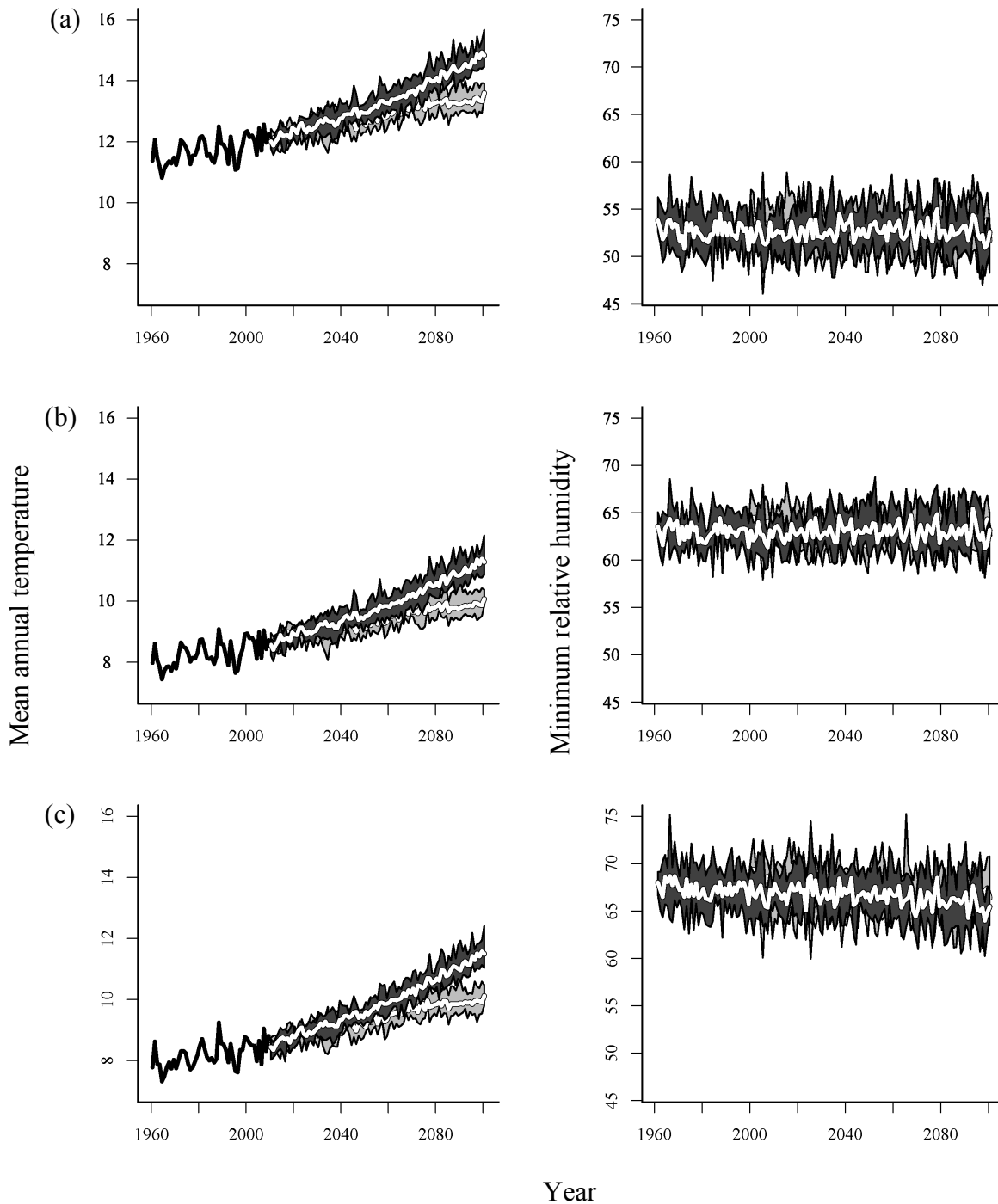


Figure 4. Historicals and predicted air temperature and minimum relative humidity from the environment for population sites of three Tasmanian snow skink species: (a) a lowland species, *Niveoscincus ocellatus* at Orford, and two highland species (b) *N. microlepidotus* at Mount Wellington and (c) *N. greeni* at Ben Lomond. Using climate predictions generated by Climate Futures for Tasmania, A2 (dark grey) and B1 (light grey) climate scenarios are presented with estimates of predicted climate tracking from 6 GCMs.



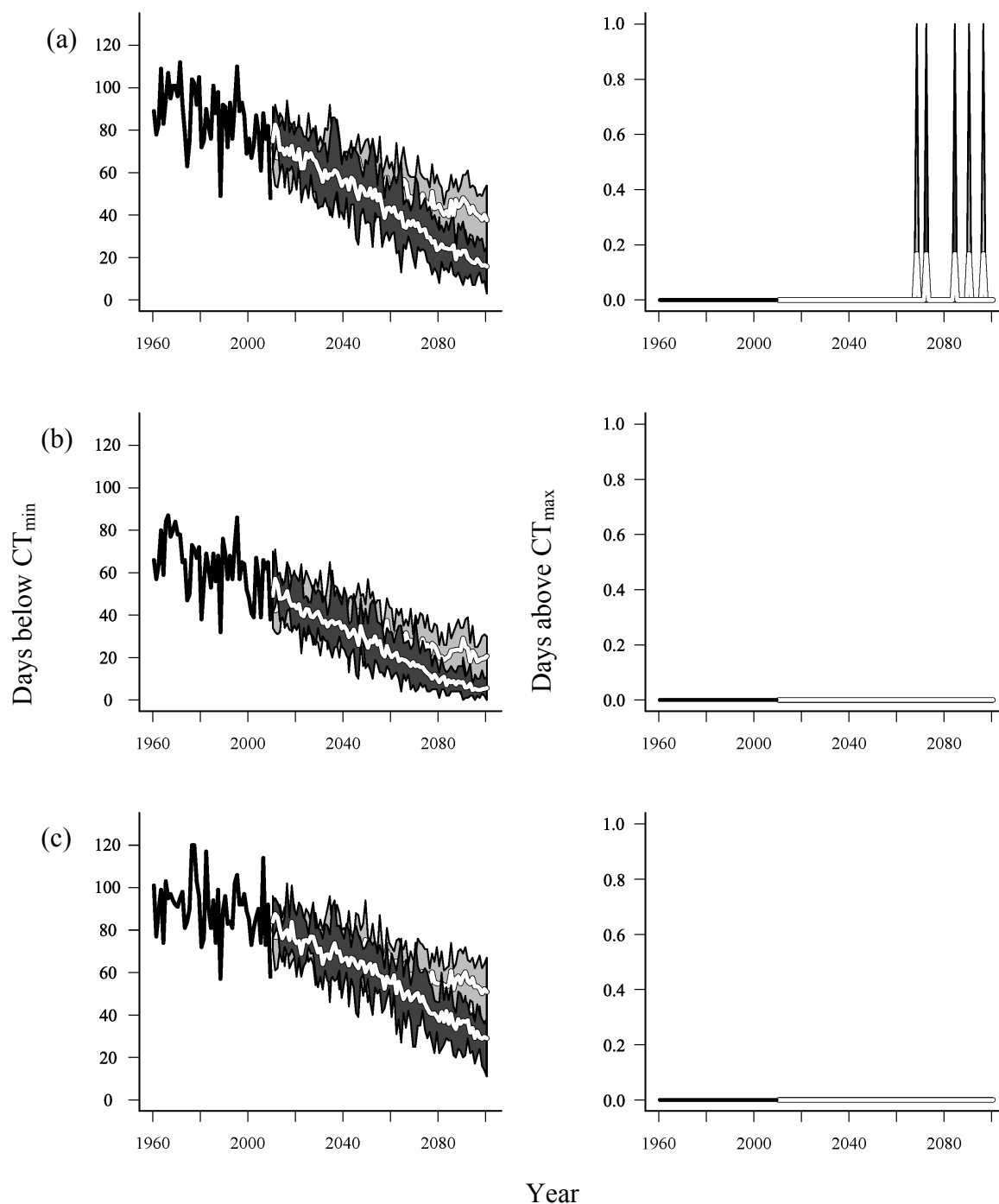


Figure 5. Number of days that air temperature is (a) above critical thermal maximum limits and (b) below critical thermal minimum limits for (i) a lowland species, *Niveoscincus ocellatus* at Orford, and two highland species (ii) *N. microlepidotus* at Mount Wellington and (iii) *N. greeni* at Ben Lomond. A2 (dark grey, extreme) and B1 (light grey, moderate) climate scenarios are presented.

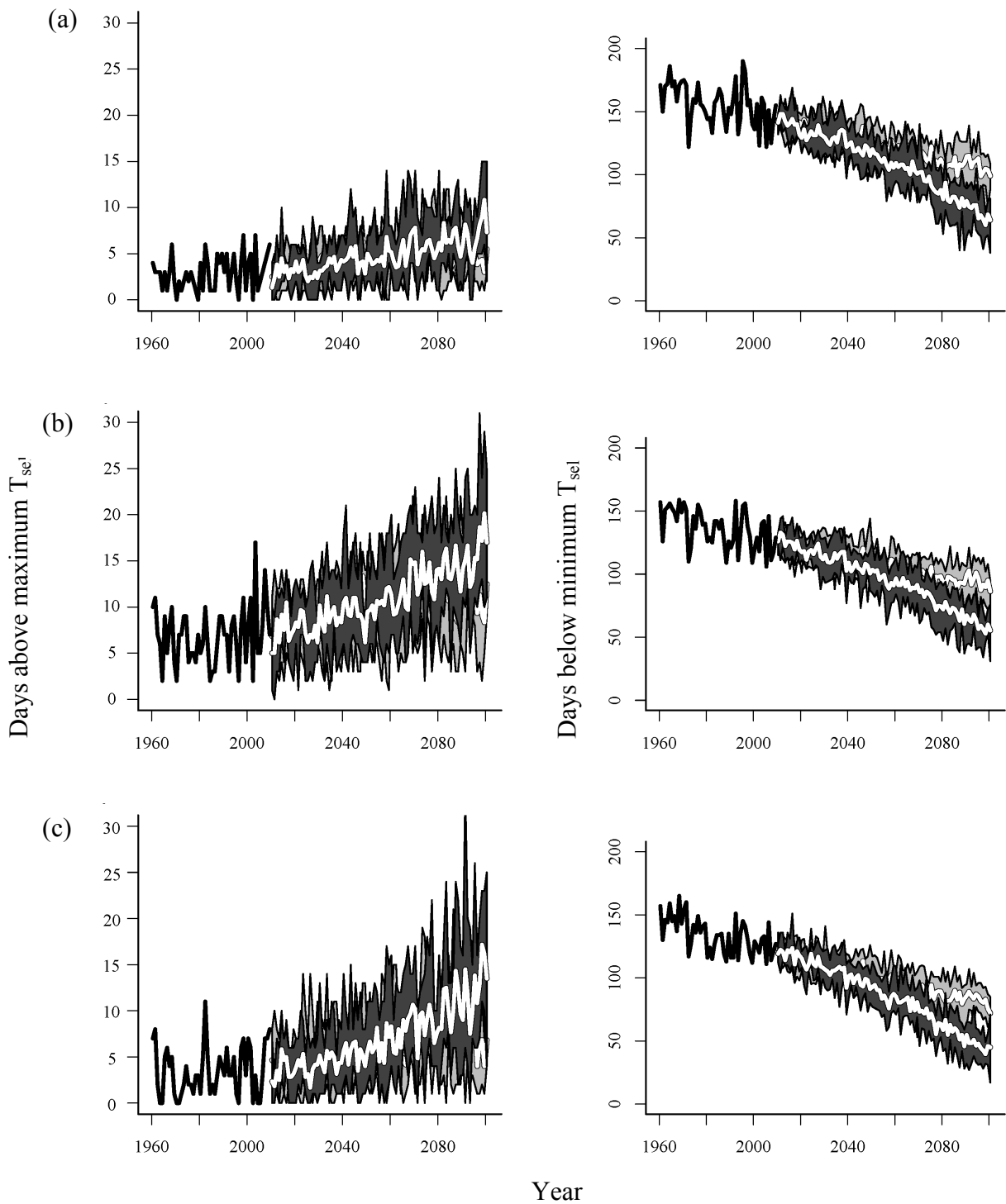


Figure 6. Number of days air temperature is below the minimum air temperature selected for activity (left) or above the maximum air temperature selected for activity (right) at the capture sites of the lowland species *N. ocellatus* at Orford (a), and the highland species *N. microlepidotus* at Mount Wellington (b) and *N. greeni* at Ben Lomond (c).

#### 4. Discussion

In accordance with our predictions, the widespread lowland *Niveoscincus* species, *N. ocellatus*, exhibited significantly higher critical thermal minimum ( $CT_{min}$ ) and significantly lower evaporative water loss rate (EWL) than both of the highland species, *N. greeni* and *N. microlepidotus*. In contrast to our hypothesis that the critical thermal maximum ( $CT_{max}$ ) would be similar across species, we found the  $CT_{max}$  of the widespread lowland species was significantly higher than both highland species. The highland species, *N. greeni* and *N. microlepidotus*, did not differ significantly from one another in  $CT_{min}$ ,  $CT_{max}$  or EWL. The thermal limits in each of these species have significant consequences for activity time under projected global climate change. Although there is relatively little likelihood of temperatures exceeding the  $CT_{max}$  of any of the species, temperatures are predicted to exceed the upper limit of temperatures selected for activity (Yuni, Jones & Wapstra Submitted). This will be offset, however, by a decreasing incidence of temperatures below the minimum temperatures suitable for activity. Overall the number of days in which the maximum predicted air temperature falls within the  $T_{sel}$  for both lowland and highland snow skink species sites is projected to increase by between 10 – 30 % under the two climate change scenarios.

Differences in  $CT_{min}$  and  $CT_{max}$  between the widespread lowland species and both highland species reflect the environmental temperatures at the respective sites. The widespread lowland species was sampled from a warm coastal site which is subject to less extreme minimum temperatures and higher mean environmental temperatures than the highland species sites. We found that the  $CT_{min}$  of the widespread lowland species and both highland species are among the lowest  $CT_{min}$  recorded for lizards (Bennett & John-Alder 1986; Clusella-Trullas & Chown 2014) probably reflecting their low latitude temperate and alpine distribution. We also found less inter-specific variation in  $CT_{max}$  than  $CT_{min}$  (~3 °C versus 1.5 °C) which is in line with recent meta-analyses on ectotherms (Chown *et al.* 2004; Sunday, Bates & Dulvy 2011; Araújo *et al.* 2013; Munoz *et al.* 2014; Sunday *et al.* 2014). Behaviours, such as regulating the timing of activity, retreat site choice and posture, enable lizards to target specific body temperatures to maximise physiological processes and avoid temperatures above their maximum critical thermal limit, resulting in a low degree of variation in this trait (Huey & Pianka 1977; Stevenson 1985b; Huey *et al.* 2012). In contrast, behaviour can only partially buffer exposure to low temperatures as these species are inactive at night and have long periods of stasis during winter (Huey, Hertz & Sinervo 2003; Munoz *et al.* 2014).

Furthermore, lizards must emerge and experience low temperatures close to  $CT_{min}$  in order to bask and reach their preferred body temperatures. Thus greater variability should exist in  $CT_{min}$  across latitudinal or altitudinal gradients than  $CT_{max}$ , because behavioural thermoregulation is more efficient at shielding organisms from selection on upper, rather than lower, thermal tolerances. Rates of evaporative water loss (EWL) between the species were also reflective of the environmental conditions experienced at each of the sites they occupy. Lizards from the lowland site experience lower relative humidity and higher mean temperatures than do lizards from the two highland sites. This is in line with previous studies of EWL that have shown that species inhabiting drier and/or warmer localities exhibit reduced water loss rates compared to their counterparts inhabiting wetter and/or cooler sites (Hillman & Gorman 1977; Perry, Dmi'el & Lazell 2000; Guillon *et al.* 2013). Changes in climate are likely to include small but significant changes to demands on water balance due to projected increases in evaporation rates, reductions in cloud cover, rising humidity and increasing winds in spring (Corney *et al.* 2010). However, at this stage the nature and level of selection acting on evaporative water loss rates due to warming environments is unclear. Combined these results suggest substantial differences between species in both thermal tolerance and EWL. At this stage we cannot establish the extent to which these differences are the result of genetic differences among populations or are the result of phenotypic plasticity in response to the prevailing environment. Separation of these two hypotheses could be achieved by examining the expression of thermal tolerance and EWL of these different species when held under a common garden.

What are the consequences for inter-specific differences in thermal tolerance and EWL for these lizards under climate change? Climate forecasts indicate that occurrences of minimum air temperatures below  $CT_{min}$  will be less frequent and there will be little to no occurrence of maximum air temperatures above  $CT_{max}$ . Furthermore, the number of days in which the maximum predicted air temperature falls within  $T_{sel}$  is forecast to increase for the species studied by between 10 – 30% within the 21<sup>st</sup> century. This suggests that, in contrast to tropical species, whose activity is predicted to decrease with climate change (Huey *et al.* 2009), temperate species may benefit, at least in the short term, from increases in temperature. This will depend on the extent to which other factors, such as competition, resource availability and offspring fitness, are influenced by changing climatic conditions (Olsson & Shine 1998; Gibbons *et al.* 2000; Wapstra *et al.* 2009; Van der Putten, Macel & Visser 2010; Wapstra *et*

*al.* 2010). A caveat to this result is that it is based on a single climate parameter (maximum daily air temperature) to estimate the potential number of days available for activity. This method excludes days on which lizards may have been active for part of the day despite the maximum air temperature ultimately exceeding maximum  $T_{sel}$ . The method also includes days on which minimum  $T_{sel}$  was exceeded but lizards may only have been able to be active for a limited part of the day. This method also excludes periods where maximum air temperature was below minimum  $T_{sel}$ , despite the lizards potentially being able to raise body temperatures above ambient via microhabitat selection (e.g. thigmothermy) to prolong activity time (Melville & Swain 1997). Our predictions are likely to be less accurate for lower air temperatures than higher air temperatures, because lizards should regulate their exposure to air temperatures above the thermal optimum for performance ( $T_{opt}$ ) more closely than air temperatures below  $T_{opt}$ , as  $T_{opt}$  is often close to  $CT_{max}$  (Logan et al., 2014). Consequently, temperatures above  $T_{opt}$  are expected to have a greater impact on lizard activity and survival (Martin and Huey, 2008). More in depth climate projections, for example minimum day time temperatures and more frequent estimations of temperatures within the diurnal activity period, would allow a more accurate estimation of the potential for activity under climate change in the future. It is important to account for several additional consequences of these shifts in temperatures for these species. While there were few instances of air temperatures exceeding the  $CT_{max}$  of the widespread lowland species, *N. ocellatus*, and these instances did not occur under all of the Global Circulation Models, temperatures forecast by Climate Futures for Tasmania were shade temperatures, with warming temperatures potentially having a greater effect in more exposed areas within the microhabitat. This would restrict activity to cooler refuges and may limit key behaviours such as foraging, territory defence and mating, with cascading effects at the population level (Sinervo et al., 2010).

Data on basal physiological traits are becoming increasingly important for comparative purposes as a growing number of authors focus on making broad inferences about potential climate change impacts (Thomas *et al.* 2004; Sinervo *et al.* 2010; Kearney *et al.* 2014; Sunday *et al.* 2014). We have demonstrated that highland and widespread lowland species within a closely related cool temperate Southern Hemisphere lizard genus display significant differences in thermal tolerances and evaporative water loss. Despite these differences all species were suggested to respond similarly to climate change in terms of an increase in the time available for activity. Changes in activity time were predicted to be most pronounced for

the widespread lowland species. However, there are additional climate change consequences which may offset any benefits from increased activity period, for example by altering the interactions occurring between these species. Incorporating an understanding of inter-specific variation in physiological traits is likely to be crucial for generating a more holistic, mechanistic understanding of the impacts of changing climates on these species and their distributions (Kearney & Porter 2004; Mitchell *et al.* 2008; Huey *et al.* 2012).

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# CHAPTER THREE





# Plasticity of thermoregulatory behaviour in response to the thermal environment by widespread and highland reptile species

*As submitted to Animal Behaviour.*

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## Abstract

Behaviour plays a central role in determining the responses of organisms to environmental change over short time scales. Despite this, our understanding of the extent to which plasticity can mediate the effects of environmental change is still relatively limited. We tested the capacity for low and high altitude populations of two widespread lowland and two highland species of a cool climate lizard genus, *Niveoscincus*, to respond to variation in basking opportunities characteristic of the group's climatic limits. We measured changes in time spent basking and preferred body temperature under controlled laboratory conditions. Highland species and high altitude populations basked more than the widespread lowland species and low altitude populations respectively. However, all *Niveoscincus* species exhibited similar levels of behavioural plasticity, responding to increased basking opportunity by reducing the time spent basking. Behavioural responses to the thermal environment translated into different effects on body temperature at the species level. However, while widespread lowland species reduced body temperatures when exposed to high basking opportunity, highland species maintained consistently high body temperatures. Our study exemplifies the importance of incorporating the potential for population and species-level differences in behaviour when examining responses to environmental change.

**Keywords:** thermoregulation; highland specialist; montane species; phenotypic plasticity; reptile.

## 1. Introduction

Human mediated impacts on the environment are placing increasing pressure on species worldwide (Leadley 2010). As a direct result of these anthropogenic effects, a large proportion of the Earth's biodiversity is threatened with extinction (e.g., Parmesan 1996; Edwards & Richardson 2004; Thomas *et al.* 2004; Pereira *et al.* 2010). Species can respond to changing environments in three ways: by adapting *in situ* (Parmesan 2006), by keeping pace with the preferred environment in physical space (e.g., dispersal), or via plastic responses (Davis, Shaw & Etterson 2005; Jump, Peñuelas & Hurr 2005). As climate change is progressing at a rate predicted to outpace evolutionary change in many species (Skelly *et al.* 2007; Huey, Losos & Moritz 2010) and habitat fragmentation and species interactions prevent many species from tracking their preferred environment in space (Chevin, Lande & Mace 2010), plasticity will be vital if species are to persist under changing environments (Davis, Shaw & Etterson 2005; Jump, Peñuelas & Hurr 2005; Hoffmann & Sgrò 2011).

Populations and species differ in the magnitude of behavioural plasticity (Coppens, de Boer & Koolhaas 2010; Dingemans & Wolf 2013). The extent to which organisms' possess an intrinsic capacity for plastic responses will depend partly on their historical exposure to different selection regimes (Komers 1997; Snell-Rood 2013). Our understanding of how environmental conditions shape plasticity in behaviour remains incomplete. On the one hand, extreme environments can result in the canalisation of behaviour (see Uller *et al.* 2011) resulting in reduced behavioural plasticity, while relatively benign environments may promote selection for behavioural plasticity (Snell-Rood, 2013). Conversely, fluctuating or changeable conditions might select for greater plasticity. Importantly, the extent of behavioural consistency / plasticity will limit the potential for behaviour to mediate responses to altered environmental conditions and ultimately its impacts on physiological processes. This may have significant implications for the extent to which populations and species can persist under ongoing environmental change (Dingemans & Wolf 2013). Therefore, research is needed which establishes the extent to which behaviours vary across populations as a result of historical selection pressures and the consequences of behavioural plasticity for fundamental physiological processes.

Squamate reptiles provide a particularly interesting test case in this context. On the one hand, a growing number of studies predict dire consequences for reptile biodiversity under climate

change (Thomas *et al.* 2004; Araújo, Thuiller & Pearson 2006; Whitfield *et al.* 2007; Bickford *et al.* 2010; Reading *et al.* 2010; Sinervo *et al.* 2010; Böhm *et al.* 2013) as reptiles rely on a narrow, species-specific range of body temperatures for activity and the proper functioning of fundamental biological processes (Sunday *et al.*, 2014). On the other hand, reptiles possess a variety of mechanisms which may allow them to persist under changing environmental conditions. In particular, behavioural thermoregulation can buffer the impact of changes in the thermal environment by allowing the maintenance of target temperatures under novel thermal environments via the modification of activity time and the exploitation of sun/shade (Porter & Tracy 1983; Kearney, Shine & Porter 2009). Therefore, plasticity in thermoregulatory behaviour may be crucial to the persistence of reptile populations under changing environmental conditions. Despite this, our understanding of the extent to which plasticity varies among or within populations and the consequences the extent to which behavioural plasticity has the potential to mediate the effects of environmental change is still relatively limited (Porter & Tracy 1983).

Here, we examined differences in the thermoregulatory behaviour of two widespread lowland species (*Niveoscincus ocellatus* and *N. metallicus*) and two highland species (*N. greeni* and *N. microlepidotus*) of a Tasmanian lizard. Widespread lowland *Niveoscincus* occur over a wide altitudinal (0 to ~1150 m above sea level) and geographic range, while highland *Niveoscincus* are limited to disjunct mountain top localities (> ~1100 m a. s. l.). As a result of their different distributional ranges, populations of the widespread lowland and highland species have experienced historically divergent local thermal environments both within and among species. Specifically, environmental conditions at high altitude sites are much cooler and variable than those at low altitude sites, resulting in shorter activity seasons and greater climate-mediated constraints on basking opportunity. This may have resulted in stronger selection to optimise basking behaviour and tightly regulate selected body temperatures in high altitude populations than low altitude populations (Uller *et al.* 2011; Cadby, Jones & Wapstra 2014). To test whether the thermoregulatory strategies of high altitude populations and highland species are more or less responsive to environmental change than low altitude populations and widespread lowland species respectively, we exposed individuals to high or low basking opportunity and examined basking behaviour and body temperature responses. We predicted that high altitude populations and highland species would spend more time basking, show greater plasticity in basking time in response to basking opportunity and

maintain higher body temperatures (irrespective of basking opportunity) than low altitude populations and widespread lowland species respectively.

## 2. Methods

### 2.1 Study species, collection and husbandry of animals

Adult male lizards of two widespread lowland species, *N. ocellatus* and *N. metallicus*, and two highland species, *N. greeni* and *N. microlepidotus*, were collected from six sites within Tasmania (see Table 1 for details of the location and habitat characteristics of each site) over a one-month period in November and December 2010. Sites differed considerably in their temperature and rainfall profiles (Fig. S1). We targeted populations at the altitudinal extremes of each species distribution, resulting in a lowland and a highland population for each species (hereafter referred to as “low” and “high” respectively; see Table 1 for details). Although, for highland species, these populations differed by only a small distance, due to the smaller geographic distributions overall (they are restricted to disjunct mountain tops), these populations still represented the altitudinal extremes of the species distributions and small changes in altitude can correspond with substantial differences in temperature (Körner, 2007; Pepin & Lundquist, 2008; Whiteman et al., 2004). There are no strong phylogenetic affiliations among species in either of the species groups, with phylogenetic analyses separating *Niveoscincus* into three sister clades, with *N. metallicus* and *N. microlepidotus* in separate clades and *N. ocellatus* and *N. greeni* grouped together (Melville and Swain, 2000). Therefore, any consistency in results gained from this study across species groups (see below) are unlikely to be driven by a shared evolutionary history. We caught adult males for this experiment to avoid the potential confounding effects of the female reproductive cycle on thermal traits (Schwarzkopf & Shine 1991; Atkins et al. 2007).

Upon capture, field active temperatures of each lizard were measured using an infrared thermometer (Testo© 805 Infrarot-Thermometer; resolution of 0.1°C, Table S1).

Temperature readings were taken at a close range (ca. 10 mm) using a consistent lateral orientation to ensure readings produce measurements of surface temperature which closely relate to core temperature (Hare, Whitworth & Cree 2007; Jones & Avery 1989). Lizards were transported to the University of Tasmania’s Terrestrial Ecology Laboratories at the School of Biological Sciences. On arrival at the laboratory lizards were weighed ( $\pm 0.01$  g), measured for snout-vent length, vent to tail length and tail regrowth ( $\pm 0.5$  mm, see Table S1



for details of differences in size among species/populations/treatments). We excluded lizards which had experienced recent tail autotomy. None of the lizards included in the study were shedding upon capture or during the experiment.

Lizards were then transferred into individual housing (30 x 20 x 10 cm) and maintained under standard laboratory conditions. Each terrarium had a mesh cover, absorbent bedding (paper pallets), a retreat for cover (wood block), a water dish and a tile beneath a basking lamp (Fig. S2). The basking lamp was suspended 120 mm above the terrarium to generate a gradient of ca. 15°C (under the retreat away from the lamp) to ca. 40°C (under the basking lamp, Wapstra 2000). During the acclimation period basking opportunity was provided between 0900 – 1600 hours. Bright UV lights at an intensity of 20 000 lux operated overhead between 0700 – 1900 hours. Lizards were fed twice weekly, 48 hours prior to each set of behavioural observations, 24 hours prior to each set of body temperature readings. This ensured lizards were in a post-absorptive state when behavioural and body temperatures were measured, as digestion has an unpredictable effect on thermal traits (Regal 1966; Van Damme, Bauwens & Verheyen 1991). Lizards were fed tenebrio larvae and fruit (Heinz<sup>®</sup> pear and banana or apple) supplemented with calcium (Repti-Cal (aristopet, Queensland)) alternating with ‘premium calcium with seaweed’ (Vetbasix<sup>™</sup>, Victoria), protein (Natures Way<sup>®</sup>, New South Wales) and multivitamins (‘Herptivite with beta carotene’, Rep-Cal, Canberra). Water was provided *ad libitum*. Lizards were oiled fortnightly to remove ectoparasites.

## 2.2 Ethical note

All procedures outlined in this study were approved by the University of Tasmania’s Animal Ethics Committee (approval number A0011478).

Table 1: Location of each field site for populations of each species, with a brief description of the vegetation of the microhabitat occupied by each population.

Study species	Study site	Pop.	Altitude (a. s. l.)	Co-ordinates	Basking surface	Undergrowth type	Canopy type
<i>N. ocellatus</i>	Central Plateau	high	1050 – 1080 m	-41.76°, 146.72°	Boulder	sub- alpine heaths (<1 m)	usually absent
	Orford	low	80 – 102 m	-42.58°, 147.85°	dolerite rocks	low shrubs (<0.8 m)	eucalypts (<15 m)
<i>N. metallicus</i>	Mt Wellington	high	1087 – 1176 m	-42.89°, 147.23°	ground/ litter/ rock	small-tall shrubs (0 – 2m)	eucalypts (15 – 40 m)
	Orford	low	80 – 102 m	-42.58°, 147.85°	ground/ litter/ rock	small shrubs (<1 m)	eucalypts (<15 m)
<i>N. greeni</i>	Ben Lomond	high	1095 – 1100 m	-41.53°, 147.66°	dolerite boulders	usually absent	absent
	Central Plateau	low	1050 – 1080 m	-41.76°, 146.72°	dolerite boulders	sub-alpine heaths (<1 m)	usually absent
<i>N. microlepidotus</i>	Mt Wellington	high	1250 – 1255 m	-43.25°, 146.77°	heath / boulder	alpine heath (0.8 m)	absent
	Hartz Peak	low	1087 – 1176 m	-42.89°, 147.23°	boulders	alpine heath (0.8 m)	absent

### 2.3 Basking opportunity treatments

Following an initial acclimation period of two weeks, lizards were randomly assigned to a prolonged or reduced basking opportunity treatment. In the prolonged basking opportunity treatment lizards were given access to the basking lamp for 8 hours per day (0900 – 1700). In the reduced basking opportunity treatment lizards were given access to the basking lamp for 4 hours per day (1000 – 1400). These experimental treatments were chosen to replicate natural basking opportunities (i.e. sunshine hours) normally experienced in coastal (prolonged basking opportunity) and mountain (reduced basking opportunity) sites (Wapstra 2000; Uller *et al.* 2011).

Lizards were able to thermoregulate freely and achieve preferred body temperatures when the basking light was on. The two basking opportunity treatments resulted in differences between the thermal treatments in the daily temperature profiles available (Fig. S3). To quantify the temperatures profiles produced by each thermal treatment, we took half hourly temperature recordings for 5 days following the experiment. Four ibuttons were positioned at locations corresponding to the four categories a – d described below, in two empty terraria for each thermal treatment (Fig. S3). The mean and standard error was calculated to produce a daily thermal profile for each treatment (Fig. S3). These basking opportunity treatments have been used in multiple laboratory studies to induce climate responses in *Niveoscincus*, such as differences in birthdate, offspring phenotype and fitness (Wapstra 2000; Cadby *et al.* 2010; Wapstra *et al.* 2010; Uller *et al.* 2011). Basking treatments have also been used to induce a climate response in other lizard species; for example to generate large differences in rates of energy acquisition (Doughty & Shine 1998), gestation length (Schwarzkopf & Shine 1991), degree of birth asynchrony, offspring phenotype (While & Wapstra 2009), date of birth, offspring growth rate and performance (Itonaga, Jones & Wapstra 2012). Terraria were positioned randomly within each basking opportunity treatment, and repositioned a day prior to each set of behavioural observations to minimize positional effects.

Basking behaviour was assessed twice a week for four weeks, resulting in a total of 8 days of behavioural observations per lizard. Basking behaviour was assessed by recording the location of each lizard relative to the basking light at 30 minute intervals from 0830 – 1800 for the prolonged basking opportunity treatment and 0930 – 1500 for the reduced basking opportunity treatment inclusive. The additional readings outside of the basking hours were

included to illustrate diurnal activity patterns; this data was not included in analyses of thermoregulatory behaviour. Each lizard's position was assigned a category: a = on the basking tile; b = not on the basking tile but within the immediate range of the basking lamp; c = in the open but out of the immediate range of the basking lamp; d = under the retreat (Fig. S2). The surface body temperature of each lizard was measured on three occasions (17, 20 and 24/1/2010) with an infrared thermometer using the method described above. On each occasion individuals were removed from their terrarium and measured immediately. Three consecutive temperature readings of the dorsum were made and the highest reading recorded. Measurements took place 3 – 4 hours after the basking lights were switched on for each basking opportunity treatment (from 1200 – 1300 h for the prolonged basking opportunity treatment and 1300 – 1400 h for the reduced basking opportunity treatment). This allowed lizards to freely thermoregulate and reach their preferred body temperature (see Table S1 for comparisons with field active temperature). Body temperatures were measured on days which basking behaviour was not monitored. All lizards were returned to their site of capture immediately following the conclusion of the study.

#### *2.4 Statistical analyses of basking behaviour and body temperature*

Basking behaviour refers to the proportion of time spent under the basking light when basking was available (from 0900 – 1700 h and 1000 – 1400 h for the prolonged and reduced basking regimes respectively). The proportion of time spent basking was estimated for all individuals which displayed basking behaviour on four or more of the eight observational days ( $n = 191$  individuals). Individuals who were never observed to bask were excluded because a lack of basking behaviour during the study period (summer) indicates abnormal behaviour (reduced basking treatment: *N. greeni*  $N_{\text{low population}} = 1$ , *N. ocellatus*  $N_{\text{high population}} = 2$ ;  $N_{\text{low population}} = 5$ ; prolonged basking treatment: *N. ocellatus*  $N_{\text{high population}} = 4$ ,  $N_{\text{low population}} = 2$ ).

We ran linear mixed-effects models that either included basking behaviour or body temperature as the response variable to assess differences among species, populations and treatments in these traits using R v3.2.5 (R Core Team 2015) and the lme4 package (Bates et al., 2014). In both of these models we included species, population, treatment and their interactions as fixed effects and individual ID as a random effect to account for multiple measurements on the same individual. Mass was initially included in these models but as it

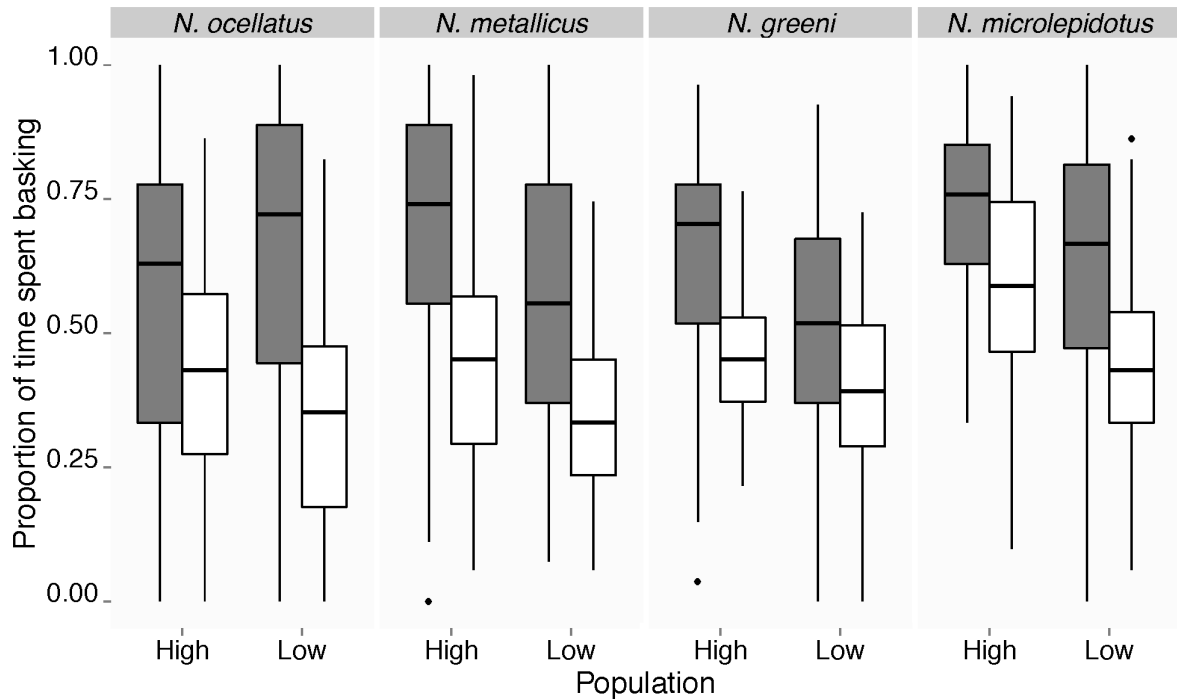
did not significantly affect basking behaviour or body temperature it was dropped from further analyses ( $p > 0.1$  in all cases). For body temperature, we also tested whether differences in basking behaviour across the day explained variation in body temperature. Specifically, we re-ran the within species linear mixed models for the proportion of time spent basking during the period body temperatures were measured for the prolonged (1200 – 1300 h) and reduced (1300 – 1400 h) basking opportunity treatments. We calculated the adjusted repeatability (intraclass correlation coefficient) for basking behaviour and body temperature using estimates of among-individual variance and unexplained within-individual (residual) variance. All models were fitted using the LmerTest package to generate type III F-tests of fixed effects. Degrees of freedom were estimated using Satterthwaites approximation. We removed all non-significant interactions via backward elimination and report results from models including all main effects and any significant interaction terms. All models were checked to ensure that they adhered to model assumptions.

### 3. Results

We found significant differences in the proportion of time spent basking across all levels of replication: species, population and treatment (Table 2). At the species level we found significant differences in the proportion of time spent basking which corresponded roughly with species group (widespread lowland species vs highland species, Figure 1). Specifically, the highland species *N. microlepidotus* spent a greater proportion of time basking than any other species (all  $p$  values  $< 0.005$ ). None of the other species differed from one another. At the population level, individuals from high altitude populations basked more than individuals from low altitude populations across all species (Table 2; Figure 1). Finally, we found strong treatment effects across all populations and all species: individuals in the reduced basking opportunity treatment spent a greater proportion of time basking compared to the prolonged basking treatment (Table 2, Figure 1). There was no significant interaction between either population and treatment or species and treatment, indicating that all species responded to the treatment effects to the same extent (e.g., there were no differences in behavioural plasticity among species or populations; Table 2). Individuals exhibited moderate repeatability in their basking behaviour across all four species; *N. ocellatus* ( $R = 0.511$ ), *N. metallicus* ( $R = 0.457$ ), *N. greeni* ( $R = 0.521$ ), and *N. microlepidotus* ( $R = 0.449$ ).

Table 2: Linear mixed-effects model analyses of the effect of basking opportunity treatment, species, and population on a) basking behaviour and b) body temperature. Individual was included as a random factor in all models.

	Basking Behaviour			Body Temperature		
	df	<i>F</i>	p	df	<i>F</i>	p
Species	<b>3, 186.26</b>	<b>8.43</b>	<b>&lt;0.001</b>	<b>3, 181.60</b>	<b>3.14</b>	<b>0.02</b>
Population	<b>1, 186.27</b>	<b>23.15</b>	<b>&lt;0.001</b>	<b>1, 181.64</b>	<b>6.64</b>	<b>0.01</b>
Treatment	<b>1, 186.29</b>	<b>80.99</b>	<b>&lt;0.001</b>	<b>1, 181.54</b>	<b>16.91</b>	<b>&lt;0.001</b>
Species x Population	3, 179.24	1.15	0.33	3, 177.60	0.56	0.64
Species x Treatment	3, 179.25	0.47	0.70	<b>3, 181.61</b>	<b>3.58</b>	<b>0.02</b>
Population x Treatment	1, 179.27	0.01	0.91	1, 177.70	0.06	0.80
Species x Population x Treatment	3, 176.25	1.81	0.32	3, 174.69	0.66	0.57

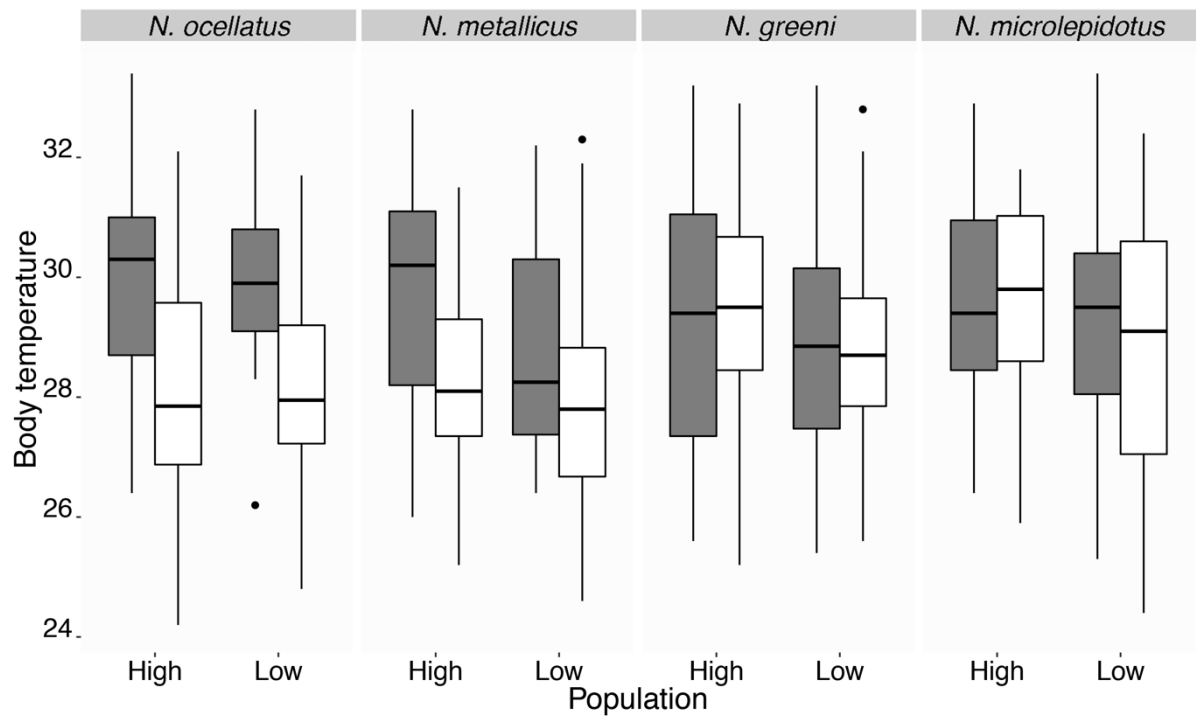


**Fig. 1** Median, upper and lower quartile of time spent basking by high and low altitude populations of two widespread lowland species, *Niveoscincus ocellatus* and *N. metallicus*, and two highland species, *N. greeni* and *N. microlepidotus*. A high and low altitude population of each species were sampled in the field (sample sizes provided in text). Lizards were then subjected to either prolonged (grey) or reduced (white) basking opportunity in a laboratory setting (8 and 4 h basking per day respectively).

As with basking behaviour, we found significant effects of all three main effects on body temperature. (Table 2, Fig. 2). Specifically, body temperatures of the widespread lowland species (*N. ocellatus* and *N. metallicus*) were lower than those of the highland species (*N. microlepidotus* and *N. greeni*). Furthermore, within species, body temperatures were higher in individuals from the high altitude population than the low population. We did, however, find that differences between the two treatments in body temperature was dependent on species (species x treatment interaction; Table 2). Specifically, while both *N. ocellatus* and *N. metallicus* exhibited higher body temperatures under the reduced basking treatment compared to the prolonged basking treatment, this was not the case for the two highland species.

We examined whether diurnal variation in lizard thermoregulatory behaviour and activity patterns may explain differences in the body temperature responses to basking treatment of highland versus widespread lowland species. Individuals of all species basked more frequently earlier in the day, this corresponded to the time when body temperature readings were taken. Basking frequency decreased later in the day with this pattern more pronounced in highland species compared to widespread lowland species (Fig. S4). Indeed, when the analysis of basking frequency was limited to the time periods during which body temperatures were measured for the high and low basking opportunity treatments (from 1200 – 1300 h and from 1300 – 1400 h respectively), we found a significant treatment effect on the proportion of time spent basking by both of the widespread lowland species, *N. ocellatus* and *N. metallicus*, but neither of the highland species (Table S2, Fig. S4) which corresponds with our body temperature results. Body temperatures exhibited low repeatability for *N. ocellatus* ( $R = 0.107$ ), *N. metallicus* ( $R = 0.232$ ) and *N. microlepidotus* ( $R = 0.266$ ). There was no evidence of repeatability of body temperature for *N. greeni* ( $R = 0.048$ ).





**Fig. 2** Mean body temperature (°C) with standard errors of two widespread lowland, *N. ocellatus* and *N. metallicus*, and two highland, *N. greeni* and *N. microlepidotus*, snow skink species. Individuals from a high and a low altitude population of each species were caught in the field and exposed to prolonged (grey) and reduced (white) basking opportunity treatments in a laboratory setting and body temperatures measured (8 and 4 h basking per day respectively).

#### 4. Discussion

Many species are experiencing novel environmental conditions as a result of climate change (Parmesan & Yohe 2003; Gienapp *et al.* 2008). The level of behavioural plasticity possessed by individuals will determine the extent to which changing thermal conditions impact on body temperature and subsequently fitness (Aubret & Shine 2010) and may be crucial to persistence during the early stages of environmental change (Beldade *et al.*, 2011; Hoffmann and Sgro, 2011; Chevin *et al.*, 2013). We show here that individuals of widespread lowland *Niveoscincus* species and low altitude populations historically exposed to warmer and more stable thermal conditions basked less overall than individuals of the highland *Niveoscincus* species and high altitude populations historically exposed to cooler and more variable thermal conditions. In contrast, we found that the extent of plasticity in thermoregulatory behaviour in response to basking opportunity was the same across all species and populations.

Interestingly, widespread lowland and highland species had different body temperature responses to the thermal treatments. While body temperatures were significantly higher in the reduced basking treatment compared to the prolonged basking treatment in the widespread lowland species, they appeared less responsive in both highland species.

Highland *Niveoscincus* species spent a greater proportion of time basking across both basking treatments compared to the widespread lowland species. Furthermore, high altitude populations of both highland and widespread lowland species spent a greater proportion of time basking than low altitude populations. This was despite the difference in altitude between sample populations of the highland species being relatively small (100 m in elevation) compared to that of the widespread lowland species (1000 m in elevation). This suggests that relatively small changes in microclimate can elicit strong differences in thermoregulatory behaviour. These results are in accordance with studies of other altitudinally divergent populations and species, which have found greater thermoregulatory behaviour in highland populations / species compared to the lowlands (Hertz & Nevo 1981; Gvoždík 2002; Samietz *et al.*, 2005; Gutiérrez, Krenz & Ibargüengoytía 2010). Combined, our results suggest that highland and lowland *Niveoscincus* populations / species have diverged in their basking behavior. While, demonstration that these patterns are the result of adaptive evolution would require assessment of the fitness consequences of differences in thermoregulatory behaviour across different environmental conditions, they are in direction expected if they were adaptive. Such divergence could be the result of genetic adaptation. This is supported to some

degree by the moderate levels of repeatability, and thus potential heritability, in basking behaviour. Alternatively it could be the result of developmental plasticity, specifically the effects of thermal regimes early in life of the developmental trajectory of specific behavioural traits (West-Eberhard, 2005; Suzuki & Nijhout, 2006). Disentangling these mechanisms was outside the scope of this study but provides an important avenue for future research.

Despite divergence in the extent of basking behaviour, both widespread lowland and highland snow skink species still exhibited considerable plasticity in basking behaviour; basking less under high basking opportunity than low basking opportunity. The similar magnitude of responses to these basking treatments suggests that both highland and lowland populations / species exhibit similar levels of plasticity in basking behavior. Interestingly, these short term responses to the current environmental conditions (e.g., the basking treatments) were in the same direction as the divergence we observed among species and populations, i.e., basking more under reduced basking opportunities. This suggests that any genetic divergence in basking behaviour observed among populations may initially be driven by plastic responses to current thermal environments. Such a response would then be followed by selection on reaction norms such that individuals that respond to the new environment in functional ways do better (West-Eberhard 2003). If there is heritable variation in reaction norms, the population may evolutionarily diverge from the ancestral population in terms of its basking behaviour (e.g., Waddington 1942; Suzuki and Nijhout 2006). The shift in basking behaviour of *Niveoscincus* species and populations in response to the thermal environment may therefore act as a precursor to evolutionary divergence among these groups. Experimental studies on female reproductive traits (e.g., clutch size, offspring size) have demonstrated similar patterns of plasticity that mirrors adaptive population divergence along temperature gradients (e.g., Shine and Downes 1999; Wapstra 2000; Warner *et al.* 2007). However, to fully understand this process we need more information on the underlying mechanisms responsible for the observed divergence in basking behaviour both among and within species (see above and also Uller and While 2015 for similar arguments).

Ultimately the function of basking behaviour is to maintain physiological processes within an optimal range. We found that lowland species / populations exhibited lower body temperatures than highland species / populations (see also Cadby *et al.* 2014; Caldwell *et al.* 2015). Despite similar behavioural responses to the basking treatments across species and

populations, the extent of plasticity in body temperature (e.g., the responses to the basking treatments) differed between widespread lowland and highland species. Specifically, the widespread lowland species exhibited changes in body temperature in response to the basking treatments whereas the body temperatures of the highland species were relatively consistent across both basking treatments. One explanation for these results is that limited and variable basking opportunity in cold highland areas may have produced greater selection pressure on highland species to maintain body temperatures within a higher preferred range during basking, regardless of basking behaviour (e.g. Hertz & Huey 1981; Grant & Dunham 1990; Diaz 1997). An alternative explanation is that the differences in response to the thermal treatment between highland and widespread lowland species are the result of more subtle shifts in basking behaviour. For example, both highland species exhibited a more concerted basking effort early in the day irrespective of thermal treatment compared to the widespread lowland species, presumably maximising their use of basking at the earliest opportunity because of the uncertainty associated with access to basking in high altitude areas (see also Cadby et al., 2014). As measurement of body temperatures coincided with the time of day when individuals of the highland species spent the greatest proportion of time basking, the lack of body temperature differences between treatments could have therefore been the result of our sampling regime rather than a result of canalisation of body temperatures with respect to thermoregulatory behaviour. This potentially fine-scale temporal influence on thermoregulatory behaviour, coupled with the co-variation between patterns of thermoregulatory behavior and thermo-physiology among species, populations, and treatments suggest that divergence among populations/species in body temperatures may largely be the result of the observed divergence in thermoregulatory behaviour. Having said that, without additional data, we cannot rule out the potential for divergence to be the result of genetic adaptation, developmental acclimation or variation in the thermal quality of the environment.

In summary, our results show that there appears to be adaptive divergence in basking behavior by *Niveoscincus* species which corresponds with historical variation in the availability of basking opportunities across sites. Despite this, all of the populations and species studied appeared to exhibit similar plasticity in basking behavior. Furthermore, small changes in basking behavior strongly influenced thermophysiology. Combined, these results suggest that plastic behavioural responses have the potential to allow *Niveoscincus*

populations to buffer changes in the environment in the short-term and thus cope with rapidly changing environmental conditions across all populations (Kearney, Shine & Porter 2009; Hof *et al.* 2011). Incorporating such behavioural plasticity and its consequences for physiology into climate models will be a crucial next step for predicting the long term ability of these species to respond to climate change.

### Data Accessibility

Behavioural, physiological and time of day data: DRYAD entry doi: xx.xxxx/dryad.xxxx

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## Supplementary Information

### *Study sites*

We examined the environmental conditions of each study population. We obtained data on the altitude and monthly mean minimum, maximum and mean air temperatures and precipitation (1960 - 1990) for Tasmania from the WorldClim database (Fig. S1). We mapped these variables across mainland Tasmania at a spatial resolution of 30 seconds ( $\sim 1 \text{ km}^2$ ) using ArcGIS software (ArcMap version 10.4.1, © 2016 Environmental Systems Research Institute, Inc.). Data for the wettest (September), coldest (July) and hottest (January) months were selected to illustrate precipitation and minimum and maximum temperatures respectively. Precipitation was lowest at the site of the low altitude populations of both widespread lowland species, Orford, and highest at the site of high altitude population 2 of the highland species, *N. microlepidotus*. The other populations experienced similar levels of precipitation during this period (Fig. S1b). All of the high altitude populations experience lower mean minimum (Fig. S1c) and maximum (Fig. S1d) air temperatures than low altitude populations. Despite differences in the thermal characteristics experienced by each population, access to substrate for basking, and presence / absence of ground cover and canopy cover, is similar (Table 1).

**Supplementary Tables**

Table S1: Mass, snout-vent length and range of field active body temperatures of males from each population of *Niveoscincus* sampled on capture. Several lizards from the low altitude populations of *N. ocellatus* (N = 20) and *N. metallicus* (N = 17) were collected opportunistically, so there is less field active temperature data for these populations. Several lizards from the high altitude populations of *N. metallicus* (N = 7) and *N. ocellatus* (N = 3) were caught by hand, and were thereby excluded from measures of field active temperature.

Species	Population	Mass (g)	SVL (mm)	N	Range F <sub>act</sub> T (°C)	N F <sub>act</sub>
<i>N. ocellatus</i>	low	4.28 ± 0.18	60.6 ± 0.8	27	28.1 - 32.9	7
	high	5.47 ± 0.27	69.0 ± 1.0	26	21.1 - 32.6	23
<i>N. metallicus</i>	low	2.77 ± 0.12	52.6 ± 0.8	25	24.1 - 32.9	8
	high	3.02 ± 0.12	56.4 ± 0.8	26	18.5 - 31.4	19
<i>N. greeni</i>	low	4.74 ± 0.20	63.9 ± 0.7	27	24.1 - 32.8	27
	high	4.49 ± 0.14	61.2 ± 0.5	26	22.0 - 28.3	26
<i>N. microlepidotus</i>	low	4.86 ± 0.15	64.1 ± 0.5	25	15.6 - 25.3	25
	high	4.51 ± 0.15	59.9 ± 0.7	27	18.7 - 30.3	27

Table S2: Sample size (N), mass and snout-vent length (SVL)  $\pm$  standard error of two widespread lowland species, *Niveoscincus ocellatus* and *N. metallicus*, and two highland species, *N. greeni* and *N. microlepidotus*. Lizards from two populations (high or low altitude) of each species were sampled and exposed to prolonged (8 h) or reduced (4 h) basking opportunity in a laboratory setting. Basking behaviour and body temperature were monitored. Non-basking lizards were excluded from the analyses.

Species	Site	Treatment	N	Mass $\pm$ SE	SVL $\pm$ SE
<i>N. ocellatus</i>	low	reduced	8	4.1 $\pm$ 0.3	60.6 $\pm$ 1.7
		prolonged	12	4.3 $\pm$ 0.3	60.4 $\pm$ 1.0
	high	reduced	8	5.7 $\pm$ 0.3	70.0 $\pm$ 1.3
		prolonged	11	4.8 $\pm$ 0.4	66.8 $\pm$ 1.9
<i>N. metallicus</i>	low	reduced	13	2.7 $\pm$ 0.2	52.3 $\pm$ 1.1
		prolonged	12	2.9 $\pm$ 0.2	52.8 $\pm$ 1.3
	high	reduced	13	3.1 $\pm$ 0.2	56.4 $\pm$ 1.2
		prolonged	13	3.0 $\pm$ 0.2	56.4 $\pm$ 1.1
<i>N. greeni</i>	high	reduced	13	4.5 $\pm$ 0.1	61.0 $\pm$ 0.8
		prolonged	13	4.5 $\pm$ 0.3	61.3 $\pm$ 0.7
	low	reduced	13	4.7 $\pm$ 0.3	63.6 $\pm$ 0.9
		prolonged	13	4.9 $\pm$ 0.2	64.5 $\pm$ 1.0
<i>N. microlepidotus</i>	high	reduced	13	4.6 $\pm$ 0.1	60.8 $\pm$ 0.8
		prolonged	14	4.4 $\pm$ 0.3	59.1 $\pm$ 1.1
	low	reduced	13	4.9 $\pm$ 0.2	65.3 $\pm$ 0.5
		prolonged	12	4.9 $\pm$ 0.2	62.8 $\pm$ 0.8

Table S3: Linear mixed-effects model analyses of the effect of basking opportunity treatment, species, and population on basking behaviour during the period of time body temperatures were measured for lizards exposed to a prolonged (8 h, 1200 – 1300 h) or reduced (4 h, 1300 – 1400 h) basking opportunity treatment. Individual was included as a random factor in all models.

	df	<i>F</i>	p
Species	<b>3, 188.71</b>	<b>12.97</b>	<b>&lt;0.001</b>
Population	<b>1, 188.71</b>	<b>8.49</b>	<b>0.004</b>
Treatment	<b>1, 188.18</b>	<b>8.18</b>	<b>0.005</b>
Species x Treatment	<b>3, 181.41</b>	<b>4.28</b>	<b>0.006</b>
Species x Population	3, 181.54	0.29	0.83
Population x Treatment	1, 181.50	0.002	0.96
Species x Population x Treatment	3, 178.26	0.61	0.61

## Supplementary Figures

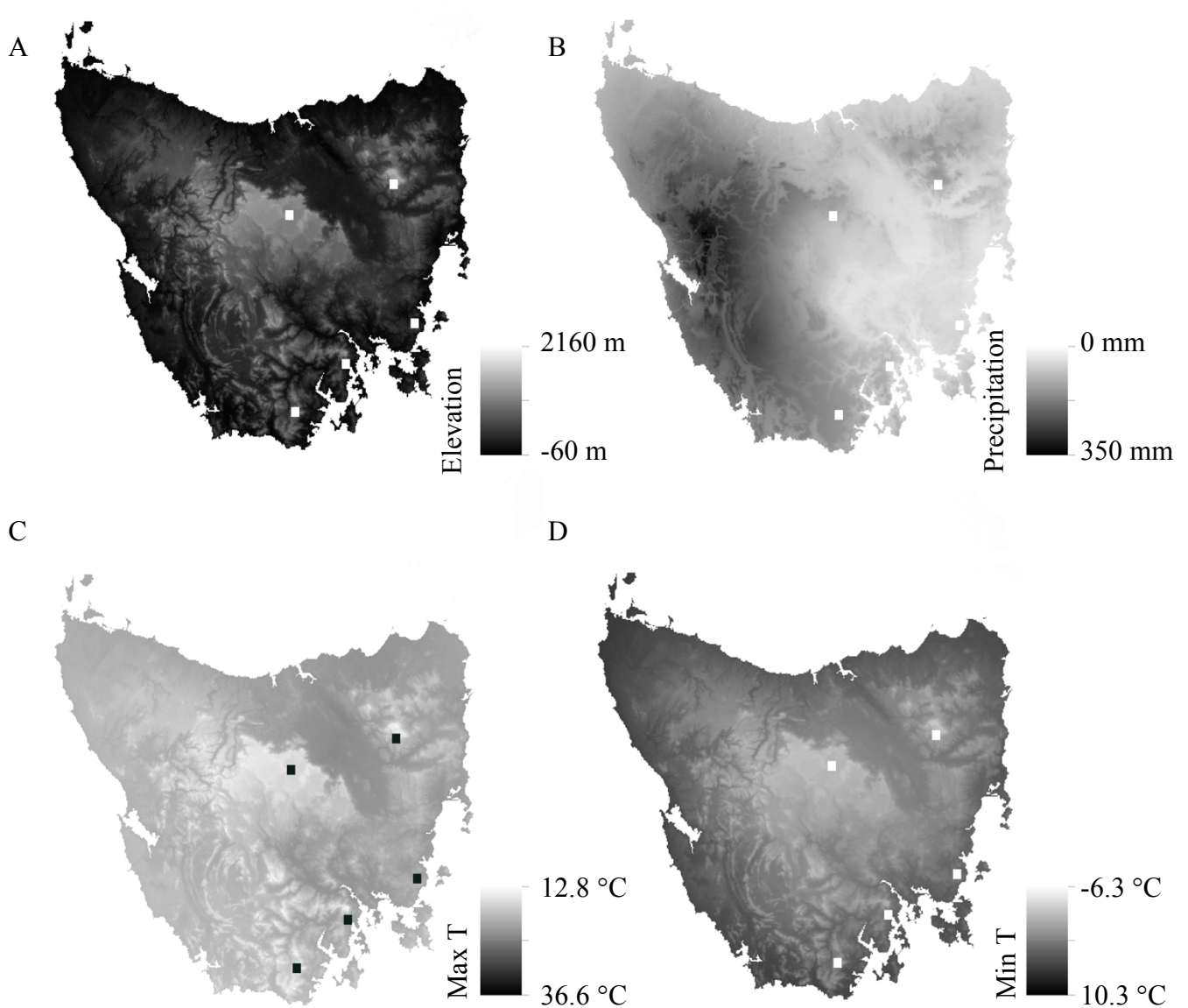


Fig. S1: Maps of mainland Tasmania with gradients illustrating altitude above sea level (A), precipitation in the wettest month (B), minimum temperature in the coldest month (July, C) and maximum temperature in the hottest month (January, D). Data was sourced from WorldClim and maps prepared using ArcMap. Lizards were sampled from five locations across Tasmania (squares). Clockwise from top left: Central Plateau; Ben Lomond, Orford, Mount Wellington, Hartz Peak.

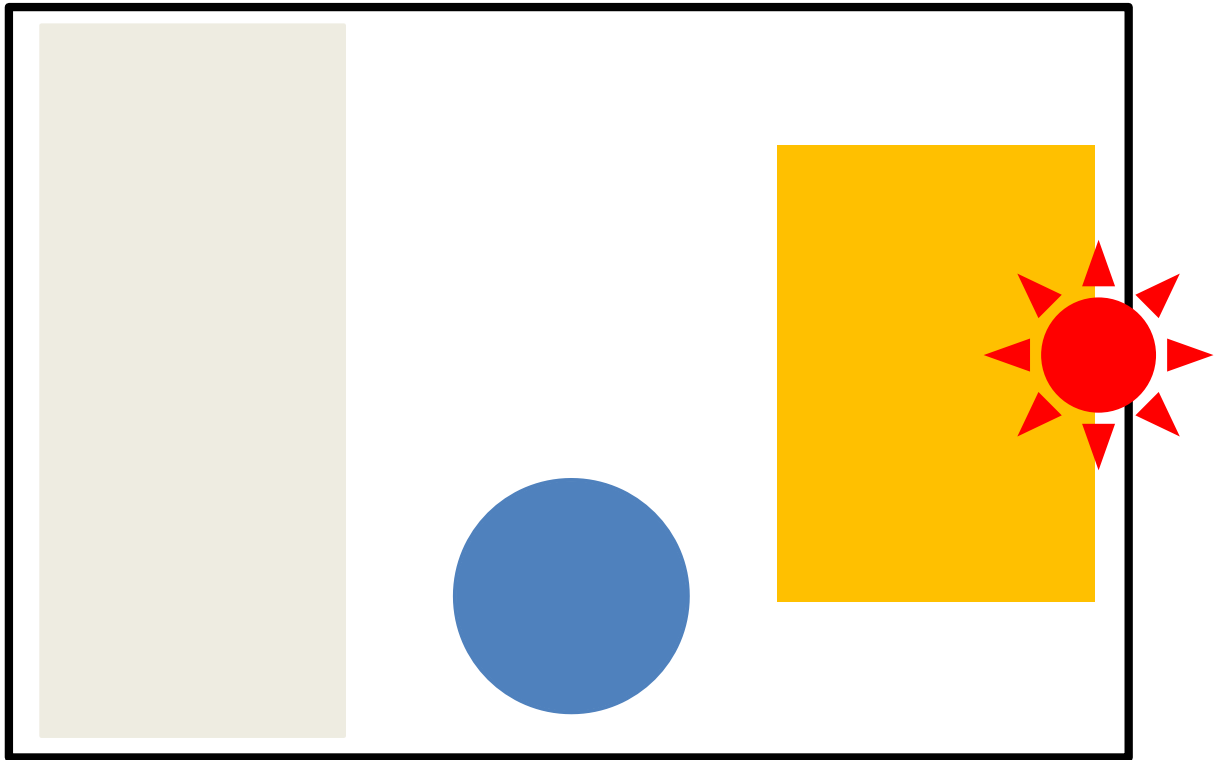


Fig. S2: Illustration of the terraria set up from above. Each terraria had a pellet substrate and contained a retreat (grey, wood block), a water dish (circle) and a basking tile (orange) under a basking lamp (red sun).



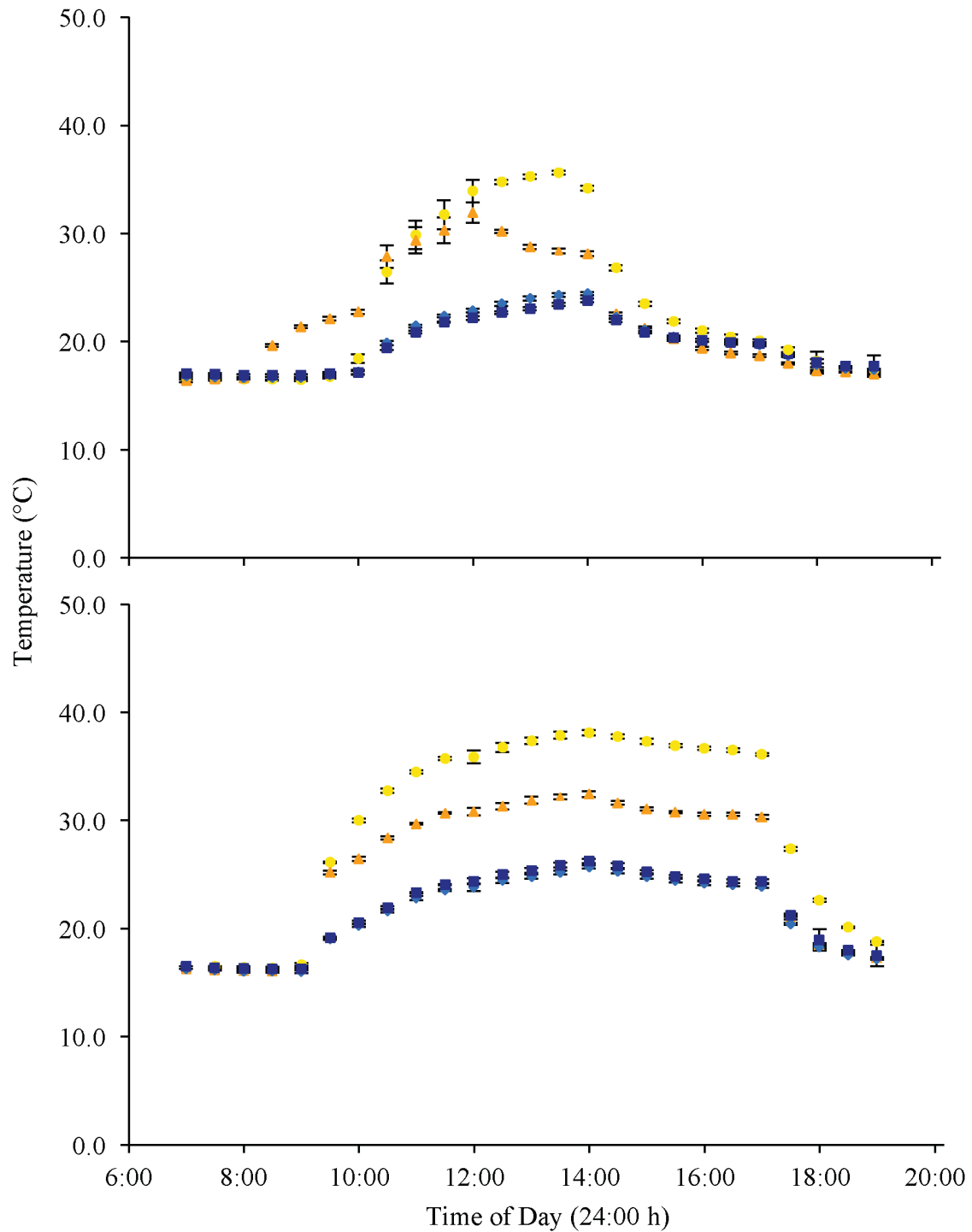


Fig. S3: Mean  $\pm$  SE temperature readings recorded in four regions: (a) under the basking light (circles); (b) near the basking light (triangles); (c) near the retreat site (diamonds); (d) under the retreat site (squares). Recordings were made under a reduced basking opportunity treatment (top, basking available 1000 – 1400 h) and a prolonged basking opportunity treatment (bottom, basking available 0900– 1800h).

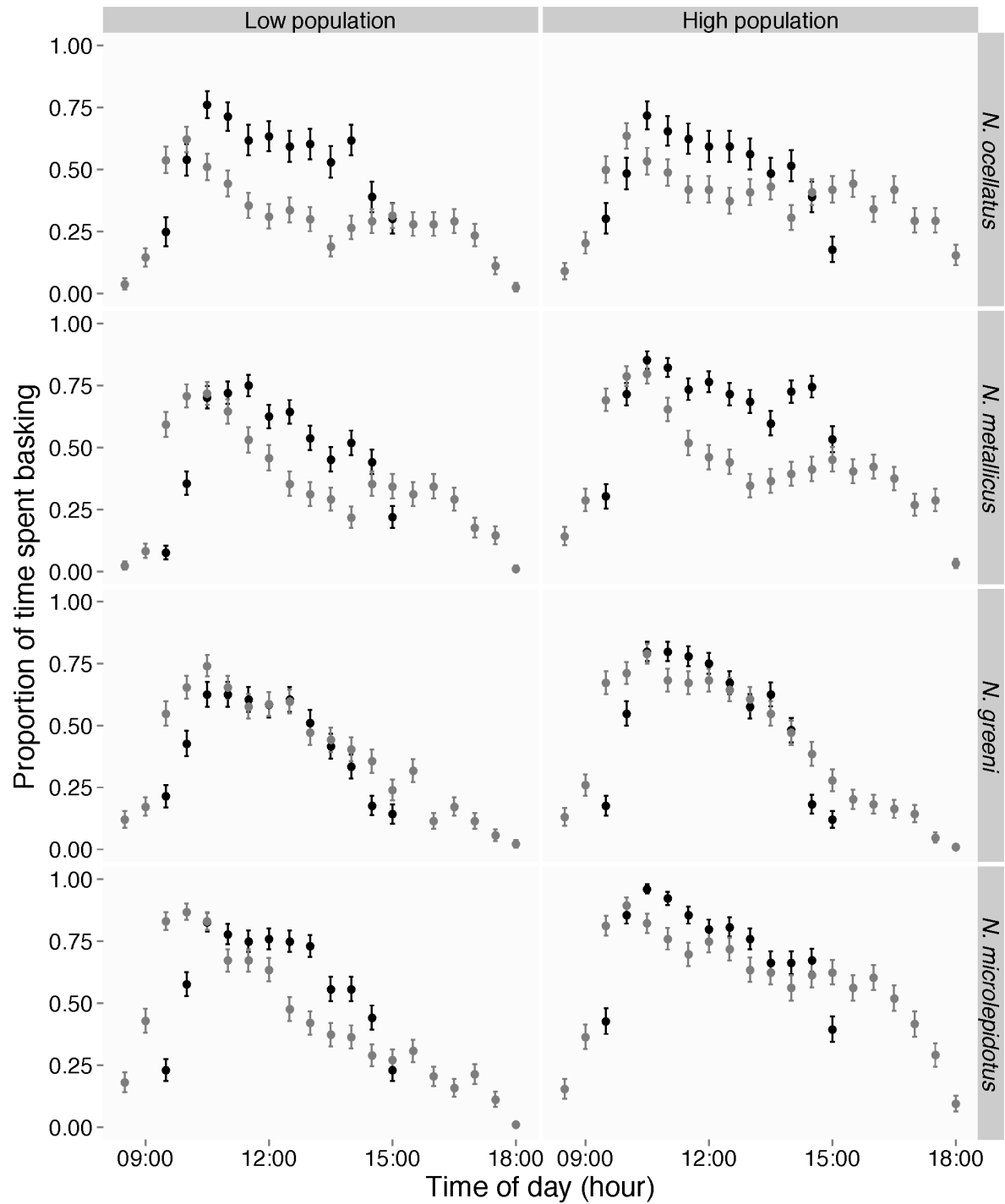


Fig. S4: Mean proportion of time spent basking at 30 minute intervals by high and low altitude populations of two widespread lowland and two highland *Niveoscincus* species. Individuals were either exposed to prolonged (grey, 0900 – 1700 h) or reduced (black, 1000 – 1400 h) basking opportunity. Mean and standard errors are based on readings across eight days.

# CHAPTER FOUR



# **Movin' on up: an individual-based model predicts climate change will alter competition between species across a mountain gradient.**

*In the final stages of preparation for submission to Ecography.*

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## **Abstract**

There is increasing evidence of upslope shifts by lowland species in response to climate change, yet the potential for such shifts to shape the persistence and distribution of alpine taxa is not well understood. To address this deficiency, we use a spatially-explicit individual-based model used to explore the effect of climate change on a hypothetical population (size and range dynamics) of two altitudinally interacting species. We used laboratory data along with data from long-term population monitoring to populate the model with two interacting widespread and highland members of the cool temperate lizard genus, *Niveoscincus*. These species have overlapping habitat requirements and compete for basking sites (a key fitness component), but co-occur only within a narrow altitudinal zone (~50 m) in Tasmania.

Increasing temperatures forecast under climate change are likely to enable widespread lowland *Niveoscincus* to colonise higher altitude sites, increasing competition for basking sites and leading to a decline in the abundance and range size of highland *Niveoscincus*. We captured the strength and nature of competitive interactions between these species, and explicitly incorporated processes determining the probability of reproduction, mortality and dispersal for each lizard, in each year of the simulation. As a result, the demography and population size and distribution of each species were a product of processes occurring at an individual level. We tested the interacting effects of competition and climate change on the persistence and distribution of populations of these species on a steep altitudinal gradient in southern Tasmania, Australia. From 2010 to 2100, the widespread lowland species was

predicted to increase in abundance by nearly 40% under a moderate scenario of climate change. In response to upward encroachment by its lowland competitor, the highland species was projected to retract its range by 27 m during this period and enter a long acting extinction vortex. Our study demonstrates that species interactions can have a detrimental impact on population viability and distribution under climate change. Process-explicit models that incorporate biotic interactions have the potential to provide critical information about the strength, nature and importance of biotic interactions for species persistence and distribution under climate change.

**Key words:** alpine specialist; species distribution model; agent-based model; lizard; climate warming; montane habitat.

## 1. Introduction

The earth's climate is changing at an unprecedented rate (Field *et al.* 2014a; Pachauri *et al.* 2014) with increasing evidence that species' distributions are shifting towards higher elevations and latitudes (Parmesan *et al.* 1999; Hickling *et al.* 2006; Jankowski, Robinson & Levey 2010; Laurance *et al.* 2011). However, these distributional shifts are not uniform, with some species responding to a greater extent than other species (Chen *et al.* 2011). As a consequence, climate change is having a significant effect on the ways in which species interact with one another (Parmesan 2006; Blois *et al.* 2013; Urban, Zarnetske & Skelly 2013). Such climate-driven changes to species interactions have the potential to drive species' range shifts (Gilman *et al.* 2010; Lambers *et al.* 2013), alter extinction risk and modify population, community and ecosystem dynamics (Hughes 2000; Thomas *et al.* 2004; Thomas, Franco & Hill 2006; IPCC 2007b). Despite this, climate-induced changes to biotic interactions are an often neglected component of research into the biological effects of climate change (Tylianakis *et al.* 2008; Valiente-Banuet *et al.* 2015).

Compared to lowland species, highland species are expected to experience a greater level of climate change (Pepin & Lundquist 2008; Rangwala, Sinsky & Miller 2013) and higher levels of habitat loss (e.g. Dirnböck, Essl & Rabitsch 2011; Parida, Hoffmann & Hill 2015). Highland species are also particularly susceptible to the indirect effects of climate change, because warming in montane landscapes allows upslope range expansion by lowland competitors (Jankowski, Robinson & Levey 2010; Laurance *et al.* 2011). Montane landscapes

are more conducive to upward range expansion by lowland competitors relative to latitudinal gradients, as distances to track changing temperatures are much less. Where lowland species are competitively superior to their high-elevation counterparts, such shifts can restrict highland species into increasingly small mountaintop habitats, compromising the viability of these populations (e.g. Jankowski, Robinson & Levey 2010; Sinervo *et al.* 2010; Buckley 2013). However, there is a large amount of interspecific variation in the rate of range shifts, which suggests that climate-driven range shifts are dependent on species-specific traits, local drivers of change and interspecific interactions (Chen *et al.* 2011). Faced with one of the most significant changes in Earth's history, reliably predicting range shifts and population dynamics is essential to conserving biodiversity, and has become a central theme in conservation biology (Dawson *et al.* 2011; Bellard *et al.* 2012).

Computer-based models are an increasingly important tool for understanding and assessing climate change effects on natural systems, yet most current approaches are considered inadequate (Evans 2012; Guillera-Aroita *et al.* 2015). Individual-based models (IBMs, or agent-based models) take a bottom up approach where individuals are treated as unique, discrete entities with properties which change with age (e.g. litter size, body size, Grimm 1999). IBMs allow an examination of the population level properties that emerge as individuals in the model not only interact with their physical and biotic environments, but also contribute to the biotic environment experienced by other individuals (Grimm 1999; Grimm & Railsback 2013). Development of IBMs which incorporate biotic interactions will increase our understanding of the potential for species interactions to affect the persistence and distribution of species under climate change (Alexander, Diez & Levine 2015). IBMs use decision rules, such as fitness maximization (Stillman & Goss-Custard 2010), to predict the behaviours of individuals and their concomitant population-level consequences. Because these decision rules are likely to remain the same, even if the environment changes (Wood, Stillman & Goss-Custard 2015), IBMs can produce realistic and robust predictions outside the range of environmental conditions in which the model was parameterized (Grimm & Railsback 2005). Hence, IBMs can provide crucial information for environmental management and enable evidence-based decision-making (DeAngelis & Mooij 2005; McLane *et al.* 2011).

We constructed a spatially-explicit IBM to explore the potential consequences of climate change and species interactions for two members of the cool temperate lizard genus, *Niveoscincus*. We focused our study on a widespread lowland species, *N. ocellatus* (the spotted skink), and a range restricted highland specialist species, *N. microlepidotus* (the southern snow skink). These species are viviparous and interact within narrow 50 m altitude zones at ~1100 m a. s. l. (Hutchinson & Schwaner 1991). Widespread lowland *Niveoscincus* species appear to exclude highland species from lower altitudes by outcompeting highland species for basking sites, which are a key component of their home range (Melville & Swain 1999a). The distribution of *N. ocellatus*, which reproduces annually throughout its range, is restricted by thermal constraints on gestation with increasing gestation length in colder years or as altitude increases (Wapstra *et al.* 1999; Cadby *et al.* 2010; Uller *et al.* 2011). However, increasing temperatures predicted under climate change are likely to improve the survival of *N. ocellatus* at higher elevations through earlier birth dates (Cadby *et al.* 2010), facilitating the colonisation of higher altitude sites. In contrast to *N. ocellatus*, *N. microlepidotus* reproduce biennially with fully developed offspring retained overwinter and born in spring after a ~ 12 month gestation (Hutchinson, Robertson & Rawlinson 1989; Olsson & Shine 1998; Olsson & Shine 1999). This protracted cycle buffers offspring from cold winter conditions, enabling highland species to successfully produce offspring within harsh montane conditions (Olsson & Shine 1998; Atkins, Swain & Jones 2007). However, a lower reproductive rate (essentially halved) may act as an evolutionary trap, preventing highland species from keeping pace with changing competitive interactions under climate change. Our aim was to assess how key demographic processes, including dispersal, mortality and competition, affect interactions between *N. ocellatus* and *N. microlepidotus* and predict the long term consequences of these interactions for these species' persistence and distribution under projected climate change.

## 2. Methods

### 2.1 Description of the study species

Both *N. ocellatus* and *N. microlepidotus* are diurnal, inhabit rocky environments and live for more than 10 years (Hutchinson & Schwaner 1991; Hudson 1997; Melville & Swain 1999a; Wapstra *et al.* 2001). However, the two species differ in a number of life history traits.

*Niveoscincus ocellatus* has a broad altitudinal range from sea level to 1150 m a. s. l. (Wapstra & Swain 2001a). This species exhibits considerable variation in life history traits across its

range. Because we are interested in interactions occurring between species occupying high altitude sites, we focussed on high-elevation populations of *N. ocellatus*. High-elevation populations reach sexual maturity later and at a larger size compared to warm lowland areas (Wapstra *et al.* 2001; Pen *et al.* 2010). Ovulation occurs in spring and gestation takes 3 – 4 months to complete (Wapstra *et al.* 1999). At high-elevation sites, low temperatures during gestation result in March born offspring, as opposed to January or February born offspring under warmer conditions (Cadby *et al.* 2010; Uller *et al.* 2011). Late-born offspring have lower survival probabilities due to a reduced time to put on condition prior to hibernation (Section 2.4.1, Atkins *et al.* 2007; Uller *et al.* 2011). *Niveoscincus microlepidotus* is an alpine specialist which occurs at altitudes above 1100 m a. s. l.. This species ovulates in spring and full embryonic development occurs prior to winter (Olsson & Shine 1998; Olsson & Shine 1999). Unlike *N. ocellatus* offspring, fully formed *N. microlepidotus* embryos are retained and born the following spring (Olsson & Shine 1998; Girling, Jones & Swain 2002a; Atkins *et al.* 2007). This has been interpreted as a “maternal care tactic” (*sensu* Olsson & Shine 1998) as offspring born in late autumn when embryo development is complete do not survive.

## 2.2 Hypothetical model space

We based the model space on the geography and the historical and projected climate of Mount Wellington, Tasmania, where *N. ocellatus* and *N. microlepidotus* co-occur (Figure 1). Mount Wellington provides our model with a realistic geographic space and has been the site of the majority of research on *N. microlepidotus*. Because the data used to parameterise our IBM are representative of general characteristics of *N. ocellatus* and *N. microlepidotus*, the simulation could be generalised to any of the high-elevation sites in Tasmania where these species interact. The modelled area is approximately 8.9 by 7.2 km (147.037 – 147.254°E, 42.853 – 42.946°S) with an altitudinal range of 700 – 1270 m a. s. l. (Figure S1). The modelled area consists of dolerite boulder fields interspersed with alpine heath, where both species occur (Melville & Swain 1999a; Melville & Swain 1999b). To set up the model space we randomly generated territories (rocks) as points across the landscape. Each territory had a fixed elevation and an associated temperature which was subject to variation (Section 2.5) according to its location within the model space (640,800 territories in total).



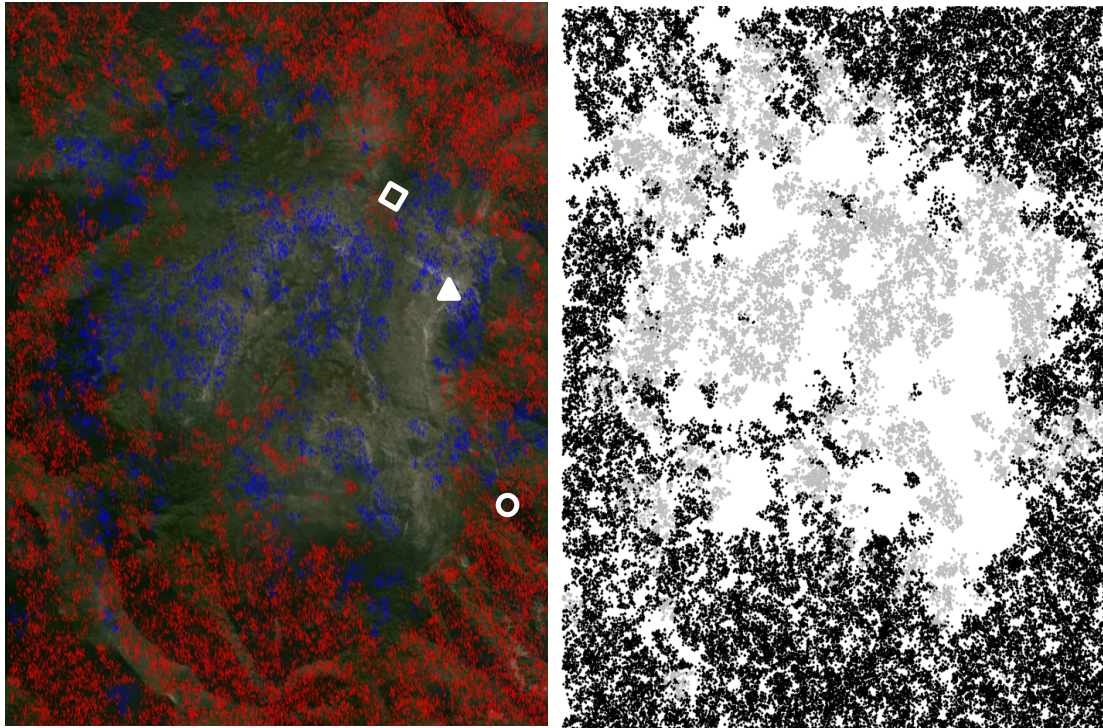


Figure 1. Predicted distribution of the widespread lowland species, *Niveoscincus ocellatus* (red / black), and the highland species, *N. microlepidotus* (blue / grey) on Mount Wellington at the end of the colonisation phase. A satellite image (left) is overlain by a map of territory occupancy (right, without satellite image). Symbols indicate the pinnacle (triangle) where *N. ocellatus* do not occur, a boulder field which is a well-studied zone of overlap (square, adjacent to the “big bend” in the road), and The Springs (circle, a local landmark), where *N. microlepidotus* do not occur (image credit: Google Maps). Altitudes and GPS coordinates of these locations are provided in Table S2.

### 2.3 Model overview and demography

We simulated interacting populations of *N. ocellatus* and *N. microlepidotus* residing on Mount Wellington using R (R Core Team 2014). For each lizard in each simulated year the IBM cycled through stages of reproduction, mortality, dispersal and ageing (Figure S2); the process and data required for each phase is outlined in Section 2.4. Each lizard was monitored from birth to death. During each year, the age, size and territory location of every lizard was recorded, along with time since last litter for females. Consequently, the demography and population sizes of *N. ocellatus* and *N. microlepidotus* were a net product of the processes governing survival and reproduction at the individual level. We modelled Mount Wellington as a closed system because dispersal among neighbouring *N. microlepidotus* populations is

essentially non-existent (except during glacial events) due to the disjunct distribution of this species, and movement of *N. ocellatus* among neighbouring populations is likely to have a limited effect on model outcomes because *N. ocellatus* populations show limited mixing (Cliff, Wapstra & Burrridge 2015). We assumed food was not limited because lizards, particularly insectivorous temperate zone species like those modelled here, are generally not food limited (Stamps, Tanaka & Krishnan 1981; Dubas & Bull 1991; King 1996) and these species are opportunistic generalist predators (Wapstra & Swain 1996; Olsson & Shine 2000a).

#### 2.4.1 Biological parameters: the reproduction stage.

The key traits required for the reproduction stage of the IBM (Figure S2) were the reproductive frequency for each species, a litter size by age distribution, the relationships between temperature and birthdate and between birthdate and the survival of *N. ocellatus* offspring.

Reproductive frequency: *N. ocellatus* has an annual reproductive rate (Wapstra *et al.* 1999). The majority of *N. microlepidotus* females give birth biennially (one litter every two years) while a small proportion of females additionally skip 1 – 2 years of reproduction, reducing reproductive frequency further. Thus, for our model, female *N. microlepidotus* had a 62% chance of giving birth every two years; a 27% chance of giving birth every three years and a 12% chance of giving birth every four years (Olsson & Shine 1999).

Litter size by age: Because *N. microlepidotus* produce comparable litter sizes to *N. ocellatus* inhabiting high altitude sites (e.g. litter sizes in: Hutchinson, Robertson & Rawlinson 1989; Olsson & Shine 1999; Wapstra & Swain 2001a; Atkins, Swain & Jones 2007), we used data from long term monitoring (15 years) of a high-elevation population of *N. ocellatus* at the Central Plateau, Tasmania, to determine age-specific litter size probabilities for both species (Table S1, see details of this monitoring in Cadby *et al.* 2010; Pen *et al.* 2010; Uller *et al.* 2011). These probabilities were produced by calculating the proportion of females giving birth to litters of a given size at a given age according to the natural population data. For each female in the model the realised litter size was determined by randomly sampling from the relevant age-specific probability distribution (Table S1).

Relationships between temperature and birthdate and between birthdate and survival: these relationships meant that survival correlated with birthdate and therefore correlated positively with temperature (Uller *et al.* 2011). For *N. ocellatus*, we incorporated the relationship between temperature and birthdate using 12 years of data from an ongoing mark and recapture study at a high-elevation site (Central Plateau, Tasmania, Uller *et al.* 2011). The relationship between birthdate and offspring survival is derived from data collected over a 3 year period within the same dataset. We made a binomial general linear model of survival and mean birthdate for *N. ocellatus* neonates (logodds survival =  $-0.499 - 0.012m$ ;  $p = 0.012$ ), where  $m$  is the numbers of days the birth occurred after the earliest birthdate observed (January 19<sup>th</sup>). We ran linear regressions of mark recapture data of birthdates from 2000 – 2012 against all available climate variables collected by the Bureau of Meteorology during the same period ( $N = 12$ ). Through this analysis we established that maximum temperature ( $T_{\max}$ ) during the second half of the year, which encompasses temperatures experienced during gestation, was the strongest climatic predictor of birthdate (adjusted  $R^2 = 0.72$ ,  $m = 92.1 - 4.5T_{\max}$ ,  $p = 0.0006$ ). We combined the preceding equations to derive the relationship between neonatal survival probability in the first year ( $s_p$ ) and  $T_{\max}$ :  $s_p = 1/(1 + \exp(1.562 - 0.052T_{\max}))$ . This relationship was used to calculate *N. ocellatus* offspring survival in conjunction with climate data (Section 2.5). Biennial reproduction with birth in early spring with all of spring, summer and autumn to feed and put on condition prior to hibernation essentially negates date dependent offspring survival for *N. microlepidotus* (Olsson and Shine 2002). While higher temperatures may result in changes in birthdate of a few weeks, shifts in birthdate have not been found to affect offspring fitness (Atkins *et al.* 2006, 2007).

#### 2.4.2 Biological parameters: constant background mortality

Mortality was the net result of two processes: (1) the effect of species- and age-specific constant background mortality (Table 1) and (2) mortality resulting from dispersal (Figure S2, Section 2.4.3). The level of background mortality for each species was constant with age. This value was established iteratively as the rate that allowed both species to reach equilibrium at known altitudes of occurrence during the colonisation phase, in line with established rates of fecundity in the field (Table S1). Neonatal *N. ocellatus* were the exception: their mortality was dealt with during the reproduction and dispersal phase, due to the temperature dependence of *N. ocellatus* birthdate and birthdate dependence of neonate survival (see above).

Table 1: Species and age-specific values for constant background mortality, snout – vent length, and dispersal distance used to parameterise the model of an interacting population of the widespread lowland species, *N. ocellatus*, and the highland species, *N. microlepidotus*. Individuals travelling 2SD or more than the average dispersal distance were counted as outliers and not included.

Species	Group	Estimate	Source
<i>Constant background mortality</i>			
<i>N. ocellatus</i>	adult	18.9%	established iteratively
	juvenile	dealt with during dispersal	
<i>N. microlepidotus</i>	adult	19.3%	established iteratively
	juvenile	28.3%	established iteratively
<i>Mean snout-vent length (cm)</i>			
<i>N. ocellatus</i>	male	68.96 ± 5.34 s. d.	Caldwell et al., unpublished data
	female	63.27 ± 4.94 s. d.	Caldwell et al., unpublished data
<i>N. microlepidotus</i>	male	59.93 ± 3.72 s. d.	Caldwell et al., unpublished data
	female	66.47 ± 7.37 s. d.	Caldwell et al., unpublished data
<i>Dispersal distance (m)</i>			
<i>N. ocellatus</i>	male	Data not available	

<i>N. microlepidotus</i>	female	$21.0 \pm 2.8$ s. e.	range of 0 – 147.1 m, GW and EW unpublished data
	juveniles	$22.1 \pm 0.9$ s. e.	range of 0 – 70.2 m, GW and EW unpublished data
	male	$9.6 \pm 1.0$ s. e.	range of 2.0 – 55.3 m, Olsson and Shine 2003
	female	$14.2 \pm 2.3$ s. e.	range of 1.6 – 52.4 m, Olsson and Shine 2003
	male juveniles	$6.0 \pm 1.1$ s. e.	range of 0.0 – 23.0 m, Olsson and Shine 2003
	female juveniles	$12.7 \pm 3.3$ s. e.	range of 1.5 – 47.5 m, Olsson and Shine 2003

### 2.4.3 Biological parameters: the process of dispersal and dispersal-related mortality

Dispersal-related mortality represented mortality resulting from predation during dispersal, exceeding energy budgets during dispersal and mortality due to competition for territory ownership. Dispersal-related mortality had an inherent density dependent component; higher densities resulted in greater competition for territories and thus a higher probability of mortality for dispersing lizards (Massot *et al.* 1992). Dispersal for each lizard was a multi-stage process based on a series of probabilistic events: (1) whether or not the lizard would disperse, (2) the distance travelled to reach a new territory and, (3) competition for territory ownership if the territory was occupied (Section 2.4.4). Dispersal steps 2 and 3 above were repeated until the lizard successfully colonised a new territory or died.

There were three processes driving lizards to disperse: (1) neonatal lizards dispersed during the first year of life, (2) three year old lizards dispersed if they failed to successfully challenge another lizard (3+ years old) inhabiting the territory they previously occupied as neonates (adults do not share territory, Section 2.4.4), and (3) when territory owners lost a competitive interaction they were forced to disperse to find a new territory. It was assumed that dispersing neonates would not attempt to occupy the territory in which they were born because *N. microlepidotus* and *N. ocellatus* neonates do not show strong philopatry (Table 1, E. Wapstra unpublished data; Olsson & Shine 2003). The process of dispersing events and dispersal behaviour followed three rules: (1) a lizard could perceive rocks up to 2.5 metres away, (2) if there were rocks in sight of the current rock, a lizard would randomly choose one of these rocks to disperse to, otherwise, the lizard dispersed in a random direction from the current territory, and (3) the lizard could only disperse 50 m in a single trip before dying (Figure S3). The maximum dispersal distance was established iteratively as the distance producing a frequency distribution of dispersal events most closely matching known dispersal distances of lizards at high altitude sites and was subject to sensitivity analyses (Table 1, Figure S3).

A constant mortality risk was assumed during travelling. Mathematically, if  $p_i$  is the probability of a lizard reaching territory  $i$  by moving in a random direction from its current position, and  $d_i$  is the distance to that territory, then the probability of a lizard surviving to reach territory  $i$  is:  $p_i \exp(-d_i / D)$  where  $D$  is a constant describing the scale over which a lizard is in danger. Consequently, the chance of survival exponentially decreased the further a lizard travelled and the more trips the lizard took to successfully colonise a territory. This

approximates what has been observed in the field: most lizards travel an average annual distance in the tens of meters, while a few travel several times the average distance (Table 1). The mean distance travelled by all dispersing lizards in the model was 14 – 16 m annually, with a range of 0 – 100 m (Figure S3). During dispersal a lizard could not avoid travelling towards unsuitable (occupied) territory. Likewise, a reproductively mature *N. ocellatus* female could not actively increase offspring survival by travelling towards and occupying territories with higher associated temperatures (Section 2.5).

#### 2.4.4 Biological parameters: competition for territory ownership

When a dispersing lizard reached a territory occupied by a lizard in the same age class (juveniles 0 – 2 years old; sub-adults and older 3+ years old), the dispersing lizard competed with the territory owner. Competition was segregated by age for both species because *N. microlepidotus* juveniles have no defined home range and appear transient (Melville & Swain 1999b). As a result, a juvenile and an adult could occupy the same territory in the model for both *N. ocellatus* and *N. microlepidotus*.

The outcome of intraspecific competition within *N. ocellatus* and interspecific competition between *N. ocellatus* and *N. microlepidotus* was assumed to be size driven, because interspecific competition between *N. microlepidotus* and another highland species, *N. greeni*, is size driven (Melville 2002). Likewise, the primary determinant of male-male contests, including interspecific contests, in other lizards and taxa is body size (Miller 1967; Abbott, Abbott & Grant 1977; Alatalo & Moreno 1987; Losos 1996; Robertson 1996; Langkilde & Shine 2004). Sex and species-specific size distributions were used to randomly determine the size of each lizard (Table 1). A strength rating was then assigned according to size. Strength ratings were subject to random variation, where a lizard with a 20 mm length advantage had a 99% probability of being assigned a higher rating than its opponent. Unlike most lizard species competition between *N. microlepidotus* is not governed by size but ownership: there was a 71.9% probability territory owners would win territorial disputes (Olsson & Shine 2000b). This is despite a lack of a statistically significant difference between resident and intruder in body size, relative head size or body condition (Olsson & Shine 2000b).

For all forms of competition, the winner occupied the territory and the loser dispersed, repeating the process as outlined above. Losing a territory dispute added a 40 m penalty to the

distance travelled to find a new territory. This penalty is less than the dangerous dispersal distance (50 m) so that it would increase, but not guarantee, the probability of mortality. This penalty reflects the potential energy loss from competing for territory that cannot be replaced by basking and subsequently foraging in the disputed territory.

### *2.5 The two phase modelling process*

Once the model space was set up and the biological parameters and demographic processes specified, the modelling process itself consisted of two phases: (i) the colonisation phase and (ii) the climate change phase. During the colonisation phase the climate of each territory was specified according to historical (1976 – 2005) annual mean temperature (AMT) data for Mount Wellington and the altitude of each territory (Figures S4 and S5). AMT data was supplied by Climate Futures for Tasmania (CFT) using ANUCLIM version 6.1 (Xu & Hutchinson 2011) at a resolution of  $0.01^\circ$  (~1 km). One second (~30 m) Digital Elevation Model (DEM) data of Mount Wellington was compared against the AMT data to find the relationship between altitude and temperature on Mount Wellington (Figure S5). Over the study region, the relationship between elevation and AMT is strongly linear ( $R^2 = 0.981$ ), because ANUCLIM uses altitude as a predictor of temperature to assist in the downscaling process (Figure S5). The relationship between elevation and temperature was used to derive the specific temperature of each territory based on its elevation according to the AMT for a given year.

When the climate change phase was initiated the temperature of each territory was altered in line with historical climate data from the Australian Water Availability Project (AWAP, 1990 – 2010) and projected CFT data from the CSIRO Mk3.5 Global Circulation Model (2011 – 2100; Figure S4). The use of AWAP data enabled empirical historical data covering the years 2005 – 2010 to be incorporated. We used the Intergovernmental Panel on Climate Change (IPCC 2007a) high (A2) and low (B1) emissions scenarios of climate change for the climate change simulations (Le Quere *et al.* 2009; Peters *et al.* 2013). This data included minimum and maximum projections for each climate scenario. Current trends of climate change and rates of greenhouse gas emissions most closely match the A2 scenario (Raupach *et al.* 2007; Field *et al.* 2014a). Because IPCC climate projections are limited to 2100, we assumed a new steady-state equilibrium for simulations after this point, where a reduction in greenhouse emissions will halt climate change post 2100 (a best-case scenario). This new steady-state



equilibrium is comparable to the WorldClim Representative Concentration Pathways (RCP) CMIP5 greenhouse gas emissions scenario RCP2.6, which predicts a halt in warming post 2100 (Stocker *et al.* 2013). To incorporate annual variability with an overall steady overall equilibrium we re-sampled the climate projections for 2090 – 2100 for years after 2100.

## 2.6 Simulations

To begin the colonisation phase a random 1% of territories were occupied by lizards, randomly allocated between each species, sex and age. These lizards were allowed to populate the model landscape for 1000 years according to demographic processes outlined in Section 2.4. This enabled the populations to reach a quasi-equilibrium state with non-directional variation in population size or range boundary movement. This state is referred to as equilibrium hereafter for simplicity. Each simulation was repeated ten times to demonstrate variability in predictions of population dynamics. We determined the predicted composition of the population at three locations at the end of the colonisation phase to compare against known species distributions on Mount Wellington (Figure 1). Species densities and the ratio of *N. ocellatus* to *N. microlepidotus* at each location was rounded to the nearest 100 lizards to each location averaged over ten model runs. We extracted the average and maximum density of each species across the model space at the end of the colonisation phase. At the end of the colonisation phase and in 2100, 2100 and 2300 we calculated the predicted proportion of the available territories occupied by each species, and the proportion of each species composing the total population, under each climate change scenario. This allowed us to determine short term (2010 – 2100) and longer term (2100 – 2300) consequences of a short period of climate change for these species' persistence and distribution. For illustrative purposes we ran simulations to the year 3000 and include these outputs in the figures. We found the altitudinal limit of the upper 90<sup>th</sup> percentile of *N. ocellatus* during each year of the colonisation and climate change phases. The change in altitude of the upper 90<sup>th</sup> percentile of *N. ocellatus* was used to estimate the rate of change in the upper elevational boundary of *N. ocellatus* per decade (m / decade) from 2010 to 2100 and from 2100 to 2300. The upper 90<sup>th</sup> percentile is hereafter referred to as the upper elevational boundary for clarity. We calculated the annual density dependent mortality rate acting on each species under each climate scenario. We illustrated the trend using a 50 year moving average to smooth out inter-annual variability in predictions.

Due to the cause and effect relationship between increases in the upper range limit of *N. ocellatus* and subsequent declines in the population size and lower range margin of *N. microlepidotus*, we further explored competition mediated changes in the thermal niche on *N. ocellatus* in response to an A2 scenario of climate change. We explored how the predicted rate of change in the upper range limit of *N. ocellatus* compared to the predicted rate of change in the potential thermal niche of this species. We used the upper range limit of 95% of *N. ocellatus* to estimate the competition-mediated range shift of this species. To estimate changes in the potential thermal niche of *N. ocellatus*, we calculated the lower thermal threshold of *N. ocellatus* which is the temperature at which the upper elevational boundary of this species ends. We assumed that the lower thermal threshold of *N. ocellatus* in the model was the minimum temperature at which 95% of *N. ocellatus* or greater were exposed to in 1990. We found the highest altitude “suitable site” which was at or above this minimum temperature for each year of the simulation to derive the annual change in the predicted thermal niche of *N. ocellatus*. We also mapped annual changes in the upper range limit of *N. ocellatus* to illustrate the effect of inter-annual variability in temperature on the maximum extent on this species. We also calculated the smoothed velocity of movement of *N. ocellatus* up the altitudinal gradient by extracting the maximum distance travelled by an *N. ocellatus* from the 1990 range for each year, and dividing this value by the number of years since 1990. From this we estimated the average velocity travelled over the preceding time period, which allowed for smoothing of stochastic changes in velocity.

## 2.7 Sensitivity analyses

We performed sensitivity analyses to test the effect of specific parameters on the proportion of each species in the total population in 2010, 2050, 2100 and 2300 under the A2 scenario. We reran the initial scenario, varying a single model input from the beginning of the climate change phase. We varied the level of constant background mortality experienced by *N. ocellatus* and *N. microlepidotus* ( $\pm 1\%$ ), the dispersal distance for a single trip before death (initially 50 m, reduced to 30 m, increased to 70 m), the dispersal distance penalty for losing a territory dispute (initially 40 m, reduced to 20 m, increased to 60 m), the size advantage which equates to a 99% probability of winning (initially 20 mm, increased to 50 mm so winning was almost entirely reliant on chance, reduced to 5 mm so winning was more size sensitive), and the territory ownership advantage of *N. microlepidotus* (advantage initially 71.9%, reduced to 55.0%, increased to 85.0%).

### 3. Results

Our model successfully allowed the widespread lowland species, *N. ocellatus*, and the highland species, *N. microlepidotus*, to colonise the model habitat (broadly analogous to a mountain gradient in southern Tasmania, Figures 1 and 2). Both species established a fluctuating equilibrium matching a narrow overlapping distribution as observed in the field (Figures 1 and 2). The upper elevational range of *N. ocellatus* rapidly reached an equilibrium at 900 – 1100 m a. s. l., with *N. microlepidotus* largely restricted to altitudes above this zone (Figure 2). By the end of the colonisation phase *N. ocellatus* occupied an average of  $9.3 \pm 0.4\%$  s. d. of the total available territories and composed  $82.2 \pm 3.3\%$  s. d. of the total population (Figure 3 and Table 2). *Niveoscincus microlepidotus* occupied an average of  $2.0 \pm 0.3\%$  s. d. of the total available territories and composed  $17.8 \pm 2.8\%$  s. d. of the total population (Figure 3 and Table 2). By the end of the colonisation phase there was an average of 10 *N. ocellatus* and 8 *N. microlepidotus* per  $10 \text{ m}^2$  in the most densely occupied area of the model and an average of 0.19 *N. ocellatus* and 0.04 *N. microlepidotus* per  $10 \text{ m}^2$  across the entire available model space. The predicted population composition of each species across the simulated mountain gradient matched observations of altitudinal clines in the density of *N. ocellatus* and *N. microlepidotus* on Mount Wellington (Figure 1). Specifically, the ratio of *N. ocellatus* to *N. microlepidotus* predicted at three locations matched observations in the field, and was lowest at the summit and several orders of magnitude greater at the Springs (Table S2). The predicted density of *N. microlepidotus* at the Big Bend matched published estimates of densities of *N. microlepidotus* at this site which range from 0.1 lizards per  $10 \text{ m}^2$  (Melville & Swain 1997) to 2.5 – 3.5 lizards per  $10 \text{ m}^2$  (Olsson and Shine, 2000). The average predicted density of *N. ocellatus* at the Big Bend was somewhat higher than field based estimates from other high altitude sites. For example, density of *N. ocellatus* at a high altitude site subject to long term population monitoring is 0.5 lizards per  $10 \text{ m}^2$  (Lake Augusta, Central Plateau), and is approximately 0.3 lizards per  $10 \text{ m}^2$  at a nearby scree (EW, pers. obs.). There are 2.0 *N. ocellatus* lizards per  $10 \text{ m}^2$  at another high altitude site in central Tasmania (Miena, EW pers. obs.). In contrast, densities of *N. ocellatus* at a low altitude site subject to long term population monitoring average an estimated 0.14 lizards per  $10 \text{ m}^2$  (EW, Orford) which is significantly lower than densities predicted by the model (Table S2).

### 3.1 Short term population responses to climate change (2010 – 2100)

After equilibrium was reached we initiated the A2 and B1 climate change scenarios. From 2010 – 2100 the population size of *N. ocellatus* increased by  $36.6 \pm 1.5\%$  s. d. and  $26.7 \pm 2.2\%$  s. d. under the A2 and B1 scenarios. This species occupied 13.1% and 12.1% of the available territories respectively by 2100. During this period the proportion of *N. ocellatus* comprising the total population increased to  $87.0 \pm 1.5\%$  and  $85.3 \pm 2.1\%$  under the A2 and B1 climate scenarios (Figure 3 and Table 2). In contrast the population size of *N. microlepidotus* showed no or little change from 2010 to 2100 under the A2 and B1 scenarios; occupying  $2.0 \pm 0.4\%$  and  $2.1 \pm 0.4\%$  of available territories in 2100 (Figure 3 and Table 2). Due to the increase in abundance of *N. ocellatus*, the relative proportion of *N. microlepidotus* comprising the total population in 2100 decreased to  $13.0 \pm 1.5\%$  and  $14.7 \pm 2.1\%$  under the A2 and B1 scenarios (Figure 3 and Table 2). From 2010 – 2100 *N. ocellatus* colonised higher altitudes at a rate of approximately 1.7 metres per decade under the A2 scenario (from 902 to 917 m a. s. l.) and 1.0 meter per decade under the B1 scenario (from 904 to 913 m a. s. l., Figure 4). During this period the lower range margin of *N. microlepidotus* retracted by 2.1 metres per decade under the A2 scenario (from 877 to 896 m a. s. l.) and 3.0 metres per decade under the B1 scenario (from 860 to 887 m a. s. l., Figure 4). From 2010 – 2100 the density dependent mortality rate experienced by both species increased under A2 and B1 scenarios of climate change, with a greater rate of change predicted for *N. ocellatus* than *N. microlepidotus* (Figure 5). In the absence of competition, the population sizes of both species are predicted to increase under climate change, though this trend is much more pronounced for *N. ocellatus* than *N. microlepidotus* (Figure S6).

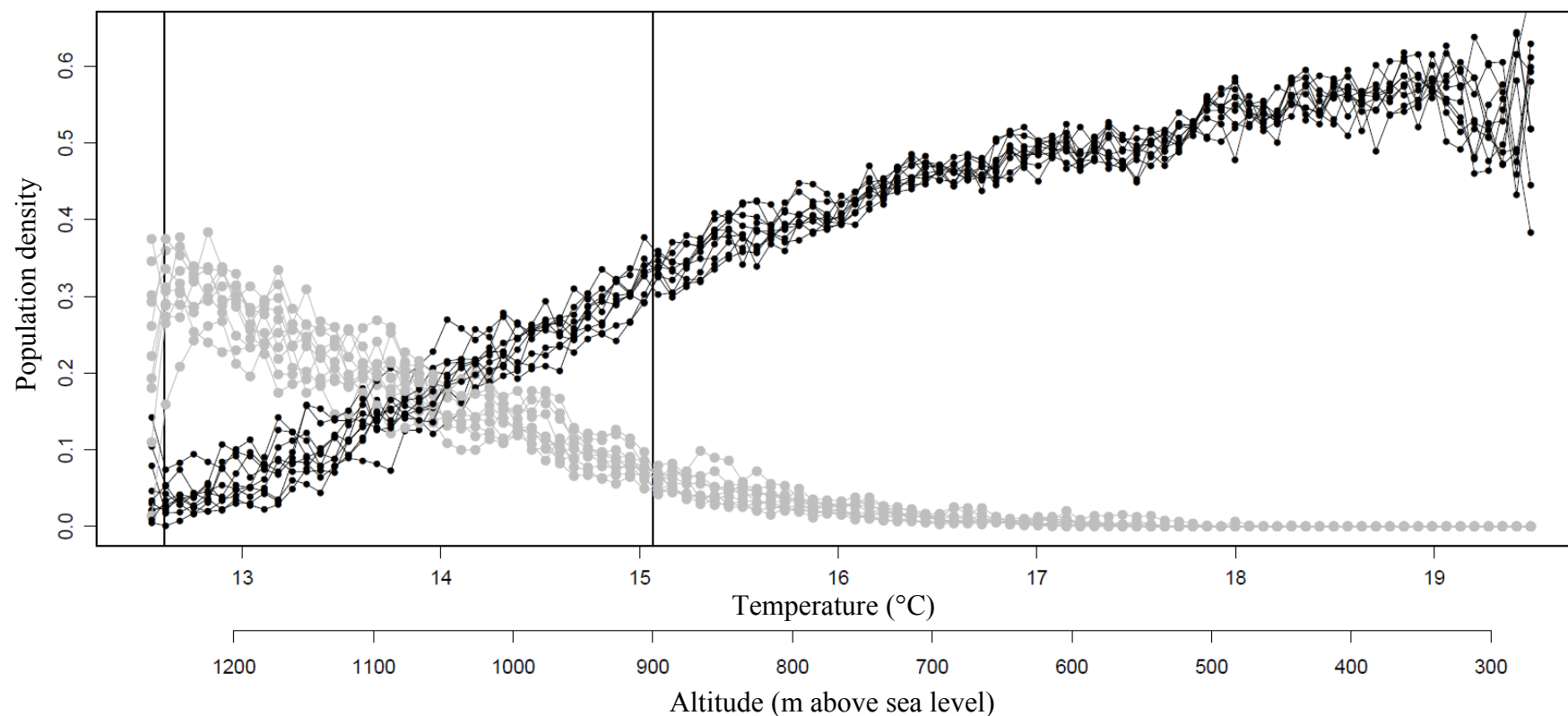


Figure 2: Altitudinal variation in the population density of interacting populations of the widespread lowland species, *Niveoscincus ocellatus* (black), and the highland species, *N. microlepidotus* (grey), residing in the hypothetical Mount Wellington model space at the end of the colonisation phase (10 model runs). Temperature has a linear relationship with altitude, with each site having an associated annual mean temperature specified according to the altitudinal location of the site (Section 2.5).

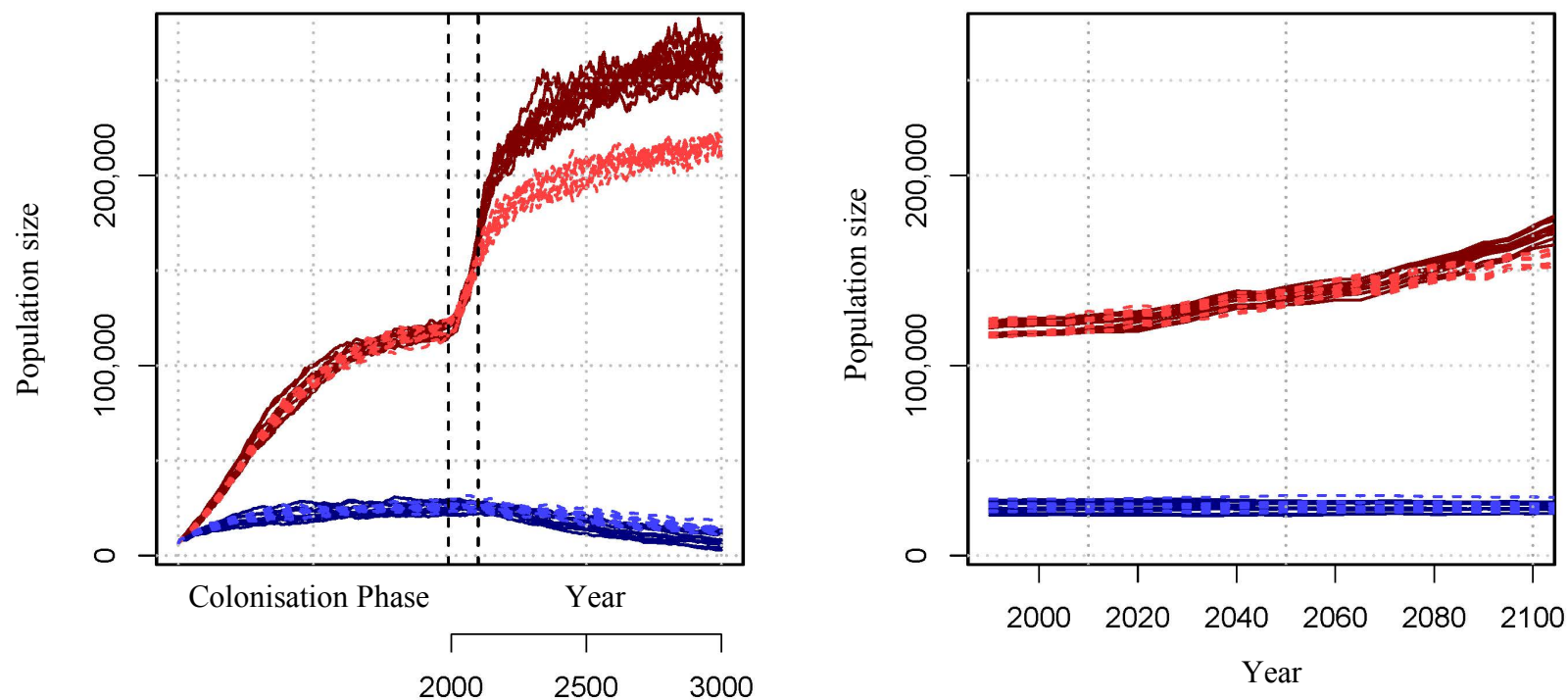


Figure 3. Projected population size of the widespread lowland species, *Niveoscincus ocellatus* (red), and the highland species, *N. microlepidotus* (blue). Left: A colonization phase (pre-1990, left of dashed line) and a warming phase (post-1990, right of dashed line) are shown under A2 (the species darker colour) and B1 (the species lighter colour) scenarios of climate change (IPCC 2007a). Dashed black lines indicate the period 1990 – 2100, which is provided at greater magnification in the right hand figure.

Table 2: Predicted proportion of the widespread lowland species, *Niveoscincus ocellatus*, and the highland species, *N. microlepidotus*, comprising the total population of lizards simulated to inhabit Mount Wellington under minimum and maximum A2 and B1 climate change scenarios (IPCC 2007a).

Scenario	Year				
	1990	2010	2050	2100	2300
<i>N. ocellatus</i>					
Min A2	84.1%	85.2%	86.6%	88.1%	92.7%
Max A2	80.7%	81.1%	82.7%	86%	90.9%
Min B1	83.3%	83.5%	85%	86.8%	90%
Max B1	80.8%	81.3%	81.3%	83.8%	88.7%
<i>N. microlepidotus</i>					
Min A2	15.9%	14.8%	13.4%	11.9%	7.30%
Max A2	19.3%	18.9%	17.3%	14.0%	9.1%
Min B1	16.7%	16.5%	15%	13.2%	10%
Max B1	19.2%	18.7%	18.7%	16.2%	11.3%

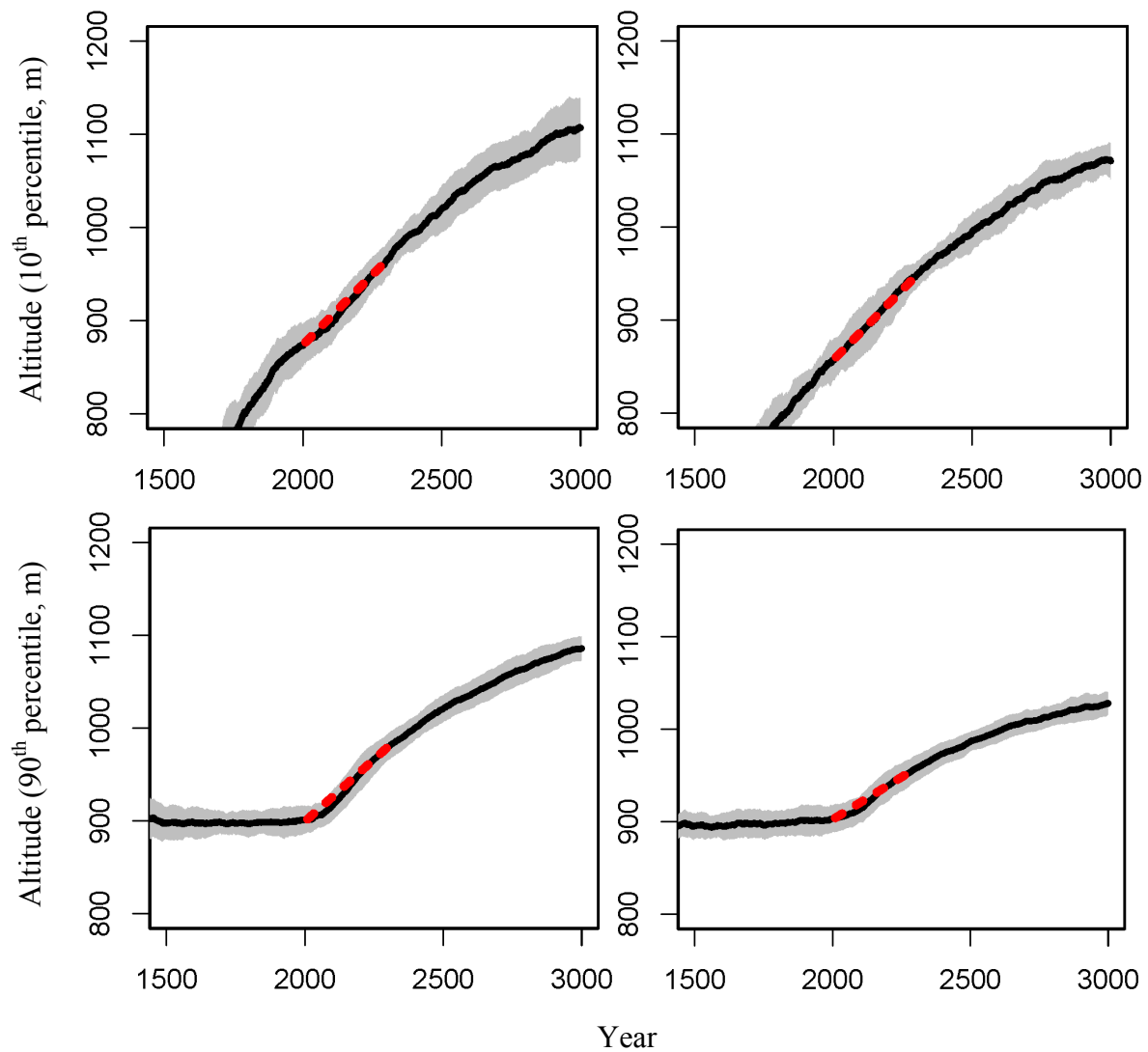


Figure 4: Predicted mean change  $\pm$  standard deviation in altitudinal range of a widespread lowland species, *Niveoscincus ocellatus* (top) and an highland species, *N. microlepidotus* (bottom). The model was run under an A2 scenario (left) and B1 scenario of climate change (right, 10 model runs, IPCC 2007a). During the colonisation phase (years 990 – 1990) lizards were able to populate the model space and the populations reach equilibrium prior to initiation of the climate change phase (1990 – 3000). The average rate of change in elevational range for the years 2010 – 2300 is shown (dashed red).



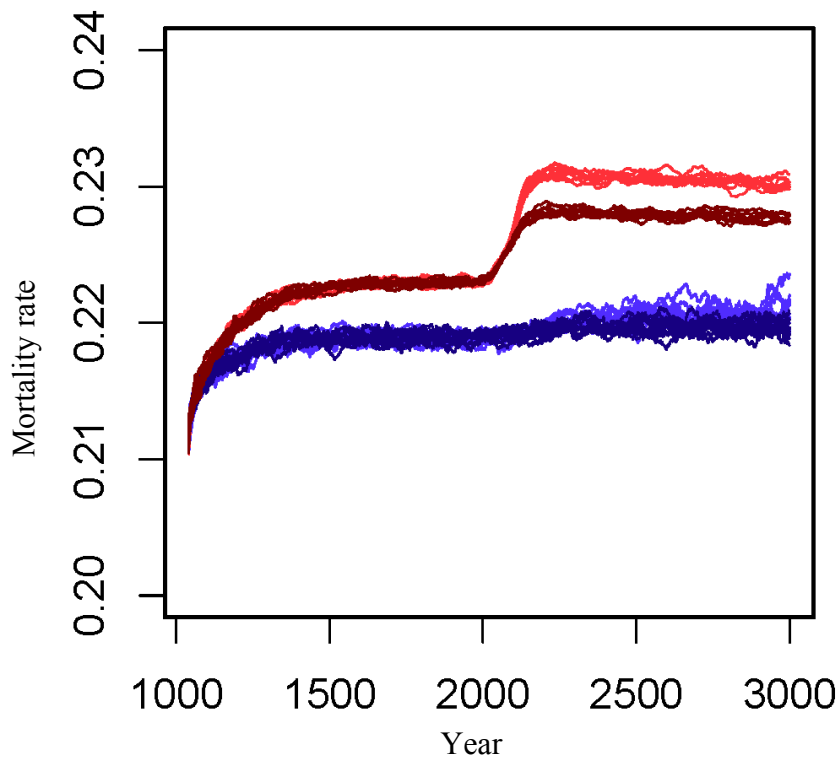


Figure 5. Density dependent mortality rate of *Niveoscincus ocellatus* (red) and *N. microlepidotus* (blue). Lizards were able to populate the model space and the populations reach equilibrium during the colonisation phase (990 – 1990), prior to initiation of the climate change phase (1990 – 3000). Ten simulations were run under an A2 (species darker colour) and B1 (species lighter colour) scenario of climate change.

### 3.2 Long term responses to a short period of climate change

After 2100 we held the climate at a new steady state equilibrium reflecting the climate projected for 2090 – 2100. By 2300 *N. ocellatus* occupied 17.8% and 15.1% of the available territories under the A2 and B1 climate scenarios, an increase from the projected population size in 2100 of  $36.0 \pm 8.7\%$  s. d. and  $24.4 \pm 4.1\%$  s. d. respectively. During this period the proportion of the population composed of *N. ocellatus* increased to  $91.8 \pm 1.3\%$  s. d. and  $89.4 \pm 0.9\%$  s. d. under the A2 and B1 climate scenarios (Figure 2 and Table 2). In contrast, *N. microlepidotus* population size decreased from 2100 to 2300 by  $17.9 \pm 3.6\%$  and  $14.3 \pm 6.7\%$  under the A2 and B1 climate scenarios respectively; occupying 1.6% and 1.8% of the available territories in 2300 (Figure 3 and Table 2). By 2300 the proportion of *N. microlepidotus* composing the total population reduced to  $8.2 \pm 1.3\%$  s. d. and  $10.6 \pm 0.9\%$  s. d. under the A2 and B1 climate scenarios (Figure 3 and Table 2). From 2100 to 2300 the rate of upward movement in the upper range margin of *N. ocellatus* increased to an average of 3.1

meters per decade under the stabilised A2 scenario (from 917 to 980 m a. s. l.) and 2.2 meters per decade under the stabilised B1 scenario (from 913 to 957 m a. s. l., Figure 4). The rate of retraction in *N. microlepidotus*' lower range margin also increased to 3.4 metres per decade under the stabilised A2 scenario (from 896 to 964 m a. s. l.) and 3.1 metres per decade under the stabilised B1 scenario (from 887 to 948 m a. s. l., Figure 4). The density dependent mortality rate of *N. ocellatus* reached equilibrium by 2300 under both the stabilised A2 and B1 scenarios (Figure 5). In contrast, the density dependent mortality rate of *N. microlepidotus* continued to increase from 2100 to 2300, despite both A2 and B1 scenarios reaching a new steady state equilibrium post 2100 (Figure 5).

### 3.3 Thermal velocity and range shifts

We examined the match between movement in *N. ocellatus* upper range limit and changes in upper limit of the thermal niche of this species under climate change. In line with inter-annual variability in projected annual temperatures, the upper limit of *N. ocellatus* thermal niche fluctuated rapidly before stabilising to include the full altitudinal range of Mount Wellington by the end of the 21<sup>st</sup> Century (Figure 5). The smoothed predicted upper range limit of *N. ocellatus* increased gradually throughout the simulated time frame (Figure 5). In line with predicted fluctuations in the range of available thermal niche, inter-annual variability in exposure to annual mean temperatures resulted in alternating periods of restriction and expansion of the upper range limit of *N. ocellatus* throughout the 21<sup>st</sup> Century (Figure 6). Consequently, the velocity of change in the upper range margin of this species was highest early in the 21<sup>st</sup> Century, rapidly declining as the simulation approached 2080 (Figure 7).

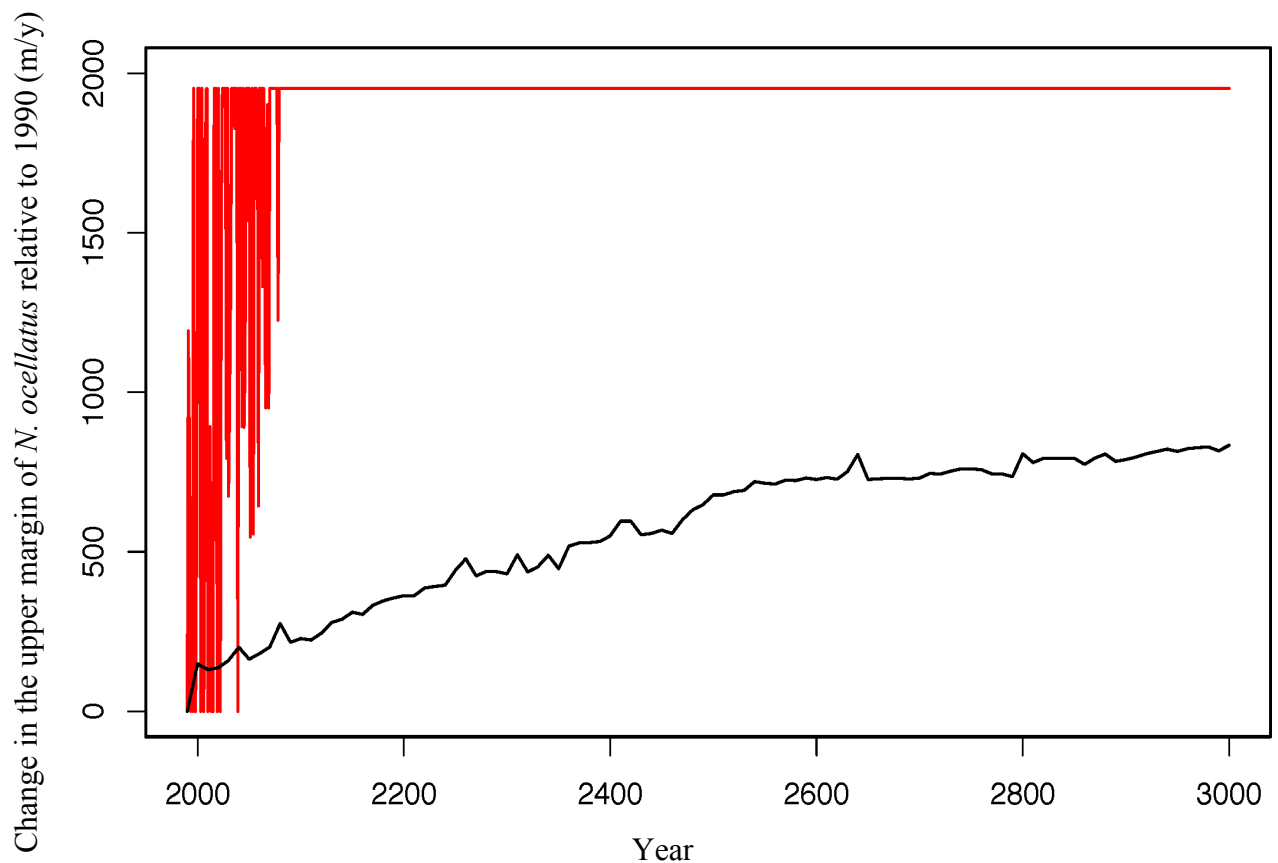


Figure 5. Smoothed rate of predicted movement in the upper range margin of *Niveoscincus ocellatus* (black line) relative to the range of this species predicted at the beginning of the climate change phase of the model process (1990 – 2100). After 2100 the climate was held at a new steady state equilibrium. The change in the location of the upper thermal limit of *N. ocellatus* is shown relative to the position of this parameter in 1990 (red line).

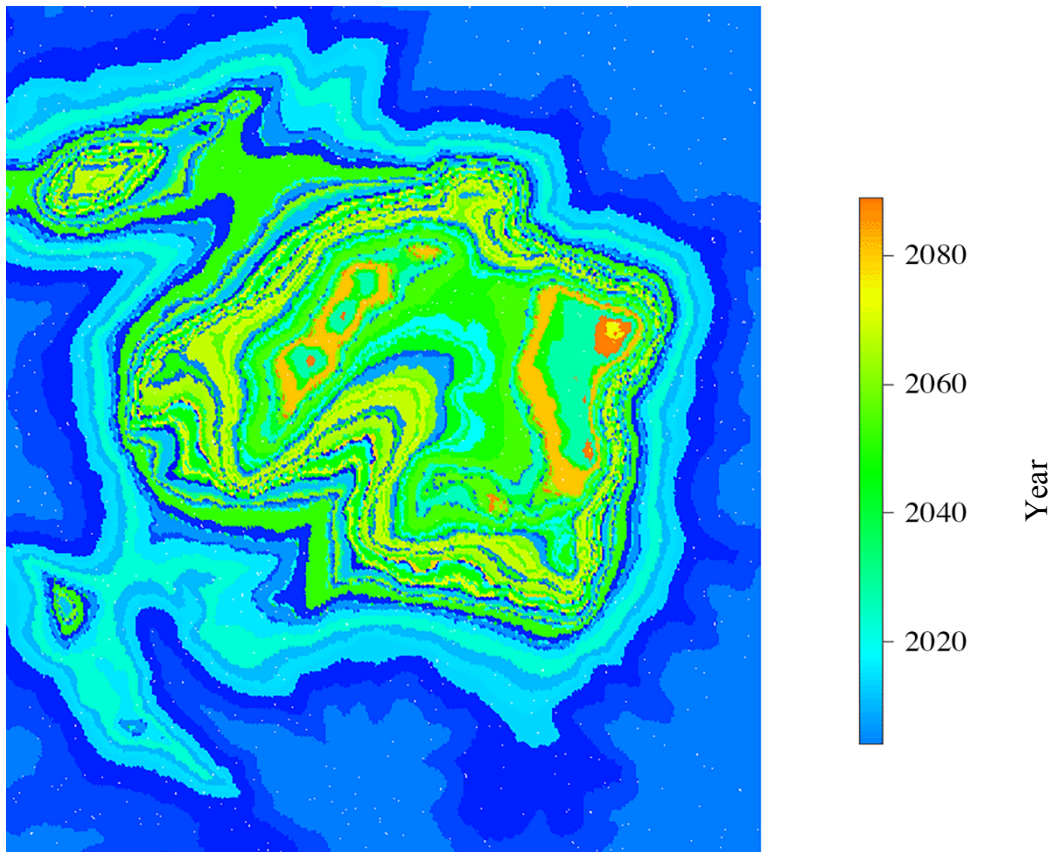


Figure 6. Map of predicted changes in the upper altitudinal range limit of *Niveoscincus ocellatus* across the model space over time following exposure to projected climate change.

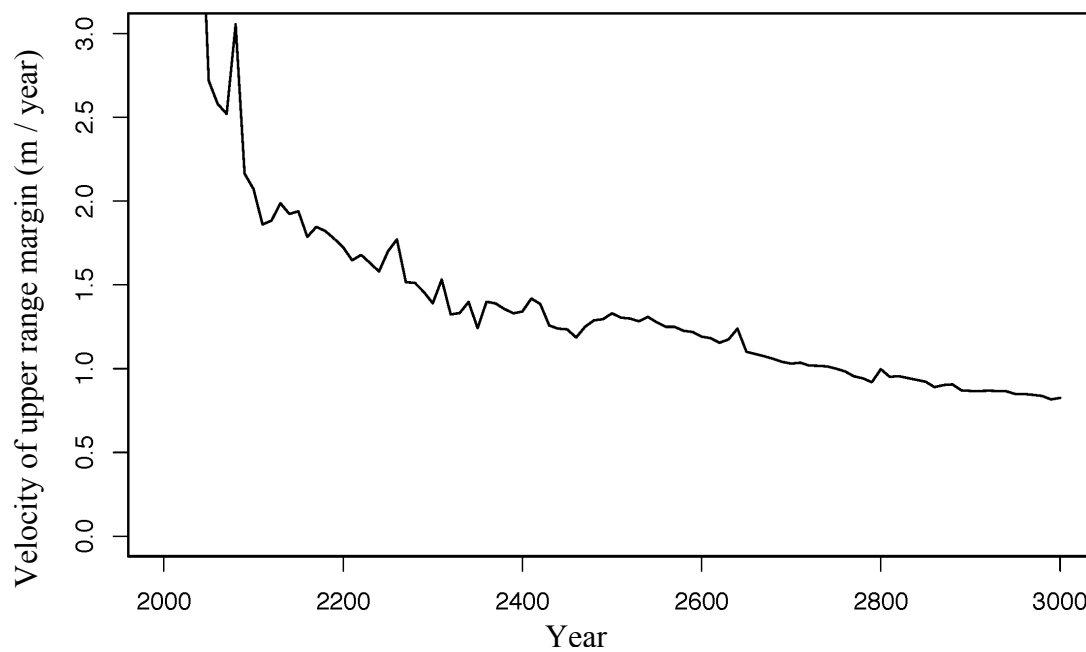


Figure 7. Predicted velocity of change in the upper range margin of *Niveoscincus ocellatus* following exposure to projected climate change from 1990 - 2100.

### 3.3 Sensitivity analyses

The model predictions were robust to changes in individual parameters in the sensitivity analyses (Table 3). The proportion of *N. ocellatus* composing the total population consistently increased for every scenario, except when the background mortality rates of *N. microlepidotus* and *N. ocellatus* were altered. Of the total population, *N. ocellatus* composed between 75.9 – 94.6% by 2100 and 69.2 – 99.0% by 2300 under the sensitivity analyses (Table 3). The level of background mortality was determined using long term fecundity data in conjunction with well-established zones of occurrence for each species and had the greatest effect on the composition of the total population. A ~1% change in the rate of background mortality of either or both species resulted in a change in the projected proportion of *N. microlepidotus* in the total population compared to initial projections of between 0.5 – 17% in 2010 and between 4.3 – 24% in 2100 (Tables 2 and 3). In contrast to background mortality, both the nature of competition for territories and the level of dispersal-related mortality risk had a limited effect on the predicted proportion of *N. microlepidotus* in the total population under projected climate change (Table 3).

Table 3: Results from sensitivity analyses of the spatially-explicit individual-based model of an interacting population of the widespread lowland species, *Niveoscincus ocellatus*, and the highland species, *N. microlepidotus*. Parameters in the initial model were varied individually and the percentage change in the proportion of *N. microlepidotus* predicted to compose the total population of lizards on Mount Wellington estimated for 2010, 2050, 2100 and 2300. An A2 scenario of climate change was used in the simulations.

Scenario	Year			
	2010	2050	2100	2300
<i>N. microlepidotus</i> mortality reduced to 18.3%	0.46%	5.23%	11.15%	27.62%
<i>N. microlepidotus</i> mortality increased to 20.3%	-4.64%	-6.87%	-7.55%	-2.18%
<i>N. ocellatus</i> mortality reduced to 17.9%	-2.74%	-3.77%	-4.25%	2.32%
<i>N. ocellatus</i> mortality increased to 19.9%	6.36%	9.03%	9.55%	14.22%
Both species mortality increased by 1%	-16.85%	-15.35%	-12.95%	-8.20%
Both species mortality reduced by 1%	26.63%	26.12%	23.95%	17.94%
Dispersal distance before death reduced to 30 m	-3.34%	-2.57%	-2.25%	2.42%
Dispersal distance before death increased to 70 m	0.26%	1.33%	1.55%	7.72%
20 m extra dispersal distance penalty for losing	-2.34%	-2.57%	-1.35%	5.02%
60 m extra dispersal distance penalty for losing	-0.44%	-0.37%	-1.55%	3.52%
50 mm size advantage = 99% chance of winning	-1.14%	-1.37%	-1.75%	4.62%
5 mm size advantage = 99% chance of winning	-2.94%	-2.17%	-1.55%	5.02%
<i>N. microlepidotus</i> home owners advantage 55%	-1.64%	-0.67%	-0.25%	6.52%
<i>N. microlepidotus</i> home owners advantage 85%	1.16%	-0.07%	-0.25%	4.72%

#### 4. Discussion

Using a spatially-explicit IBM we investigated the potential for interspecific interactions and temperature dependent processes to mediate climate change impacts on the persistence and distribution of a range restricted highland specialist, *N. microlepidotus*, and its widespread lowland competitor, *N. ocellatus*, on Mount Wellington, Tasmania. We found that the warmer conditions predicted under climate change facilitated an increase in both the density and upper elevational boundary of *N. ocellatus*. While the population size of *N. microlepidotus* was predicted to remain relatively stable in the short term (2010 – 2100), increasing competitive pressure from *N. ocellatus* ultimately drove a decline in *N. microlepidotus*' population size over the long term (2100 – 2300). The predicted population sizes of both species were sensitive to levels of background mortality, however, the direction of the model results were otherwise robust to changes in individual model parameters. Although reptiles are vulnerable to changes in the thermal environment (Thomas *et al.* 2004; Sinervo *et al.* 2010) to our knowledge there has been no previous attempt to model the distribution and population size of interacting reptile species subject to climate change. Though methods to incorporate biotic interactions into species distribution models are still under development, studies which explicitly capture biotic interactions have the potential to: (a) provide information about the strength and nature of mechanisms underlying changes in species' persistence and distribution, (b) indicate potential timeframes in which changes will occur, (c) predict the level of match / mismatch between changes in thermal niche available to a species and competition mediated changes in realised distributional range, and (d) identify target species for conservation management.

##### 4.1 Climate driven shifts in *N. ocellatus* upper elevational range boundary

The relationships between temperature and birthdate, and birthdate and offspring survival are well documented in *N. ocellatus*, and improve offspring survival rates under warming conditions in the field (Atkins *et al.* 2007; Cadby *et al.* 2010; Wapstra *et al.* 2010; Uller *et al.* 2011). Positive covariation between these parameters in the model facilitated an increase in the population size and upper elevational boundary of *N. ocellatus* under projected climate change, as has been found in other taxa (e.g. warm water fishes, Alheit & Hagen 1997; Holbrook, Schmitt & Stephens Jr 1997). In line with the general trend of species expanding their upper elevational boundary in conjunction with climate warming (Pounds, Fogden & Campbell 1999; Hill *et al.* 2002; Klanderud & Birks 2003; Konvicka *et al.* 2003; Parmesan &

Yohe 2003; Grabherr, Gottfried & Pauli 2009) we found that the upper elevational boundary of *N. ocellatus* is likely to increase under projected climate change. The predicted rate of increase in the upper elevational boundary of *N. ocellatus* is broadly comparable to results from recent meta-analyses, with estimated mean upward shifts in elevation by terrestrial organisms of 11.1 metres per decade (Chen *et al.* 2011) or 6.1 m per decade (Parmesan & Yohe 2003; Hickling *et al.* 2006). The slower upward shift we predicted for *N. ocellatus* is not surprising, given lizards are slow dispersers in general and the average shifts estimated elsewhere incorporate species with more rapid colonisation rates (e.g. birds and mammals, Chen *et al.* 2011; Parmesan & Yohe 2003; Hickling *et al.* 2006) which may result, for example, from greater dispersal ability, reproductive rate and ecological generalization (Angert *et al.*, 2011). Range changes enable species to track their preferred climate niche through space, counteracting some of the detrimental effects of climate change (Somero 2012). However, a great deal of variation exists between species in the rate and direction of climate change effects (Chen *et al.* 2011). Furthermore, as we found for *N. ocellatus*, inter-annual variability in temperature can drive alternating periods of expansion and contraction in the upper range limit of a species under climate change. Indeed, as temperatures across the mountain were more consistently predicted to be above the minimum thermal limit of *N. ocellatus*, the velocity of change in the upper range limit of this species rapidly declined.

#### 4.2 The lag in elevation response by *N. ocellatus*; a sustained distributional shift

The upper elevational boundary of *N. ocellatus* was predicted to continue to shift upward in longer term projections (2100 – 2300) despite the climate being assumed to reach a new steady state post-2100. The lag in the distributional shift in the upper elevational boundary of *N. ocellatus* is surprising, because the distances involved in tracking projected changes in climate were small (< 500 m) relative to maximum annual dispersal distances observed ( $\leq 100$  meters). A number of other species have shown lags in elevational response to climate change (Grabherr, Gottfried & Pauli 2009; Savage & Vellend 2014), despite the distances involved being within the dispersal capabilities of many species (reviewed by Chen *et al.* 2011). In our case study it is likely that high levels of mortality were responsible for the slow rate of upward movement by *N. ocellatus*, because mortality was a key determinant of *N. ocellatus*' population size. High mortality drove low territory occupation in the model, reducing competition for territories and resulting in lizard densities similar to those observed in the field. Low levels of competition for territories are likely to have resulted in lag in the



competitive exclusion of *N. microlepidotus*, as discussed below. The significant influence of mortality on both species' population size suggests that any secondary effects of climate change on mortality rate will play a large and as yet indefinite role in shaping species' persistence and distribution under climate change. For example, rising temperatures are projected to increase the number of days available for activity for both of the model species (Chapter 2) which will increase time available for foraging and likely reduce mortality, improving the survival of upward dispersing *N. ocellatus*. This type of climate change induced reduction in mortality would promote greater rates of increase in the upper elevational boundary of *N. ocellatus* than those modelled here. This is in contrast to predictions for tropical lizard species (sensu Sinervo *et al.* 2010), which are expected to experience declines in available activity period leading to reduced foraging time and unmet energy requirements, ultimately increasing mortality under projected climate change. A greater understanding of the pathways through which climate change will impact on mortality rates is required, with effects likely to be broadly different between temperate, tropical and desert taxa (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009; Sunday, Bates & Dulvy 2011; Sunday *et al.* 2014).

#### 4.3 Climate mediated competition drives *N. microlepidotus* into an extinction vortex

Overall, our findings agree with the expectation that interspecific interactions will be key determinants of climate change effects on highland species (Mason *et al.* 2014). Increasing densities of *N. ocellatus* under projected climate change increased competition for territories, raising the level of density dependent dispersal-related mortality experienced by both species. The increase in the rate of dispersal-related mortality was greater for *N. ocellatus* than for *N. microlepidotus*. However, while this change was offset by improved offspring survival under climate change for *N. ocellatus*, this was not the case for *N. microlepidotus*. Consequently, projected climate change acted as a forcing event which, mediated by competitive interactions with more rapidly reproducing *N. ocellatus*, was predicted to drive *N. microlepidotus* into a long acting extinction vortex (>300 years). Unlike the increase in the population size of *N. ocellatus* size, the decline in abundance of *N. microlepidotus* was not immediately apparent. Several frameworks have been developed which propose a temporal hierarchy of response to environmental change (Shaver *et al.* 2000; Smith, Knapp & Collins 2009; Farrer *et al.* 2015). These frameworks posit that responses to environmental change occur at the level of the individual first, followed by alterations in species abundances and subsequently the strength

of density dependent competitive effects (e.g. competition for a limited resource such as territory sites, Kardol *et al.* 2010; Adler, Dalglish & Ellner 2012; Farrer *et al.* 2014). As a result, the indirect effects of climate change are likely to take longer to manifest than more direct physiological responses (Suttle, Thomsen & Power 2007). This appeared to be the case in our study, with distributional changes occurring at a greater rate after the climate reached a new steady state equilibrium post 2100. While the decline in *N. microlepidotus* population size provided insights into the potential for biotic interactions to alter climate change impacts on this species, it occurred outside the timeframe considered by the vast majority of current species distribution models (i.e. up to 2100). Species distribution modelling on a longer time scale would benefit from increased availability of long term climate modelling data. In our example, the rate of decline in *N. microlepidotus*' population size is likely to be more rapid if the climate does not stabilise at the end of the 21<sup>st</sup> century.

#### 4.4 Caveats and future directions

While our model captured the core processes which are likely to mediate these species responses to climate change, several factors were not incorporated into the model which may influence real-world outcomes. We blanketed the model space with habitat that was potentially suitable and assumed a complete niche overlap between *N. ocellatus* and *N. microlepidotus*, yet neither may be true in reality. For example, while both species are saxicolous, *N. microlepidotus* inhabit sites with up to 75% vegetation cover, whereas *N. ocellatus* occupy sites with less than 20% shade (Melville & Swain 1999a). While the patchiness in territory occupation predicted by the model reflected that not all of the model space is habitable, where possible future work should explicitly incorporate variation in microhabitat and thereby variation in habitat suitability. Mountain characteristics are likely to slow the movement of low-elevation species into higher altitude sites, slowing the competitive exclusion of high-elevation species. For example, *N. microlepidotus* may persist longer on poleward-facing slopes, because cooler temperatures at more shaded locations will reduce *N. ocellatus*' potential to colonise these sites. This would require detailed information on species habitat preferences and high resolution spatially-explicit microhabitat data, which could be derived from satellite imagery and ground surveys. Incorporating microhabitat variation would enable subtle differences in habitat preferences to be accounted for in the model (e.g. Monasterio *et al.* 2009). This would also enable tests of the potential for changes in land use, such as vegetation clearance, and habitat suitability, such as tree line shifts, to

impact on the persistence and distribution of *N. ocellatus* and *N. microlepidotus* under climate change. These models would provide valuable insights for conservation managers and policy makers.

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## Supplementary Figures



Figure S1. Map of the area of Mount Wellington modelled in the simulation. The region within the square was included in finding territories of 700m elevation and above the model space. The blue circle denotes the pinnacle of Mount Wellington.

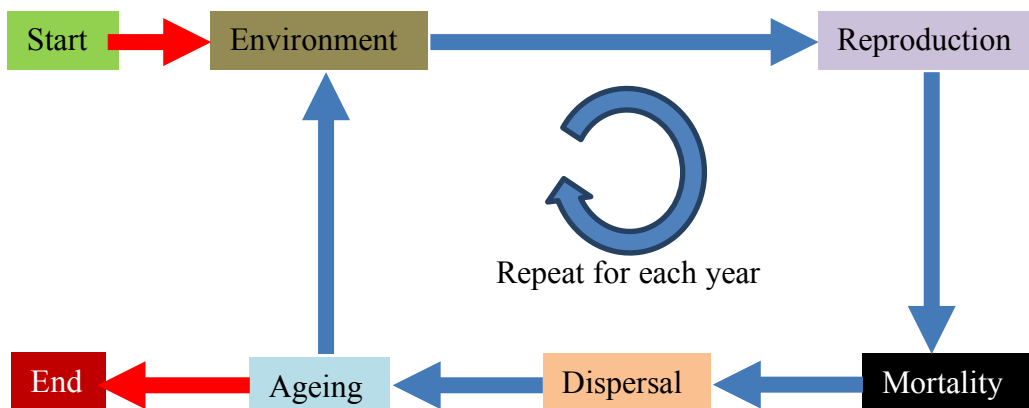


Figure S2. The modelling process, which is repeated for each year of the simulation. The model calculates the temperature of each territory (Section 2.5), then calculates each lizard's reproduction, mortality, dispersal and ageing component according to probabilistic calculations and biological parameters outlined in Section 2.4. The dispersal phase also contains a mortality component. At the end of each cycle all surviving lizards are aged by one year and the cycle repeats.

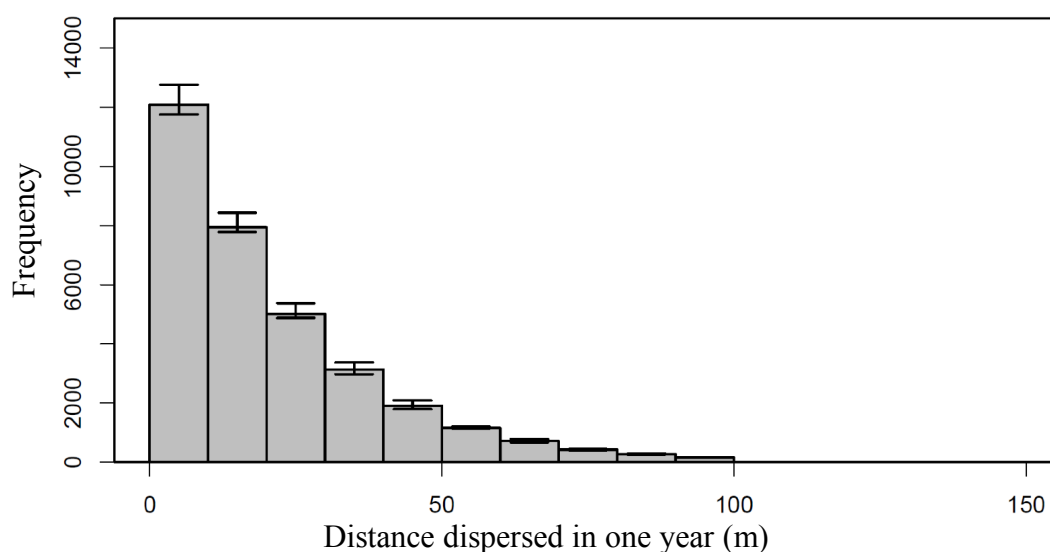


Figure S3: Frequency distribution of the annual dispersal distances (m) predicted for individuals of the widespread lowland species, *Niveoscincus ocellatus*, from ten model runs.

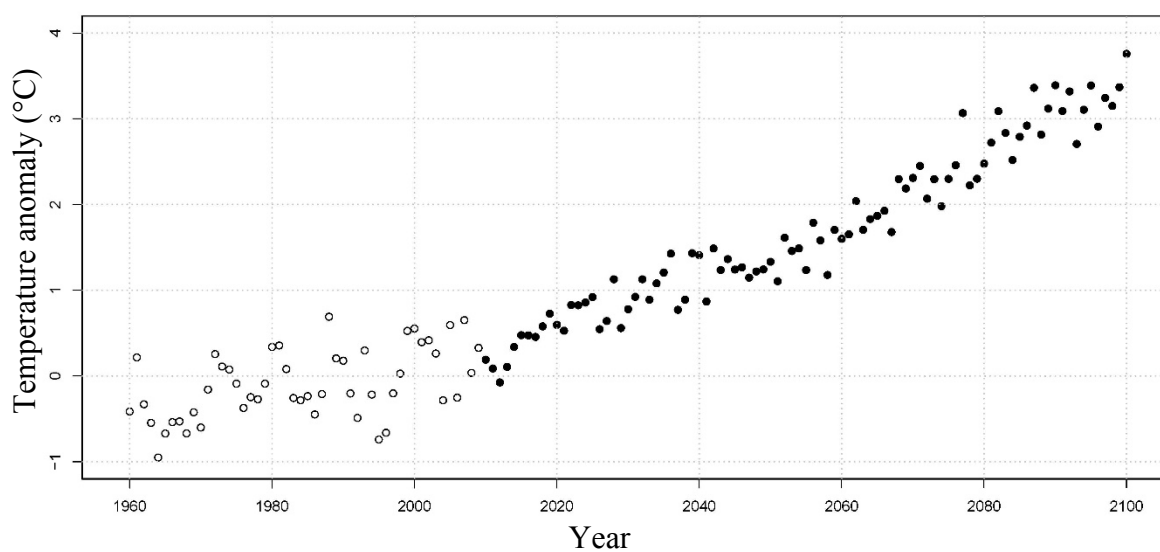


Figure S4. Annual mean temperature (AMT) for 1960 – 2010 (observations, open circles) was derived from Climate Futures for Tasmania data which was used to predict AMT for the years 2011 – 2100 (closed circles) for Mount Wellington.

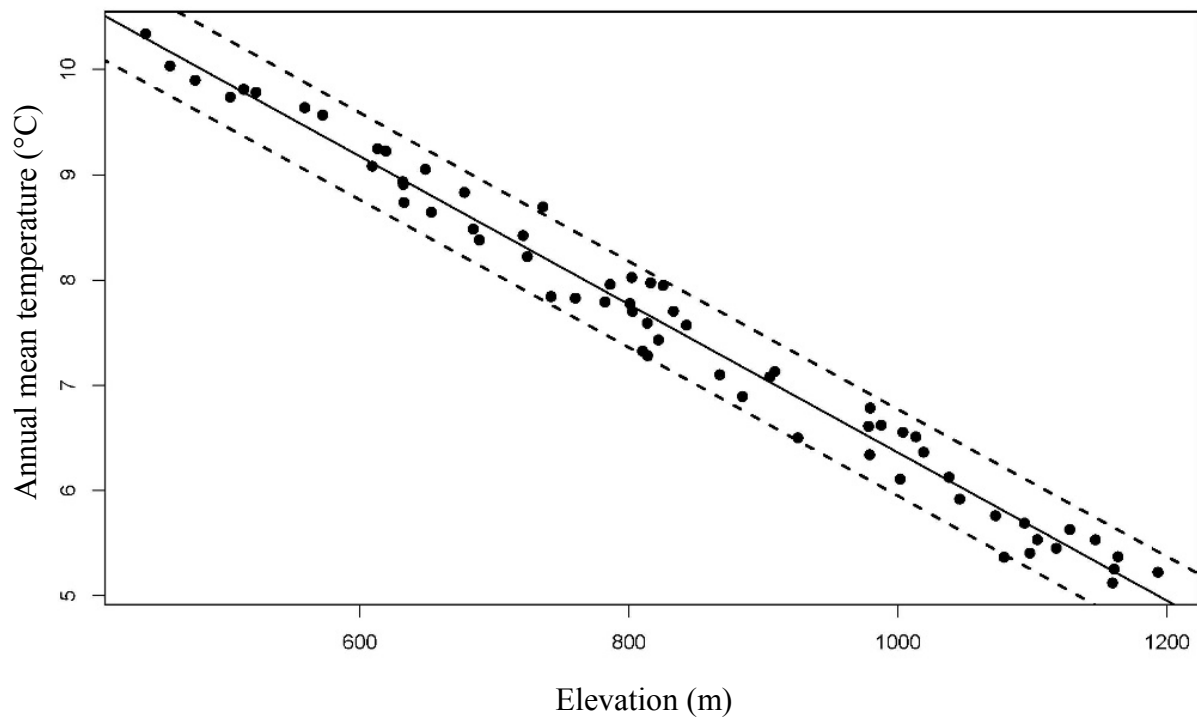


Figure S5. The relationship between elevation (m) and annual mean temperature (°C).

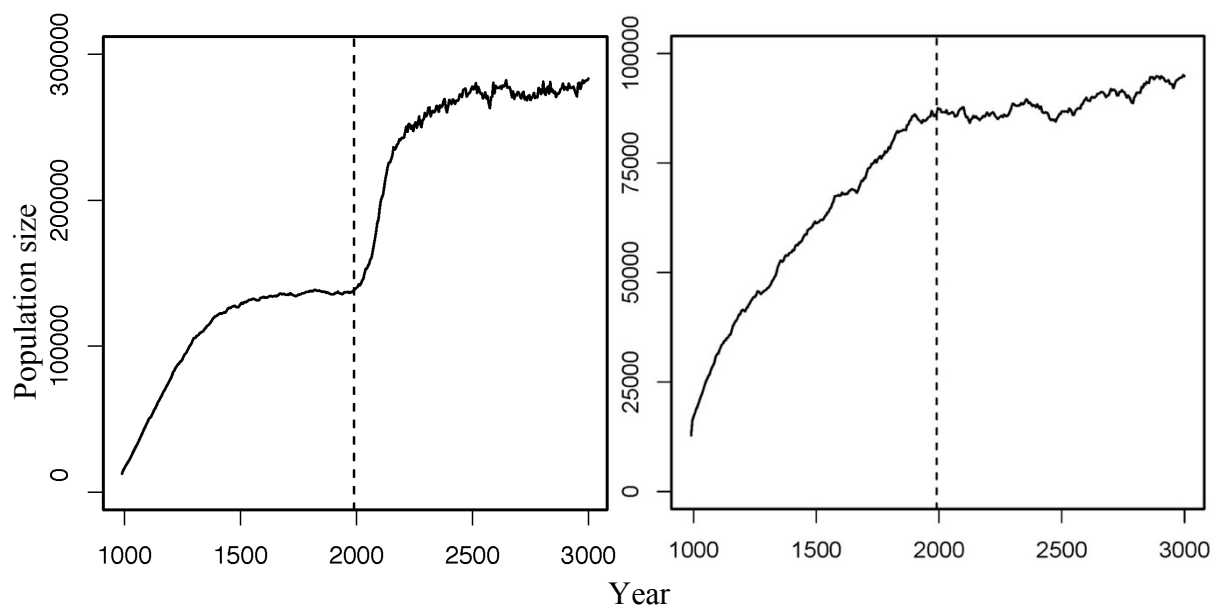


Figure S6. Population sizes of the widespread lowland species, *N. ocellatus* (left) and the alpine species, *Niveoscincus microlepidotus* (right) in the absence of competition. Left of dashed line: colonisation phase. Right of dashed line: climate change phase.

### Supplementary Tables

Table S1: Probability distribution of a given litter size for females of a given age for widespread species, *Niveoscincus ocellatus*, and the highland species, *N. microlepidotus*. Data was collected from a natural population of *N. ocellatus* at a high altitude site by EW and GW from 2001 – 2010. Females were born in the laboratory, so have a known age.

Litter size	Age										
	0	1	2	3	4	5	6	7	8	9	10
0	1	1	0.93	0.36	0.28	0.31	0.34	0.46	0.47	0.00	0.00
1	0	0	0.00	0.03	0.03	0.04	0.00	0.00	0.00	0.00	0.00
2	0	0	0.06	0.18	0.09	0.15	0.10	0.00	0.00	0.13	0.00
3	0	0	0.01	0.30	0.28	0.17	0.24	0.12	0.12	0.13	0.00
4	0	0	0.00	0.10	0.27	0.26	0.27	0.27	0.12	0.25	0.00
5	0	0	0.00	0.02	0.03	0.06	0.05	0.04	0.18	0.38	0.33
6	0	0	0.00	0.00	0.01	0.01	0.00	0.12	0.12	0.13	0.33
7	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33

Table S2: Average density per hectare and ratio of *N. ocellatus* and *N. microlepidotus* at three point locations on Mount Wellington. Estimates are averaged over ten simulations, with the range provided in brackets.

	Altitude	Coordinates	<i>N. ocellatus</i>	<i>N. microlepidotus</i>	Ratio <i>N. ocellatus</i> : <i>N. microlepidotus</i>
Summit	1270 m a. s. l.	-42.89603°, 147.237332°	1.4 (0.5 – 2.9)	7.9 (1.6 – 16.6)	0.31 (0.05 – 1.18)
Big bend	1150 – 1200 m a. s. l.	-42.887419°, 147.22317°	2.9 (0.7 – 9.7)	2.9 (1.0 – 6.7)	2.10 (0.13 – 9.59)
Springs	1000 m a. s. l.	-42.915452°, 147.248662°	19.0 (6.3 – 32.2)	0.5 (0.1 – 2.1)	67.23 (8.26 – 131.05)



# CHAPTER FIVE



# Towards a mechanistic framework for interpreting climatic effects on widespread and highland temperate reptile species.

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## Abstract

Process-based approaches provide insight into pathways of climatic effects by explicitly incorporating the mechanisms (e.g. climate, phenological cues, physiology) underlying geographic variation in life history between populations and species (e.g. parturition date, growth and fecundity). We outline a state-of-the-art mechanistic model, NicheMapR, to identify mechanisms underlying differences in life history (e.g. growth, age at maturity, fecundity, longevity) and activity between low and high altitude populations of a widespread lowland species, *Niveoscincus ocellatus*, and a range-restricted highland species, *N. microlepidotus*, of viviparous Tasmanian snow skink. The model accurately predicted reduced activity, growth, and fecundity for a high altitude population of *N. ocellatus* compared to its low altitude counterpart. Changes to the reproductive window at the high altitude site induced a number of major changes in life history representative of *N. microlepidotus*, including a transition from an annual to a biennial reproductive frequency and prolonged overwinter gestation. Under projected climate change every population experienced increased growth and fecundity, with effects most pronounced at the high altitude site. When simulated across an altitudinal transect, the models predicted that *N. ocellatus* would be largely limited to sites below 1010 m above sea level under historical climates. Under a moderate (3°C) scenario of climate change the widespread lowland species, *N. ocellatus*, was predicted to successfully reproduce and experience enhanced fitness (e.g. increased fecundity) up to 1200 m a. s. l. by 2080. Although *N. microlepidotus* was predicted to experience fitness gains under climate

change, due to asymmetric territory competition, expansion of the upper range boundary by *N. ocellatus* is likely to have negative implications for the long term viability of this species.

## 1. Introduction

Climate change is impacting terrestrial organisms worldwide (Parmesan 2006; Moritz & Agudo 2013; Pauchard *et al.* 2015). The biological impacts of climate change depend on organisms' physiological sensitivities to warming temperatures and behavioural and physiological capacities to buffer changing temperature (Huey *et al.* 2009; Seebacher, White & Franklin 2015; Kubisch, Fernández & Ibargüengoytia 2016). Despite this, the potential for adaptive phenotypic responses to climate change (e.g. behavioural and physiological buffering) are often ignored in models of species distributions under climate change (but see Sunday *et al.* 2014; Walker, Stuart-Fox & Kearney 2015; Levy *et al.* 2016). Furthermore, interspecific differences in life history traits alter climatic effects on species. Models capable of explicitly incorporating these differences will provide a more realistic basis from which to predict the magnitude of climate change effects on natural systems (Bernardo *et al.* 2007; Bozinovic, Calosi & Spicer 2011).

To reliably predict the extinction risk and responsiveness of species to projected climate change, ideally we should model the impact of projected climate change on a full range of species traits (e.g. activity, fecundity, and longevity) and life history processes (e.g. growth and gestation length). Projections should incorporate data on environmental biophysics together with the behaviour, physiology, operative body temperatures and ecology of the organism (Buckley 2008; Kearney, Shine & Porter 2009; Sunday *et al.* 2014). Mechanistic species distribution modelling is an emerging approach able to incorporate such data and can be used to describe fundamental linkages between an organism and its environment into a spatially-explicit framework (Dormann *et al.* 2012; Kearney, Matzelle & Helmuth 2012; Ehrlén & Morris 2015). Life history can be estimated based on the environmental conditions and resource levels experienced by an organism at a particular location (Kearney & Porter 2009). The explicit nature of this approach enables the specific mechanisms (e.g. photoperiod, temperature, physiology) driving differences among species among populations within species life history to be identified. This can then be used to broaden our understanding of past and future pathways of climate effects by quantifying the nature and strength of relationships between individual environmental parameters and the life history and activity of

a specific species. This framework allows a realistic representation of the ecological processes governing the responses of a species to the novel environments predicted under climate change (Kearney & Porter 2004; Mitchell *et al.* 2008; Huey *et al.* 2012; Kearney 2013).

NicheMapR (<https://github.com/mrke/NicheMapR>) is a mechanistic niche modelling software package which integrates models of metabolism, thermoregulation and the biophysical environment in R (M.R. Kearney and W.P. Porter, Submitted). This package utilises a Dynamic Energy Budget (DEB) model of growth and reproduction via a ‘thermodynamic niche’ modelling approach (Kearney *et al.* 2013). This approach has been successfully used to model climatic constraints on, and the energetic and reproductive biology of, several lizard species (Kearney 2012; Moritz *et al.* 2012; Kearney 2013; Schwarzkopf, Caley & Kearney 2015). Unlike other energy budgeting approaches (van der Meer 2006b; Kearney 2013), DEB theory models the mass and energy budget of an organism as discrete pools of biomass which have a constant chemical composition and are expressed as elemental ratios (Kooijman 1995). The DEB is modelled across the entire life cycle of the organism according to exposure to a range of nutritional and thermal environments (Kooijman 2010). As a result DEB provides a powerful tool to model interactions between heat, water and nutritional constraints (Kearney *et al.* 2013).

In this study, we apply NicheMapR to model the current and future activity, life history and altitudinal distribution of two species of the temperate lizard genus, *Niveoscincus*.

*Niveoscincus* is composed of several widespread lowland species and several highland species. We modelled a high and low altitude population of a widespread lowland species, *N. ocellatus*, and a high altitude population of an highland species, *N. microlepidotus*. Long term population monitoring data for *N. ocellatus* and field and laboratory studies of *N. microlepidotus* makes these species ideal candidates to (1) determine the role that climate, physiology and phenology have in driving geographic variation between populations and species’ life history traits and activity and (2) use this information to identify potential pathways of climate change effects on the life history, activity and distribution of these species (Chapter 2, Calosi, Bilton & Spicer 2008; Angert *et al.* 2011; Huey *et al.* 2012).

Contemporary species of the *Niveoscincus* genus appear to have arisen from a widespread lowland ancestor after the last glacial maximum, which colonized increasingly higher

elevation areas previously too cold to be habitable (Melville & Swain 2000b; Cliff, Wapstra & Burridge 2015). Widespread lowland *Niveoscincus* species are broadly distributed within Tasmania from lowland coastal sites to subalpine sites approximately 1150 meters above sea level. Highland *Niveoscincus* species have more restricted distributions and occur in disjunct mountain-top populations above 1100 m a. s. l. While lowland populations of widespread lowland *Niveoscincus* species experience warm and less variable thermal conditions, mountain populations of both widespread lowland and highland *Niveoscincus* species experience cold and highly variable temperatures (Pen *et al.* 2010). The upper range margin of widespread lowland *Niveoscincus* appears to be temperature limited, whereas the lower range margin of highland *Niveoscincus* appears to be mediated by competition with widespread lowland *Niveoscincus* (Chapter 4). High altitude populations and species possess a number of behavioural, physiological and phenological adaptations to the cold alpine environment (Atkins, Swain & Jones 2007; Pen *et al.* 2010; Cadby, Jones & Wapstra 2014). For example, high altitude *N. ocellatus* and highland *Niveoscincus* bask more and have lower selected body temperatures than their low altitude counterparts (Chapter 2, Yuni, Jones & Wapstra 2015; Yuni, Jones & Wapstra Submitted). For high altitude *N. ocellatus* these adaptations result in a gestation length which is the same as their low altitude counterparts, despite exposure to vastly different climatic regimes (Wapstra *et al.* 1999). Furthermore, while widespread lowland species reproduce annually, highland species (e.g. *N. microlepidotus*) overwinter fully developed embryos *in utero* (Olsson & Shine 1999). Widespread lowland and highland *Niveoscincus* co-occur within a narrow zone of overlap. The zone of overlap of these species indicates that the biennial reproductive frequency of the highland species is maintained at lower altitudes by factors other than temperature alone (e.g. costs of a poorly timed parturition, Schwarzkopf, Caley & Kearney 2015). Indeed, *N. microlepidotus* can reproduce annually, but do not do so in natural populations (Olsson & Shine 1998). Climate-mediated life history traits (e.g. offspring birth date, size and sex), along with intra- and inter-specific differences in behaviour, physiology and phenology are likely to impact the responses of these population and species to climate change (Olsson & Shine 1998; Atkins *et al.* 2007; Pen *et al.* 2010; Uller *et al.* 2011; Cadby, Jones & Wapstra 2014). Increasing temperatures are likely to enable upwards encroachment by the widespread lowland species, with asymmetric territory competition between highland and widespread lowland species negatively affecting the distributional range and abundance of the highland species under climate change (Chapter 4).

We parameterised a mechanistic model of a low and high altitude population of *N. ocellatus* and a high altitude population of *N. microlepidotus*. Specifically, we produced a dynamic energy budget model based on a low altitude population of *Niveoscincus ocellatus*. This model included relationships between temperature and temperature dependent life history processes such as gestation length, age at maturity, longevity and growth. We tested the ability of this model to simulate the life history, activity and phenology of a large (>1000 individuals) population of *N. ocellatus* at a low altitude site where a long term dataset (>14 years) is available to verify the predictive accuracy of the model. We then applied the model to a high altitude site and explored the role of climate, physiology and phenology in driving differences between low and high altitude populations of *N. ocellatus*. We determined the predictive ability of the model by comparing the model predictions at the high altitude site with another long term dataset (>14 years) collected from a large (>1000 individuals) high altitude population of *N. ocellatus*. An advantage of the mechanistic approach is that the effect of specific components can be manipulated in isolation. For example, simple changes to the timing of key life history events have the potential to drive the differences observed in reproductive frequency between *N. ocellatus* and *N. microlepidotus*. Specifically, the biennial reproductive frequency and prolonged gestation of *N. microlepidotus* appear to be maintained by photoperiod and temperatures associated with photoperiod (Girling, Jones & Swain 2002b; Girling, Jones & Swain 2002a; Atkins, Jones & Guillette Jr 2006). We tested whether simple changes in the timing of the initiation and termination of breeding could produce the observed differences in reproductive rate between *N. ocellatus* and *N. microlepidotus*.

We then examined how climate change is likely to affect the life history, activity and distribution of low and high altitude populations of *N. ocellatus* and populations of *N. microlepidotus*. We compared model predictions for these species using historical and projected climate data, to determine the effect of projected climate change on the life history (e.g. fecundity, reproductive frequency, age at maturity) and activity of these populations and species. We reran the model of the high altitude population of *N. ocellatus* at discrete sites across an altitudinal transect under historical and projected climates. We examined variation between predictions produced under historical and projected climates in the altitudinal clines of a wide range of life history traits (e.g. fecundity, parturition date, mass at one year of age). This allowed us to robustly predict the potential for the widespread lowland species to expand

its upper altitudinal range boundary in response to the warming conditions projected under climate change.

## 2. Methods

NicheMapR is an R (R Core Team 2015) implementation of the NicheMapper<sup>TM</sup> biophysical modelling software (details in Porter *et al.* 1973; Porter & Mitchell 2006; Kearney *et al.* 2009). We followed the ‘thermodynamic niche’ modelling approach (described in detail by Kearney 2012; Kearney 2013; Kearney *et al.* 2013). NicheMapR consists of two interacting parts: an ectotherm model of an organism (Section 2.3) and a biophysical model (Section 2.4, Figure 1). The ectotherm model incorporates a thermophysiological component describing the preferred thermal environment (Section 2.3.1) and a reproduction component describing the potential timing of reproduction, rate of development and possible litter sizes (Section 2.3.2). An ageing component incorporated in the ectotherm model tracks the energy of the lizard from vitellogenesis to maturity. Energy acquired from feeding is allocated to indeterminate growth, movement and storage, along with reproduction post-maturation. The energy/mass budget of the ectotherm model was calculated following the principles outlined by DEB theory. DEB theory is described extensively in Kooijman (2010), with further helpful reviews in van der Meer (2006a) and Sousa, Domingos and Kooijman (2008). Detail on the standard DEB model used here along with the associated theory underlying this model is also provided in Kearney (2012, Table S1). The ectotherm model calculates energy/mass budgets (Section 2.2) according to the microclimate conditions at specific sites, supplied to the ectotherm model by the biophysical model (Figure 1, described by Kearney *et al.* 2014). The location and microhabitat characteristics of a site were inputted into NicheMapR via ArcMap at a resolution of 0.04° (~5 km). Microhabitat data for each site includes the properties of the substrate (e.g. conductivity, density, soil-specific heat) and slope, aspect and percentage of shade (via GIS data on vegetation density). Together the ectotherm model and biophysical model generate site-specific information about available activity periods for basking and foraging (according to the thermal constraints Section 2.3.1), mass and length trajectories, time to maturity, realized reproductive output, and energy buffers for structural and reproductive processes (Figure 1).

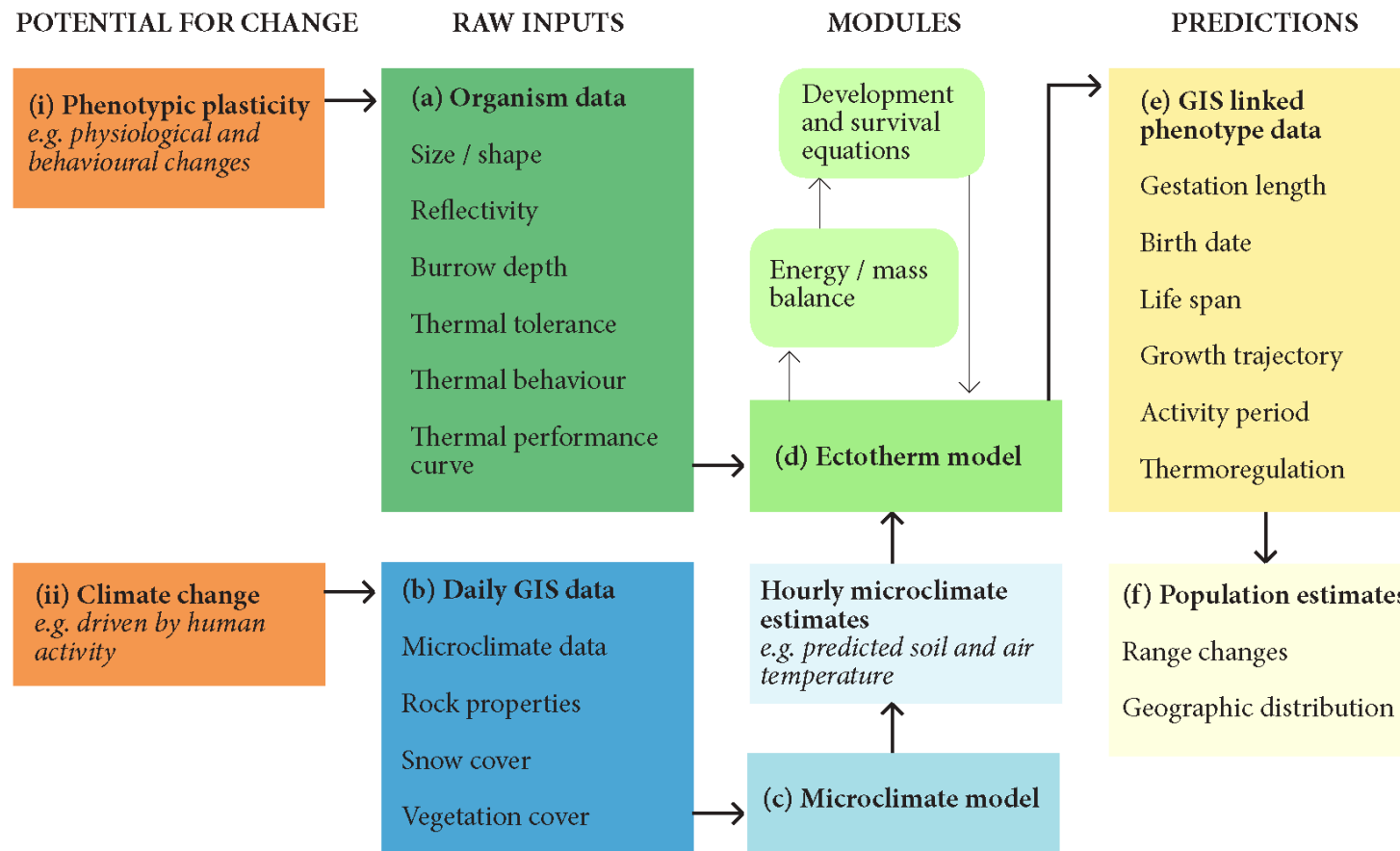


Figure 1. Summary of the mechanistic modelling process as it relates to a thermoregulating ectotherm with the potential to seek shelter in deep rock crevices. The energy mass balance of the organism is calculated using Dynamic Energy Budget theory.



## 2.1 Study species

*Niveoscincus ocellatus* and *N. microlepidotus* are diurnally thermoregulating, rock dwelling lizards. Spotted snow skinks, *N. ocellatus*, are small-to-medium-sized lizards (adults 3 – 12 g, Wapstra *et al.* 1999) inhabiting a wide altitudinal (0 – 1150 m above sea level) and geographic range in Tasmania (Cliff, Wapstra & Burridge 2015). This species has an annual reproductive strategy throughout its range. Mating occurs in autumn with obligate over-winter sperm storage by females (Jones, Wapstra & Swain 1997; Wapstra *et al.* 1999; Cadby *et al.* 2010; Wapstra *et al.* 2010; Uller *et al.* 2011). Vitellogenesis and ovulation predominantly occur in spring and are followed by a temperature dependent 3 – 4 month gestation and parturition in summer (Jones, Wapstra & Swain 1997; Wapstra *et al.* 1999; Cadby *et al.* 2010; Wapstra *et al.* 2010; Uller *et al.* 2011). There are clear differences in life history and reproductive timing between low and high altitude populations of *N. ocellatus* (Wapstra *et al.* 1999; Wapstra & Swain 2001a; Wapstra *et al.* 2001; Atkins *et al.* 2007; Wapstra *et al.* 2009; Cadby *et al.* 2010; Pen *et al.* 2010; Uller *et al.* 2011). Lizards inhabiting low elevation sites grow more quickly, mature earlier at a smaller size and produce smaller litters than lizards inhabiting high altitude sites (Wapstra *et al.* 2001; Pen *et al.* 2010). Low altitude populations also ovulate and give birth 1 month earlier than their high altitude counterparts (Wapstra *et al.* 1999; Pen *et al.* 2010; Uller *et al.* 2011). Offspring survival probabilities decline with proximity of birth to winter, as the necessary time to increase condition prior to hibernation declines (Atkins *et al.* 2007; Uller *et al.* 2011). These effects drive selection against late-born offspring, such that births after the first week of March are not observed in natural populations (Uller *et al.* 2011).

The southern snow skink, *N. microlepidotus*, replaces widespread lowland *Niveoscincus* species at altitudes above ~1100 m above sea level at sites in southwest and central west Tasmania (Hutchinson & Schwaner 1991; Melville & Swain 1999a; Melville & Swain 2000a; Wapstra & Swain 2001a; Olsson & Shine 2002; Atkins, Jones & Guillelte Jr 2006). This species exhibits summer mating, spring ovulation and fertilization, with full embryonic development completed prior to winter (Olsson & Shine 1998; Girling, Jones & Swain 2002a; Girling, Jones & Swain 2002b). Overwintering fully developed embryos results in a protracted ~ 12 month gestation (Olsson & Shine 1998; Olsson & Shine 1999). This has been interpreted as a maternal care tactic to buffer offspring from harsh high alpine conditions (Olsson & Shine 1998) but it does have a cost, reducing reproductive frequency (and lifetime reproductive output) by more than 50% (Olsson and Shine 1999). Female *N. microlepidotus*

also exhibit skipped years of reproduction, producing young every 2 – 4 years (Olsson & Shine 1999).

## 2.2 DEB parameter estimation

We applied the covariation method to estimate parameters used by the DEB model (Lika *et al.* 2011). This method simultaneously estimates the DEB model parameters based on empirical observations of physiological processes (Table 1, Kearney 2012). The covariation method is used to estimate DEB parameters because these parameters are not directly observable, but are abstract state variables of structure, reserve and maturity. In essence, the covariation method attempts to simultaneously estimate all of the DEB parameters from empirical observations of physiological processes. ‘Core’ and ‘auxillary’ parameters (defined in Kearney, 2012) are combined with state variables to define mapping functions from abstract considerations (e.g. structural volume) to field and laboratory based observations (e.g. wet mass). In essence, the covariation method allows competition between all of the available information to generate the parameter set with the best fit, as a result all DEB parameters must be simultaneously estimated from all data sets.

Observational data for *N. ocellatus* used in DEB parameter estimation were collected from large natural populations at low and high elevation sites from 2000 – 2015 (referred to as natural population data, Table 1). Females are caught in the field each year and brought into the laboratory to give birth. Females and their offspring are then weighed and measured and offspring toe clipped for future identification. As a result of the long term nature of this dataset lizards have a known age, parentage and reproductive history.

Observational data used to fit the DEB model included: ages (days) at birth and maturity and masses (g) and snout-vent lengths (SVL) at birth, maturity and ultimate size, annual reproductive output (litter size) and longevity (Table 1). A standard conversion factor was used to convert wet mass (m) to dry mass for use in the model ( $m_{\text{dry}} = 0.3m_{\text{wet}}$ ). We used age – SVL trajectories and SVL – mass relationships from birth to adulthood to describe potential developmental trajectories (natural population data, Wapstra *et al.* 2001). Because fecundity is strongly related to SVL (Jones, Wapstra & Swain 1997; Wapstra & O'Reilly 2001; Wapstra & Swain 2001b), we made litter size dependent on SVL based on observations of the low altitude population of *N. ocellatus*.

Table 1. Comparison of observed and predicted parameters used in the dynamic energy budget model. Observational data was from a long term study of thousands of *N. ocellatus* at a low elevation site collected by GW and EW from 2000 – 2015. Length is snout-vent length.

Data	obs.	pred.	units	Source
$a_b$ , age at birth	98	92	days (20°C)	(Wapstra <i>et al.</i> 1999)
$a_p$ , age at puberty	457	465	days (20°C)	(Wapstra <i>et al.</i> 1999)
$a_m$ , longevity	4745	4745	days (20°C)	natural population data
$l_b$ , length at birth	29.62	31.44	mm	natural population data
$l_p$ , length at puberty	50	49	mm	estimated
$l_\infty$ , maximum length	73	75	mm	natural population data
$W_b$ , dry mass at birth	0.165	0.175	g, dry	natural population data
$W_p$ , dry mass at puberty	0.9	0.7	g, dry	estimated
$W_\infty$ , maximum mass	2.13	2.35	g, dry	natural population data
$R_\infty$ , max. reproductive rate	0.0137	0.0131	# d <sup>-1</sup> (20 °C)	natural population data

DEB parameterisation requires an associated temperature for ages at birth and maturity, length-at-age, reproductive rate and longevity. An Arrhenius thermal response curve describing the temperature dependence of reaction rates is also required. Together, the associated temperature and the Arrhenius thermal response curve allows the model to estimate the life history of the lizard, according to the environmental conditions experienced at the site of interest (Section 2.4). We used data on gestation length collected under laboratory conditions from Wapstra (2000) to estimate the ‘constant temperature equivalent,’ which enables a direct comparison between the rate of biological processes under fluctuating temperatures in the field, with the rate at constant temperatures in the laboratory (CTE, Orchard 1975). Because observations of gestation length were made under diurnally fluctuating conditions we estimated a mean Arrhenius temperature correction factor across gestation and then back-calculated the temperature necessary to produce the CTE. We produced an Arrhenius thermal response curve using the 5-parameter model (for more detail on this model see Sharpe & DeMichele 1977; Schoolfield, Sharpe & Magnuson 1981). We estimated the Arrhenius temperature  $T_A$  using observations of maximal sprint speed (ms<sup>-1</sup>) against body temperatures of 21 °C, 23 °C, 26 °C, 29 °C, 31 °C, 33 °C and 35 °C (described in Yuni, Jones & Wapstra Submitted). We assumed that the lower threshold temperature for enzyme deactivation  $T_L$  corresponded with the critical thermal minimum and that the upper

threshold temperature  $T_H$  at which the performance curve is reduced to zero corresponded with the critical thermal maximum (Table S1, Chapter 2).

### 2.3 The ectotherm model

The ectotherm model uses the physical properties of the lizard in combination with a behavioural component to calculate the heat / activity budget of the ectotherm (Tables 2 and S2, described in Kearney *et al.* 2013). A thermophysiological component specified preferred and tolerable environmental conditions while a reproduction component defined potential reproductive output and timeframes for the initiation and termination of reproduction.

#### 2.3.1 Thermophysiological component

The lizard model was specified to thermoregulate diurnally. Data on the thermoregulatory behaviour of low and high altitude populations of *N. ocellatus* were collected in the laboratory and field (Table 2, Yuni, Jones & Wapstra Submitted). In the model, body temperature had to reach a series of temperature thresholds during daylight hours to initiate emergence, basking and foraging / feeding (Table 2, Kearney *et al.* 2013). The lizard could shelter in rock crevices at certain depths (5 to 30 mm deep) or shade (0 – 90%) to avoid temperatures outside the critical thermal limits. Any period of exposure to temperatures at or above the critical thermal maximum ( $CT_{max}$ ) was lethal (Chapter 2). As these species recover from freezing temperatures, 12 h of continuous exposure to temperatures below the critical thermal minimum ( $CT_{min}$ ) were required for exposure to temperatures at or below the  $CT_{min}$  to be lethal.

#### 2.3.2 Reproduction component

We used the batch reproduction model to calculate reproductive output (Pecquerie, Petitgas & Kooijman 2009) following Kearney (2012). After maturity a reproduction buffer continues to accumulate at all times (with feeding throughout pregnancy), but is only drawn on to produce offspring according to species and population-specific dates (Table 3, Olsson & Shine 1998). While the model accurately represented the overall energy flow required to produce an embryo, the process of embryonic development was more rapid than occurs in reality (Wapstra *et al.* 1999). Consequently, the date reproduction was able to commence in the model corresponded with the date ovulation occurs in the natural population. Offspring born late in the season have severely reduced survival, so a second cut-off date was used to prevent reproduction after a specified date (Table 3, Olsson & Shine 1999).

Table 2. Population-specific thermal traits for low and high altitude populations of *Niveoscincus ocellatus*. Minimum emergence temperature and minimum basking temperature were estimated based on laboratory studies by A Caldwell, unpublished data.

Temperature threshold	units	low	high	source
$T_{RB}^{min}$ , min emergence	°C	10.0	7.0	estimated
$T_B^{min}$ , min basking	°C	23.0	18.0	estimated
$T_F^{min}$ , min foraging	°C	29.1	22.3	(Yuni, Jones & Wapstra Submitted)
$T_F^{max}$ , max foraging T	°C	34.7	33.9	(Yuni, Jones & Wapstra 2015)
$T_{pref}$ , preferred	°C	32.7	30.4	(Yuni, Jones & Wapstra Submitted)
$CT_{min}$ , critical min	°C	4.3	4.3	Chapter 2
$CT_{max}$ , critical max	°C	41.8	41.8	Chapter 2

Table 3. Dates for the reproductive phenology of low and high altitude populations of *Niveoscincus ocellatus* and *N. microlepidotus*.

Parameter	low <i>N. ocellatus</i>	high <i>N. ocellatus</i>	Source	<i>N. microlepidotus</i>	Source
Median birth date	20 Jan	14 Feb	natural population data	14 Nov	(Olsson & Shine 1998)
Initiation of reproduction	11 Oct	1 Nov	established iteratively	11 Feb	established iteratively
Reproduction cut off	11 Nov	1 Dec	established iteratively	7 May	established iteratively

While litter size was dependent on SVL, we allowed smaller litters for *N. ocellatus* if the energy required to produce the expected litter size exceeded the amount of energy available for reproduction. As *N. microlepidotus* exhibits skipped years of reproduction, smaller litters were not allowed if the energy required to produce the expected litter size was not reached (Olsson & Shine 1999). The dates used for the reproductive window of high altitude *N. ocellatus* and for *N. microlepidotus* were established iteratively as the dates which produced the most realistic representation of these species reproductive phenology and reproductive output.

#### 2.4 Microclimate model

Given the physical properties of the model lizard (Table 1) and its microhabitat, the microclimate model (described in Porter *et al.* 1973) computes hourly steady-state body temperatures from actual and interpolated weather station records (Kearney *et al.* 2014). To drive the microclimate model we used historical (1990 – 2009) 0.05° gridded environmental data for Tasmania from the Australian Water Availability Project (AWAP, Raupach *et al.* 2011). Data included daily minimum and maximum temperature, vapour pressure, rainfall and daily solar radiation. Projections were centred on the year 2000, with simulations post-2009 looping back to climate data from pre-2000 to provide a constant block of climate data. To calculate the microclimate available to a thermoregulating lizard at a height of 10 mm above the ground we solved partial differential equations using the AWAP data recorded 2 m above the ground. This enabled the conditions in minimum and maximum sun to be estimated and the position of a thermoregulating lizard within the environment to be predicted.

##### 2.4.1 Climate projections

We assessed the impacts of projected climate change on the life history of low and high altitude populations of *N. ocellatus* and *N. microlepidotus*. We adjusted the daily air temperature inputs for the microclimate model based on a 3°C projected increase in air temperature for 2080 under the Representative Concentration Pathway (RCP) 6.0 scenario of climate change (Nakicenovic & Swart 2000; Moss *et al.* 2010; Field *et al.* 2014b). The RCP6.0 scenario is a moderate scenario of climate change (Van Vuuren *et al.* 2011), which is based on a revised and extended storyline of the Intergovernmental Panel on Climate Change A2 climate scenario published in Riahi, Grubler and Nakicenovic (2007). Current climate trends and greenhouse gas emissions most closely match the A2 scenario (Raupach *et al.* 2007; Field *et al.* 2014a).

### 2.5 Site choice and simulations

We first simulated *N. ocellatus* at Orford, a warm low altitude site on the East Coast of Tasmania ( $-42.56^{\circ}$ ,  $147.83^{\circ}$ , 50 m above sea level). This is the site of the large natural population of *N. ocellatus* used to parameterise the model, and is typical of the coastal cool temperate region of Tasmania (Pen *et al.* 2010). We then transplanted the initial model to the shores of Lake Augusta, a cold high altitude site in Tasmania ( $-41.85^{\circ}$ ,  $146.57^{\circ}$ , 1050 m a. s. l.). Lake Augusta is the site of a large natural population of *N. ocellatus* subject to ongoing monitoring since the year 2000. This allowed us to determine how much of the differences in life history between low and high altitude populations of *N. ocellatus* could be explained by climate. We examined traits that may have diverged from low altitude populations of *N. ocellatus* to produce the observed life history and activity of high altitude populations of this species. We reran the initial model at the high altitude site with (a) high altitude *N. ocellatus* preferred temperatures for basking and foraging (Section 2.3.1, Table 2) and then (b) a change in the dates that initiated and terminated reproduction (Section 2.3.2, Table 3) to test the potential for these traits to alter the life history and activity of *N. ocellatus* observed at this location.

We reran the initial model of low altitude *N. ocellatus* at sites across Tasmania to compare the predicted distribution of annual and biennial reproductive frequency with the observed distribution of *N. ocellatus* and *N. microlepidotus* respectively. We generated a map of the continuous, non-threshold value of mean number of litters per reproductive year for Tasmania. We overlaid the map with the known distribution of *N. ocellatus* and *N. microlepidotus* using observational data from the Natural Values Atlas (Department of Primary Industries, Parks, Water & Environment, Tasmania). The match between the predicted distribution of annual and biennial reproduction and the distribution of *N. ocellatus* and *N. microlepidotus* species illustrated the effect of climate on these species life history and subsequent distribution. We then tested whether simple changes to reproductive phenology could produce the biennial reproductive mode of *N. microlepidotus* at sites at the lower altitudinal range boundary of *N. microlepidotus* by altering the dates that reproduction was initiated and terminated in the initial model (Table 3).

Simulations were commenced on the same day of the year as the observed median parturition date (Table 3). For each simulation we ran the model for fifteen years. We compared predictions of growth rate, maximum SVL, age at first reproduction, reproductive frequency, activity period, parturition dates, litter size and life span with observations from the corresponding natural population of *N. ocellatus*. Growth trajectories were compared with skeletochronology data (Wapstra *et al.* 2001). Skeletochronology data was derived using lines of arrested growth (LAGs) on the femur of a selection of individuals from the low (N = 53) and high altitude site (N = 103, Wapstra *et al.* 2001). Mean gestation length and associated standard error were calculated by averaging predictions across years. There are no observations of age – SVL trajectories or SVL – mass relationships available for *N. microlepidotus* for comparison with model predictions. We recorded life span, reproductive life history, birth dates and activity predicted by the model for *N. microlepidotus*. Each simulation was run under historical and projected climate change, with one exception. The models of *N. ocellatus* run at the high altitude site using population-specific thermal traits and reproductive phenology were combined.

#### 2.5.1 Climate change effects across an altitudinal transect

We simulated the high altitude population of *N. ocellatus* at several discrete sites across an altitudinal transect on Mount Wellington under historical and projected climate change (Section 2.4.1, Figure S1). We chose Mount Wellington as a well-studied site with known range boundaries for *N. ocellatus* (~1150 m a. s. l.) and *N. microlepidotus* (1100 – 1250 m a. s. l.). This allowed us to examine altitudinal variation in climate driven impacts on activity, birthdate, mass at one year of age, fecundity, gestation length and time to maturity. We used model predictions of fecundity and birthdate to indicate whether a viable population could establish at each site along the transect.



### 3. Results

To establish the reliability of the dynamic energy budget model at reproducing the life history of low altitude *N. ocellatus*, we compared predictions of key life history traits used for the Dynamic Energy Budget procedure (Figure 1) with observations from a large low altitude population of *N. ocellatus*. The DEB model estimates of life history parameters, including mass, length and age at birth and maturity, had a close fit to field based observations (Table 1). The DEB model successfully captured empirical relationships between snout-vent length and age, temperature and metabolic rate, and wet mass and snout-vent length (Figures S2a – c). When used within NicheMapR, life history predictions based on the DEB model closely matched field based observations of growth rate (Figure 2, Wapstra *et al.* 2001), and parturition date of the low altitude population of *N. ocellatus* (17 December – 25 January versus 17 December – 10 February). The model predicted a larger-than-average maximum snout-vent length (Figure 2) comparable to the largest lizards observed in the field (75 mm versus 73 mm). Gestation length was shorter than observed in the field (42 days  $\pm$  1 s. e. versus 92 - 126 days, Wapstra *et al.* 1999). The predicted lifespan was the same as the maximum longevity observed in the field (13 years). Predictions matched age at first reproduction (3 years of age versus 2 – 3 years of age), reproductive frequency (both annual with no skipped years of reproduction), clutch size (both 1 – 5 offspring, Figure 3), and activity period (Figure 4, activity from August to May with some winter emergence, Wapstra & Swain 1996). Except for gestation length, predictions indicate that using first principles, the mechanistic model successfully captured processes underlying the life history, activity and reproductive phenology of a low altitude population of *N. ocellatus*.

When the initial model was applied to a high altitude site predictions closely matched field based observations of growth at the high altitude site until 3 years of age, after which the modelled rate was slower than in reality. This resulted in a smaller predicted maximum size than occurs in the natural population (73 mm versus 92 mm, Figure 2). There was a close match between predicted and observed age at first reproduction (age 4 versus 3 – 5 years of age) and reproductive frequency (both annual with 1 – 2 years of skipped reproduction across the lifetime, Figure 3). Litter sizes were generally predicted to be smaller than is observed at the high altitude site (1 – 2 offspring versus 1 – 6 offspring, Figure 3). Gestation length was predicted to be shorter than occurs at the high altitude site (72 days  $\pm$  4 s. e. versus 92 - 126 days, Wapstra *et al.* 1999). The model lizard did not die within the simulated time frame, exhibiting a slightly longer lifespan than has been observed in the natural population (15 years

versus 14 years). Parturition was predicted to occur two weeks earlier than is observed at the high altitude site (3 January – 22 February versus 20 January – 26 February). Predictions of activity period largely matched field based observations of activity (both October to April), but emergence was delayed by 1 – 2 weeks compared to the natural population. Both the model lizard and the natural population exhibited unbroken winter torpor at the high altitude site (Figure 4, Wapstra *et al.* 1999).

When thermal traits of the high altitude population of *N. ocellatus* were specified (Table 2), predictions of activity period and the timing of emergence better matched field based observations (Figure 4). Hibernation was predicted to occur up to 6 days later than generally occurs in the field (Figure 4). This adjustment had no effect on growth rate, maximum size, age at first reproduction, reproductive frequency, litter size or longevity. Gestation length increased ( $74 \pm 4$  s. e. days) and parturition was delayed (7 January – 24 February), more closely matching field based observations than the initial climate transplant. Delaying the initiation and termination of reproduction (Table 3) produced birthdates within the range observed in the field (29 January – 15 February versus 20 January – 26 February), increased fecundity (Figure 3) and reduced gestation length ( $62 \pm 3$  s. e. days). Otherwise this change did not result in a notable deviation from the life history traits or activity period reported for the simulation of *N. ocellatus* at the high altitude site.

### 3.1 Simulating *N. microlepidotus* reproductive phenology under historical climates

We simulated the initial model of low altitude *N. ocellatus* across mainland Tasmania. The predicted distribution of annual and biennial reproductive frequency aligned well with the observed distribution of *N. ocellatus* and *N. microlepidotus* respectively (Figure 5).

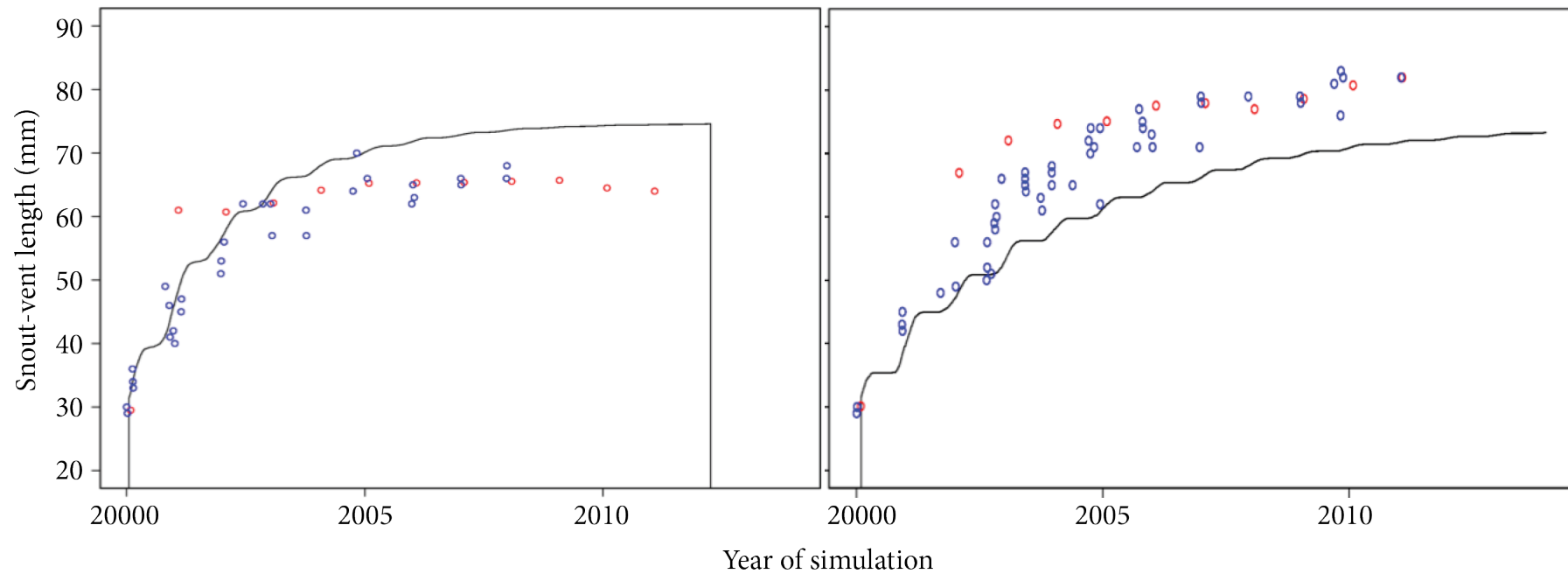


Figure 2. Growth trajectories (wet mass) predicted for a low (left) and high (right) altitude population of the widespread lowland species, *N. ocellatus* based on modelled data from Dynamic Energy Budget models (black line), skeletochronology data (blue, Wapstra *et al.* 2001) and natural population data (red, collected by EW and GW). Pauses in growth during hibernation are reflected in annual growth plateaus.

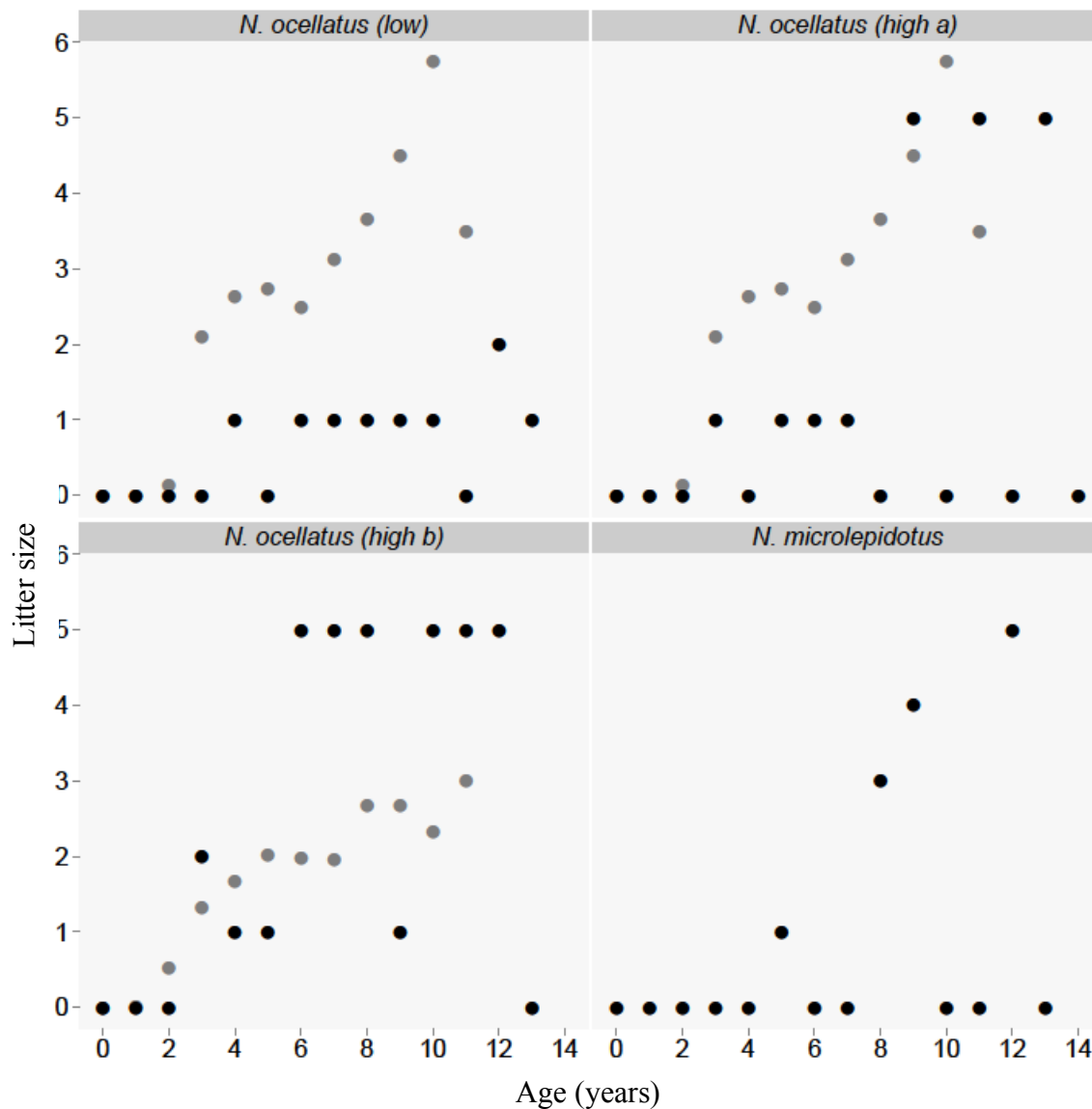


Figure 3: Predicted (black) versus average observed (grey) age based fecundity of *N. ocellatus* at a low and high altitude site and *N. microlepidotus* at a high altitude site. The initial simulation of *N. ocellatus* was transplanted to the high altitude site (a), then rerun (b) with altered dates for the initiation and termination of reproduction and again rerun with an altered window for reproduction to produce a reproductive frequency and duration similar to *N. microlepidotus*.

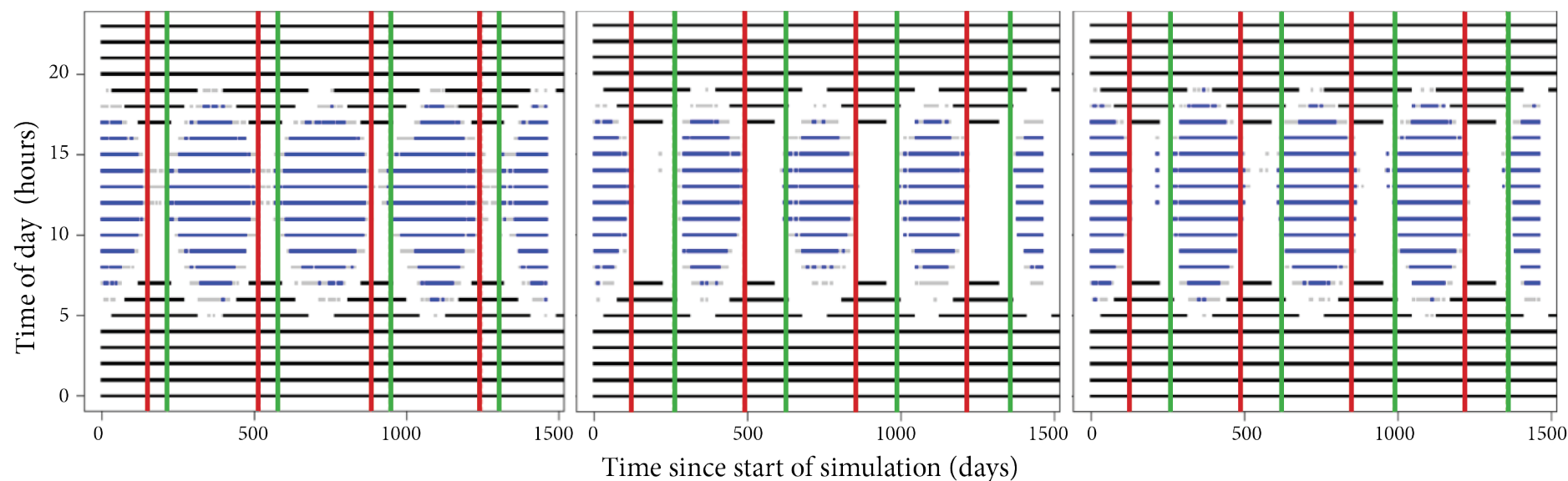


Figure 4: Predicted foraging activity (blue) and basking activity (grey, overlaid by foraging activity) of *N. ocellatus* for the first four years of the simulation. Each ellipsoid represents one annual activity period. The initial model was run at a low altitude site (left), a high altitude site (middle), and again at a high altitude site with population-specific thermal traits (right). Dashed lines indicate the approximate timing of emergence (green, 1 August low altitude site; 1 October high altitude site) and hibernation (red, 31 May at the low altitude site; 30 April high altitude site) as occurs in reality.

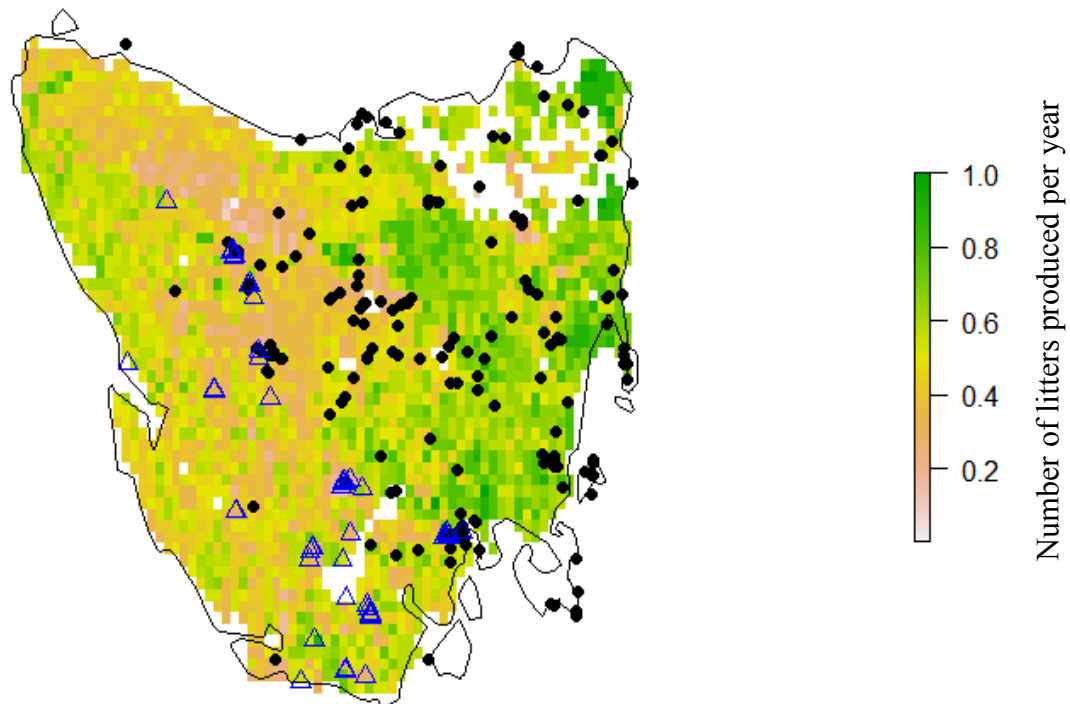


Figure 5: Map of litter frequency predicted by the model (green to white) overlaid by distribution data of annually reproducing *Niveoscincus ocellatus* (black circles) and biennially reproducing *N. microlepidotus* (blue triangles).

When the reproductive window was altered to simulate a biennial reproductive mode the lizard reached a maximum size similar to that of *N. microlepidotus* in the field (69 mm versus 73 mm, Caldwell unpublished data). Reproductive frequency closely matched field based observations (biennial reproductive rate with occasional skipped years of reproduction, Figure 3, Olsson & Shine 1998; Olsson & Shine 1999). The first litter was produced at age 5 (age at maturity in the field is not known) and the maximum litter size predicted was greater than has been observed in the field (5 offspring versus 4 offspring, Atkins, Swain & Jones 2007). The model predicted prolonged overwinter gestation, shorter than that observed in the field ( $273 \text{ days} \pm 4 \text{ s. e. days}$  versus  $\sim 12$  months, Olsson & Shine 1998). Unlike reality, only partial instead of full offspring development occurred prior to hibernation (Olsson & Shine 1998; Olsson & Shine 1999). The model lizard did not die within the simulated timeframe (15 years). Predicted birthdates were similar to those observed in the field (9 November - 18 December versus late October - early December, Olsson & Shine 1998). Predicted and observed activity period aligned well (September – April, Figure 4, Olsson & Shine 1998).

### 3.2 Effects of projected climate change on life history and activity

Under a realistic scenario of climate change (3°C warming) centred on 2080, the model lizard at the low altitude site was predicted to grow more rapidly to its maximal size (75 mm), mature earlier (2 years of age), reproduce annually (with an extra litter at age three) and consistently produce larger litters (5 offspring from age 4 onward) than was predicted under historical climates. The model lizard died at 12 years of age, one year earlier than in the initial simulation. Gestation lengths shortened ( $39 \pm 1$  s. e. days) and litters were produced up to 8 days earlier (9 December – 13 January). Activity was extended under climate change, continuing throughout the year. We reran the model at the high altitude site with the thermal traits and reproductive phenology of high altitude *N. ocellatus*. Under projected climate change this model predicted more rapid growth to maximum size (74 mm), earlier age at first reproduction (age 3), reproduction of larger litters (up to 5 offspring), several missed years of reproduction, earlier birthdates (20 January – 3 February), shorter gestation ( $55 \pm 1$  s. e. days) and an extended activity period (mid-September – mid-May) compared to the initial models. As in the initial simulation, the lizard did not die within the modelled timeframe. Under climate change, the model altered to reflect *N. microlepidotus* reproductive biology predicted more rapid growth to maximum size (74 mm), earlier maturity (4 years old) and greater fecundity (1 – 5 offspring from age 4 onward) than predicted under historical climates. As in the initial simulation, the lizard did not die within the simulated time frame. Like the initial simulation the model predicted biennial reproduction, although there was one instance of litters produced in consecutive years. Gestation lengths were shorter and more variable ( $238 \text{ days} \pm 7$  s. e. days) and accompanied by a greater birth dates spread (7 September to 30 November). Activity was extended (late August – early June) with some winter emergence.

### 3.3 Climatic effects on life history across an altitudinal transect

We reran the model of the low altitude population of *N. ocellatus* across an altitudinal transect on Mount Wellington in 2000 and 2080 (Table 4). Under historical climates, gestation took 75 days or more to complete at altitudes above 1010 m a. s. l. (Figure 6). At altitudes above 1040 m a. s. l. only one offspring was able to be produced before mid-March under historical climates in the simulated timeframe, so offspring survival probabilities at these sites would be very low (Table 4, Atkins *et al.* 2007; Uller *et al.* 2011). This supports the hypothesis that the effect of low temperatures on embryonic development makes annual reproduction unviable at higher altitudes for the widespread lowland species, *N. ocellatus*. Under projected climate change gestation lengths were reduced and parturition date brought forward, which suggests

viable offspring would be produced at all altitudes (Table 4 and Figure 6). Under projected climate change across the transect, age at maturity decreased, mass at one year increased and reproductive output more than doubled (Figure 6). Life span remained consistently greater than 13 years across the transect regardless of the climate scenario experienced. While litters were predicted to be produced biennially across the transect under historical climate change, instances of annual and even double litters were predicted under projected climate change.

Table 4: Predicted birth dates and activity across an altitudinal transect on Mount Wellington.

<sup>1</sup>A product of overwinter gestation. <sup>2</sup> Excluding overwinter gestation. <sup>3</sup> Litter size of 1.

Altitude:	900 m	1010 m	1040 m	1070 m	1100 m	1200 m
<i>Year 2000 subjected to historical climates</i>						
Earliest birth	10 Jan	29 Oct <sup>1</sup>	5 Nov <sup>1</sup>	5 Nov <sup>1</sup>	2 Dec <sup>1</sup>	24 Nov <sup>1</sup>
Earliest birth 2 <sup>2</sup>	10 Jan	24 Feb	5 Feb	7 Feb <sup>3</sup>	27 Feb <sup>3</sup>	6 Feb <sup>3</sup>
Latest birth	31 Mar	11 Mar	3 Mar	22 Mar	27 Feb	20 Apr
Emergence	mid Oct	mid Oct	late Oct	early Nov	early Nov	mid Nov
Hibernation	late Apr	mid Apr	mid Apr	mid Apr	early Apr	early Apr
<i>Year 2080 subjected to moderate climate change (3°C)</i>						
Earliest birth	29 Dec	1 Sep <sup>1</sup>	3 Oct <sup>1</sup>	28 Oct <sup>1</sup>	3 Jan	3 Jan
Earliest birth 2 <sup>2</sup>	29 Dec	29 Dec	3 Jan	3 Jan	3 Jan	3 Jan
Latest birth	19 Mar	10 Mar	12 Mar	14 Mar	14 Mar	4 Apr
Emergence	late Aug	mid Sep	mid Sep	mid Sep	mid Sep	late Sep
Hibernation	late May	mid May	mid May	early May	early May	early May



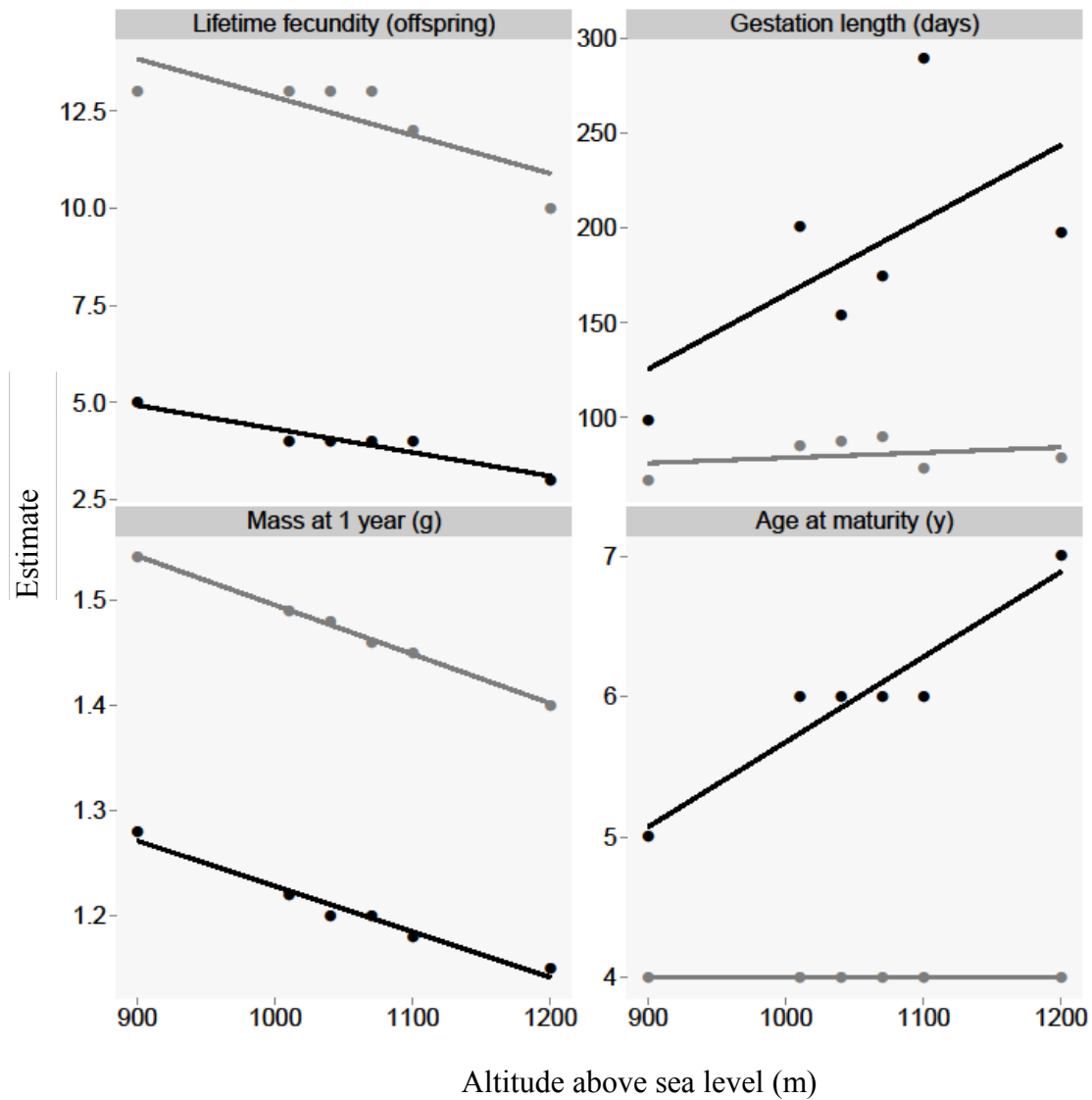


Figure 6: Clinal variation in total life time fecundity, gestation length, mass at one year of age and age at maturity under historical climates centred on the year 2000 (black) and under projected climate change centred on the year 2080 (grey).

#### 4. Discussion

Modelling techniques to identify the mechanisms and constraints underlying geographic variation in life history and activity patterns are in their infancy (but see Kearney & Porter 2004; Huey *et al.* 2012; Kearney 2013; Levy *et al.* 2015; Levy *et al.* 2016). Lizards are especially useful within the modelling context because their thermal biology is well studied and their biological processes are closely linked with environmental temperature (Huey *et al.* 2009; Gunderson & Leal 2016). We parameterised a mechanistic model of a low altitude population of a widespread lowland lizard species, *Niveoscincus ocellatus*, using NicheMapR. This model successfully predicted a wide range of life history traits, activity and thermodynamic processes. When transplanted to a high altitude site the model successfully predicted a number of life history traits and processes specific to high altitude populations of *N. ocellatus*, which indicates climate plays a central role in shaping the life history of this species. Using population-specific data for the thermophysiological and reproductive components of the model improved predictions of activity period and the timing of parturition for *N. ocellatus* at high altitude. However, climate, together with population-specific thermal traits and reproductive phenology, did not fully explain observed life history patterns. This suggests a level of adaptation at high altitude sites to compensate for the effect of low temperatures on life history. Furthermore, we found that a simple change in the timing of reproductive events at the high altitude site could induce a shift from annual to biennial reproduction, representative of the highland species, *N. microlepidotus*. Following this change, model predictions closely resembled the reproductive biology of highland *N. microlepidotus* under alpine climatic conditions. Taken together, our data suggest that a number of the differences in life history between and within *Niveoscincus* species result from climatic effects offset by relatively minor adjustments to the mechanisms underpinning these traits. Warmer temperatures projected under climate change were forecast to have a number of fitness benefits for both *N. ocellatus* and *N. microlepidotus*. In particular, both *N. ocellatus* and *N. microlepidotus* were predicted to successfully reproduce at a higher rate. Furthermore, *N. ocellatus* were forecast to reproduce successfully at higher altitudes (up to 1200 m a. s. l.) and thereby expand their range under climate change. As a result of the forecast range expansion of *N. ocellatus*, *N. microlepidotus* is likely to experience increased competition and thereby density dependent mortality (Chapter 4). Therefore, a contraction of the lower range margin of *N. microlepidotus* is likely under climate change (Chapter 4).

The dynamic energy budget (DEB) model accurately captured empirical relationships between phenotypic and physiological traits of a low altitude population of *N. ocellatus*. When used in conjunction with the microclimate model, the DEB model realistically predicted the growth, development, reproductive output and seasonal activity patterns of *N. ocellatus* at a low altitude site. Several species-specific traits were not represented in our model, yet did not appear to greatly affect the model predictions. For example, the offspring lacked a placenta to simulate placental transfer, which does occur in *N. ocellatus* (Thompson *et al.* 2001; Jones & Swain 2006). The model outputs suggest that based on their metabolic processes, and in the absence of predation and disease, these lizards can live longer than has thus far been observed in the wild. The model also estimated an overly rapid rate of development based on the constant temperature equivalent we estimated (Wapstra 2000). This resulted in shorter gestation lengths than is observed in the wild and could be corrected in future versions through further iterative sensitivity analyses to establish a CTE which produces gestation lengths more closely representative of natural populations. However, the overall close match between model predictions and observations demonstrates that the integration of DEB models and biophysical ecology provides a powerful platform for hypothesis testing. Unlike the majority of readily available species distribution modelling packages, the mechanistic basis of NicheMapR affords it a wide range of applications in inferring roles of evolutionary and ecological processes in novel environments.

When transplanted to a high altitude site, the DEB model of *N. ocellatus* accurately predicted the reduced growth, fecundity and activity, and delayed reproductive maturity and parturition date observed for lizards at that site. These changes represent plastic phenotypic responses to the local climate in the same direction as field based observations for this species. However, the effect of temperature on these life history traits was overestimated by the model. Specifically, the model under-predicted growth rate, fecundity and activity, and over-predicted time to reproductive maturity. Given that the model reliably captured many of the life history processes of the low altitude population, differences between predictions and observations at the high altitude site indicate that adjustments to underlying DEB parameters are required to better represent high altitude *N. ocellatus*. Temperature effects on life history in the model and in reality are underlain by the thermal response curve, which determines the effectiveness of metabolic processes at different temperatures. Overestimation of temperature effects on life history traits suggests that the thermal response curve is downregulated in high altitude populations of *N. ocellatus*. This would enable more effective metabolic activity at

lower temperatures (i.e. metabolic cold adaptation). This hypothesis is supported by evidence of thermal adaptation to low temperatures by high altitude populations of *N. ocellatus*, particularly to reduce gestation length, which does not vary with altitude (Uller *et al.* 2011; Cadby, Jones & Wapstra 2014; Yuni, Jones & Wapstra 2015). Physiological adaptations to increase metabolic efficiency at low temperatures are common in cold living species and populations (Addo-Bediako, Chown & Gaston 2002; McConnachie, Alexander & Whiting 2009; Bonino *et al.* 2011). Our hypothesis is also in line with a recent study by Yuni, Jones and Wapstra (2015) who found evidence that *N. ocellatus* at a high altitude site are able to upregulate metabolism to compensate for low temperatures. This may represent an adaptive response to low temperatures in the alpine environment, and is likely to be a crucial factor underlying the wide altitudinal and distributional range of *N. ocellatus*. Future modelling work could adjust the lower bounds of the thermal response curve to allow increased metabolic activity at lower temperatures, and test the importance of this parameter to mediating reproductive output and growth at high altitude sites. While there is a reasonable amount of research on altitude-related variation in the metabolic mechanisms underpinning life history processes in plants, insects and birds, little study has been made of reptiles (but see Walker, Stuart-Fox & Kearney 2015). Such taxonomic biases reduce our understanding of how certain taxa may respond to changing thermal environments (Walsh *et al.* 2013).

An advantage of mechanistic species distribution models is the ability to manipulate traits individually (Kearney & Porter 2004; Mitchell *et al.* 2012; Huang *et al.* 2013; Kearney *et al.* 2014). When the thermal traits were adjusted to represent observations from a high altitude population of *N. ocellatus* (Yuni, Jones & Wapstra Submitted) the model predictions converged with observations of activity periods at the high altitude site, although hibernation was delayed. However, changes to thermal preferences (and thereby activity period and subsequent body temperatures) were not predicted to alter development rate or fecundity. This may be a product of the idealised model scenario, which specified abundant food, lack of predation threat and no impact of parturition date on offspring fitness. Future studies could test various states of food limitation and predation to gain a more realistic estimate of the importance of activity for mediating the life history of these species at cold high altitude sites. By changing the timing of the initiation and termination of reproduction the model was able to accurately predict birthdates of the high altitude population of *N. ocellatus*. This suggests that unlike life history, differences in reproductive timing between low and high altitude populations of *N. ocellatus* may be the result of relatively simple evolutionary changes in

response to climate, as opposed to more complex metabolic changes (as the DEB model was based on low altitude *N. ocellatus*).

The timing and process of gestation of highland *Niveoscincus* species occurs due to strong selection in high altitude sites to buffer the detrimental effects of low temperatures on offspring fitness (Atkins, Swain & Jones 2007; Cadby *et al.* 2010; Uller *et al.* 2011; Cadby, Jones & Wapstra 2014). Evidence from phylogeographic studies suggests that widespread lowland and highland *Niveoscincus* species have undergone long periods of divergence as a result of geographic isolation driven by separation within glacial refugia and mountaintop habitats (Hutchinson & Schwaner 1991; Melville & Swain 1998; Melville & Swain 2000b; Cliff, Wapstra & Burridge 2015). Yet despite the underlying metabolic and heat/activity budgets being parameterised to represent low altitude *N. ocellatus*, we found small changes to the dates on which reproduction was initiated and terminated were able to produce biennial reproduction approximating the process observed in *N. microlepidotus*. This suggests that the ancestral colonisation of high altitude sites may have been accompanied by relatively simple changes to the timing of reproduction to maintain the biennial reproductive rate under fluctuating conditions to avoid wasted reproductive investment (Schwarzkopf, Caley & Kearney 2015). This change in reproductive frequency is likely to be underpinned by concomitant changes to hormonal pathways, mating systems and uterine structure to support prolonged gestation (Girling, Jones & Swain 2002a; Girling, Jones & Swain 2002b; Atkins, Jones & Guillelte Jr 2006; Atkins, Swain & Jones 2006). In our model, changes to the timing of reproduction resulted in increased litter sizes and gestation lengths, which more closely reflected observations of *N. microlepidotus*. However, unlike field based observations, gestation was not predicted to be complete prior to hibernation. Offspring born late in the season have severely reduced survival (Olsson & Shine 1999), but in the simulation for *N. ocellatus* the cut-off date for reproduction was relaxed to enable *N. microlepidotus* to breed more frequently (established via sensitivity analyses). In reality severe restrictions on the timing of parturition are likely to be a key selective force driving the overwintering of fully developed offspring *in utero* (Olsson & Shine 1998; Schwarzkopf, Caley & Kearney 2015). Completing embryonic development prior to winter allows the parturition of offspring within days of emergence, increasing the time available for offspring to put on mass prior to winter (Atkins, Swain & Jones 2007).

A process-based approach has benefits in both explaining the adaptive significance of life history differences between species, and realistically forecasting the potential for these differences to alter the responses of species to climate change. We explored the potential impact of a realistic (3°C) scenario of global warming on the life history, activity and distribution of *N. ocellatus* and *N. microlepidotus* by the year 2080. When subject to climate warming, all of the populations experienced a number of beneficial effects. These effects included more rapid growth, reduced time to maturity, earlier birthdates (or a greater spread in the case of *N. microlepidotus*), increased fecundity and extended activity periods. These changes stem from enhanced metabolic activity under warmer temperatures, which is congruent with recent experimental evidence (Seebacher, White & Franklin 2015). Specifically, physiological rates of ectothermic species have increased by up to 20% in response to climatic changes over the last 20 years, and are expected to continue to increase under climate change (Seebacher, White & Franklin 2015). Our findings are also in line with recent experimental evidence, which suggests that warming temperatures promote a change in the life history strategy of ectothermic species to a live fast, die young tactic (Bestion *et al.* 2015; Martinez *et al.* 2016), though only low altitude *N. ocellatus* were predicted to experience reduced longevity under climate change. As in our study, exposure of the common lizard, *Zootoca vivipara*, to warming conditions over a two year period promoted more rapid growth, earlier onset of reproduction and decreased longevity (also see Chamaillé-Jammes *et al.* 2006; Bestion *et al.* 2015). Earlier death in this experiment was suggested to result from unmet increases in energetic demands due to warmer temperatures (Bestion *et al.* 2015). However, we suggest that decreased longevity predicted for one of the populations we examined was underpinned by accelerated metabolic senescence due to warm temperatures, as food was not limited in our model.

The majority of the life history traits that we examined were highly plastic in response to temperature. This suggests that both *N. ocellatus* and *N. microlepidotus* are well placed to experience fitness gains under climate change, as warming conditions increase the activity periods and physiological rates of these cool temperate ectotherms. This is in line with recent studies, which predict that while tropical ectotherms are at high risk from the effects of global warming, temperate ectotherms will either resist or benefit from rising temperatures (Deutsch *et al.* 2008; Sunday *et al.* 2014; Brusch IV, Taylor & Whitfield 2016). Using an altitudinal transect, we found that the effects of low temperatures at higher altitude sites on gestation and offspring fitness is likely to have historically limited *N. ocellatus* to lower altitude sites.

Temperature increases under a moderate scenario of climate change are predicted to enable *N. ocellatus* to successfully reproduce across the entire available altitudinal range (~1200 m a. s. l.). The model suggests that warming conditions will more than double the fecundity, and significantly reduce gestation length and age at maturity across the transect. Changes in these life history traits were particularly pronounced at higher altitude sites. As a result, it appears that fitness gains under climate change will translate into an increase in the upper range margin of *N. ocellatus*. Increased abundance due to greater fecundity is also likely, contingent on the effect of other density dependent processes (such as competition for basking sites). Together these changes suggest that *N. ocellatus* will be able to colonise higher altitude sites under climate change. An important implication of this finding is the potential for competition from upward encroaching *N. ocellatus* to detrimentally affect the range size and abundance of *N. microlepidotus* under climate change. The niches of these species appear to overlap, with increased competition for basking sites at high altitudes likely to increase the density dependent mortality experience by both species (Chapter 4, Melville & Swain 1999a). This trend is increasingly evident in alpine habitats worldwide as lowland species invade increasingly higher altitude areas and are able to outcompete resident cold adapted species in newly benign environments (Huey *et al.* 2009; Jankowski, Robinson & Levey 2010; Gallagher *et al.* 2015). Ultimately the effect of climate change on species' persistence and distribution will depend on the underlying processes which effect change, yet there have been few mechanistic analyses of the potential effects of climate change, particularly involving reptile taxa (but see Kearney & Porter 2004; Levy *et al.* 2015; Levy *et al.* 2016). The large degree of plasticity in the life history, activity and reproductive phenology of these species is likely to result in fitness benefits for both of these temperate lizard species under future climates.

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**Supplementary Tables**

Table S1: Dynamic energy budget parameters.

parameter	value	units	source
$z$ , zoom factor (relative volumetric length)	1.815	-	estimated
$\delta_M$ , shape correction factor	0.2429	-	default
$\nu$ , energy conductance	0.04184	cm d <sup>-1</sup>	estimated
$\kappa$ , allocation fraction to soma	0.6433	-	estimated
$[p_M]$ , somatic maintenance	31.82	J cm <sup>-3</sup> d <sup>-1</sup>	estimated
$[E_G]$ , cost of structure	7793	J cm <sup>-3</sup>	estimated
$E_H^b$ , maturity at birth	2068	J	estimated
$E_H^p$ , maturity at puberty	$1.05 \times 10^4$	J	estimated
$\kappa_X$ , digestion efficiency	0.8	-	(Shine 1971)
$\kappa_R$ , reproduction efficiency	0.95	-	default
$[E_s^m]$ , maximum specific stomach energy	350	J cm <sup>-3</sup>	(Kearney 2012)
$E_0$ , energy content of ‘egg’	9220	J	estimated
$\{\dot{p}_{Xm}\}$ , maximum specific food intake	12420	J cm <sup>-2</sup>	assumed
$X_K$ , half saturation constant	10	J ha <sup>-1</sup>	assumed
$d_V$ , density of structure	0.3	g cm <sup>-3</sup>	assumed
$W_V$ , molecular weight of structure	23.9	g C-mol <sup>-1</sup>	default
$\mu_X$ , chemical potential of food	525000	J C-mol <sup>-1</sup>	default
$\mu_E$ , chemical potential of reserve	585000	J C-mol <sup>-1</sup>	default
$\mu_V$ , chemical potential of structure	500000	J C-mol <sup>-1</sup>	default
$\mu_P$ , chemical potential of faeces	480000	J C-mol <sup>-1</sup>	default
$\kappa_{XP}$ , fraction of food energy into faeces	0.1	-	default
$T_L$ , lower bound for $T_A$	283.1	K	Chapter 2
$T_H$ , upper bound for $T_A$	310.1	K	Chapter 2
$T_A$ , value of $T_A$	10,190	K	(Yuni, Jones & Wapstra Submitted)

$T_{AL}$ , value of $T_A$ below lower bound	50,000	K	(Kearney 2012)
$T_{AH}$ , value of $T_A$ above upper bound	90,000	K	(Kearney 2012)

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Table S2. The physical properties of the lizard used in the heat/activity budget model.  $W_w$  is wet weight in grams.

Parameter	units	value	source
$\epsilon_{\text{body}}$ , skin longwave infrared emissivity	-	1.0	default
$\alpha_{\text{body}}$ , skin solar absorptivity	-	0.857	(Spellerberg 1972)
$\rho_{\text{body}}$ , flesh density	kg m <sup>3</sup>	1000	default
$k_{\text{body}}$ , flesh thermal conductivity	W m <sup>-1</sup> °C <sup>-1</sup>	0.5	default
$C_{\text{body}}$ , flesh specific heat capacity	J kg <sup>-1</sup> °K <sup>-1</sup>	4185	default
$F_{\text{body,sky}}$ , configuration factor body to sky	-	0.4	(Porter <i>et al.</i> 1973)
$F_{\text{body,sub}}$ , configuration factor body to substrate	-	0.4	(Porter <i>et al.</i> 1973)
$A$ , lizard surface area	cm <sup>2</sup>	$10.4713W_w^{0.688}$	(Porter <i>et al.</i> 1973)
$A_{\text{sil}}$ , silhouette area normal to the sun	cm <sup>2</sup>	$3.798W_w^{0.683}$	(Porter <i>et al.</i> 1973)
$F_{\text{sub}}$ , fraction of surface area contacting the substrate	-	0.1	assumed
$F_{\text{wet}}$ , fraction of surface area that is wet	-	0.01	assumed

## Supplementary Figures

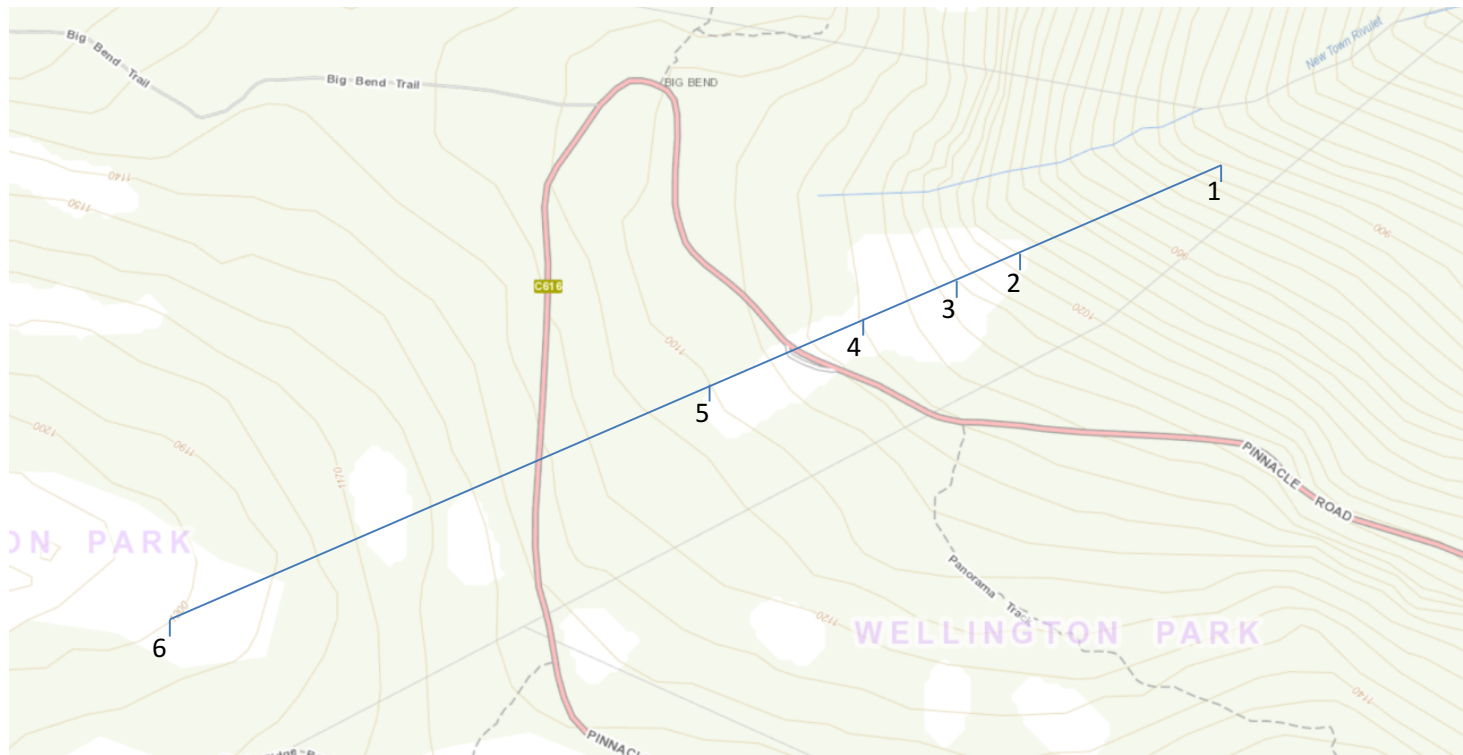


Figure S1: Sites used for the altitudinal transect of a high altitude population of *Niveoscincus ocellatus* and for *N. microlepidotus* subject to historical (2000) and projected climates (2080): 1) 900 m above sea level ( $-42.88572^{\circ}$ ,  $147.22792^{\circ}$ ), 2) 1010 m a. s. l. ( $-42.88642^{\circ}$ ,  $147.22585^{\circ}$ ), 3) 1040 m a. s. l. ( $-42.88663^{\circ}$ ,  $147.22518^{\circ}$ ), 4) 1070 m a. s. l. ( $-42.88693^{\circ}$ ,  $147.22413^{\circ}$ ), 5) 1100 m a. s. l. ( $-42.88746^{\circ}$ ,  $147.22259^{\circ}$ ) and 6) 1200 m a. s. l. ( $-42.88925^{\circ}$ ,  $147.21695^{\circ}$ ).

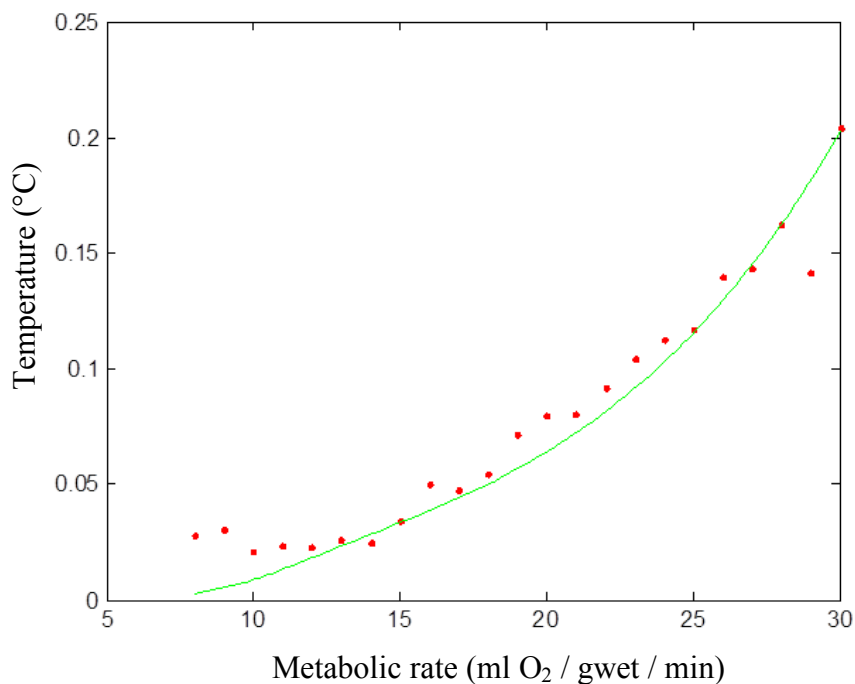


Figure 2a: Observed (red dots) and captured (green line) metabolic rate (ml O<sub>2</sub> / gwet / min) versus temperature (°C) for *Niveoscincus ocellatus* at a low altitude site used to parameterise the dynamic energy budget model.

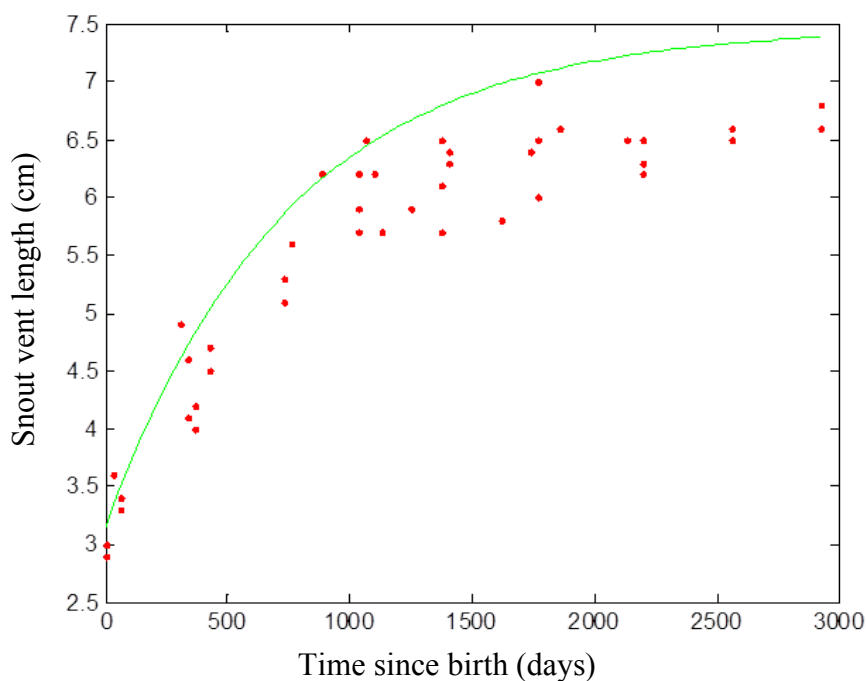


Figure 2b: Observed (red dots) and captured (green line) time since birth (days) versus snout to vent length (cm) for *Niveoscincus ocellatus* at a low altitude site used to parameterise the dynamic energy budget model.

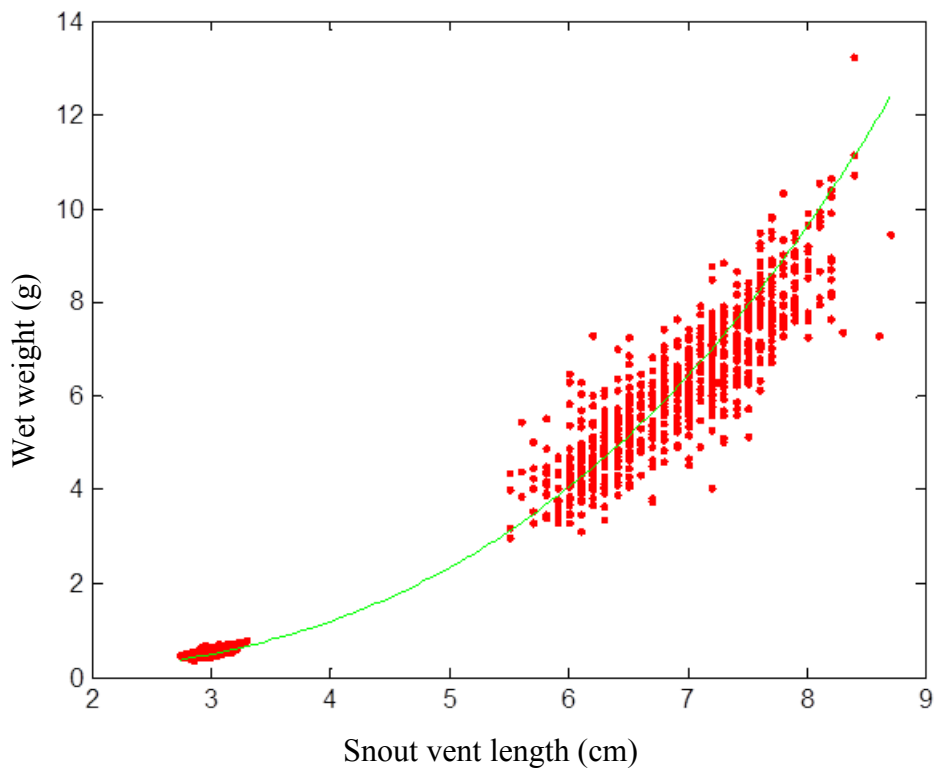


Figure 2c: Observed (red dots) and captured (green line) snout vent length (cm) versus wet weight (g) for *Niveoscincus ocellatus* at a low altitude site used to parameterise the dynamic energy budget model.

# CHAPTER SIX





## General Discussion

*“Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is this problem compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!”*

– Charles Darwin (1859).

As Darwin acknowledged, it is fundamentally difficult to predict the ecological and evolutionary dynamics of natural systems. Yet as the earth continues to undergo rapid and unprecedented climatic change (Schneider 2001; Moritz & Agudo 2013), predicting ecological and evolutionary responses to this change has become a global priority (Botkin *et al.* 2007; Williams *et al.* 2008; Sunday *et al.* 2014). Despite this, significant gaps remain in our understanding of the factors governing the responses of organisms to climate change (c, Figure 1; Lambers 2015; Urban 2015). The challenge to ecologists and physiologists is to identify species’ sensitivities to climate change and the potential for adaptive responses (a and b, Figure 1; Williams *et al.* 2008; Dawson *et al.* 2011; Bellard *et al.* 2012; Moritz *et al.* 2012). This challenge was well articulated by Hughes (2000) who outlined four categories of predictions of climate change effects on species: (1) effects on physiology, (2) effects on distributions, (3) effects on phenology, and potential for (4) *in situ* adaptation (Figure 1). Hughes (2000) also noted the importance of secondary effects of these processes on species’ interactions, distributions and persistence. Models of species’ distributions and persistence under projected climate change must incorporate the potential for phenotypic traits, phenotypic plasticity and inter-specific interactions to mediate climate change effects to produce reliable, realistic projections.

My thesis took up the first three aspects of Hughes (2000) challenge using a two-tiered approach: (1) by determining the potential for physiology (Chapter 2), behaviour (Chapter 3), inter-specific interactions (Chapter 4), and phenology (Chapter 5), to alter the responses of species to the thermal environment, and (2) by exploring the potential for these responses to decrease or increase the effects of climate change on the activity, life history, distribution and persistence of several reptile species (Chapters 2 – 5, Figure 1). An examination of adaptive evolutionary responses to climate change (i.e. Hughes 2000, the fourth potential response by

species to climate change) was outside the scope of this thesis although underpinning much of the work was an understanding of local adaptation by populations and species to the thermal environment. I took a comparative approach to explore the potential for historical exposure to different climates to shape the responses of species to projected climate change. To achieve this, I used four members of a temperate Tasmanian reptile genus, *Niveoscincus*. *Niveoscincus* includes several species with widespread lowland distributions (from sea level to ~1150 m) and several species with restricted highland distributions (~1100 m above sea level). The *Niveoscincus* genus provided two major advantages for the purpose of this thesis. Firstly, while low altitude populations are exposed to warm and predictable climatic conditions, high altitude populations inhabit cooler sites subject to highly variable temperatures (Pen *et al.* 2010). Exposure to different climatic regimes has resulted in highly variable life-history and reproductive traits between species and populations, with clinal trends evident in growth rate, fecundity and reproductive frequency (Wapstra *et al.* 1999; Melville & Swain 2000a; Wapstra & Swain 2001a; Cadby, Jones & Wapstra 2014). Secondly, the evolutionary history of this genus is well documented, with molecular evidence indicating that present day species arose from a widespread lowland ancestor which colonised high altitude areas after the last glacial maximum (Melville & Swain 2000b; Cliff, Wapstra & Burridge 2015). The evolutionary and ecological context of the *Niveoscincus* genus allowed me to examine both the historical and contemporary factors which may influence population and species level responses to climate change. My thesis was focused on elucidating information central to producing realistic predictions of the vulnerability of widespread lowland and highland *Niveoscincus* species to climate change effects (Figure 1). Here, I synthesise the main outcomes of my research and discuss the specific mechanisms by which climate change may impact the activity, life history, distribution and persistence of *Niveoscincus* species, and reptiles in general. I then suggest approaches which have the potential to advance the field of species distribution modelling and further our understanding of the vulnerability of species to climate change.

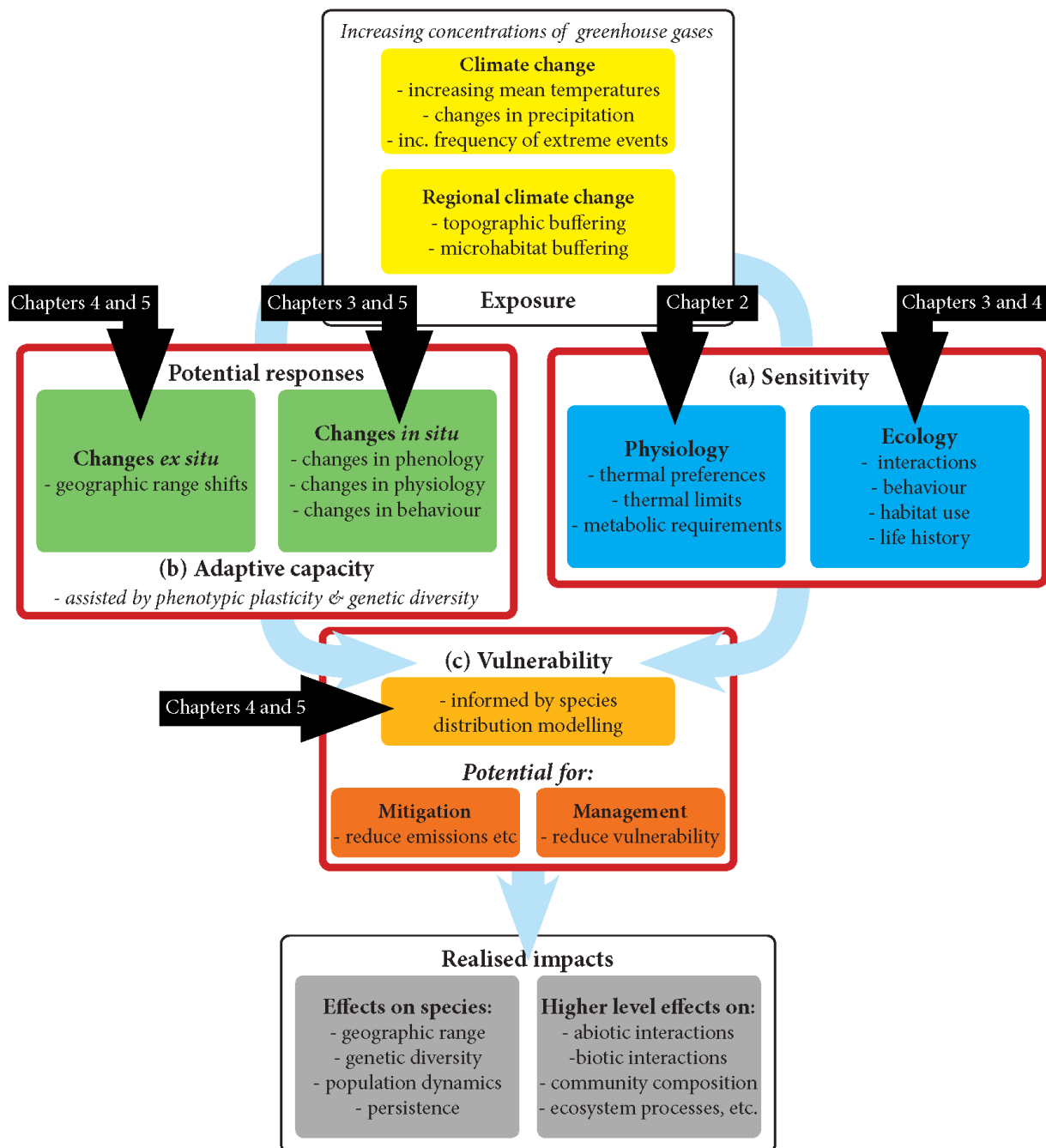


Figure 1: Revisited conceptual diagram from Chapter 1. This thesis adds to the understanding of the processes outlined in the red boxes. Specifically, I examined widespread lowland and highland *Niveoscincus* species (a) sensitivity and (b) adaptive capacity in response to climate change. I used this data to parameterise species distribution models, which have different capacities to assess (c) species' vulnerabilities to climate change. *Niveoscincus* was an excellent candidate genus for this work. The inclusion of widespread lowland and highland members enabled a comparative approach from which a broader discussion of the potential impacts of climate change on reptiles can develop.

### *1.1 The state of research into the effects of climate change on reptiles*

Reptiles are integral components of natural systems and are often bio-indicators of environmental health (Read 1998; Gibbons *et al.* 2000; Varela & Bucher 2002; Olesen & Valido 2003; Godinez-Alvarez 2004; Böhm *et al.* 2013). However, “taxonomic chauvinism” continues to pervade the research and conservation arena. Compared to other terrestrial vertebrates, reptiles receive the least investigation and representation in both the scientific literature and in terms of conservation effort (Bonnet, Shine & Lourdais 2002; Walsh *et al.* 2013; Cronin *et al.* 2014; Clemann 2015). Taxonomic biases in research and conservation are likely to culminate in lost opportunities to achieve the optimal conservation outcomes, because some threatened species receive little attention despite their potential for recovery (Walsh *et al.* 2013). The relative neglect of reptiles in the research and conservation arena is particularly concerning in the context of climate change, because reptiles are especially vulnerable to the effects of changing environmental temperatures (Huey & Slatkin 1976; Huey *et al.* 2009; Sinervo *et al.* 2010). Effects of warming temperatures on reptiles are diverse, and include increased rates of metabolism and growth, decreased time to maturity, altered reproductive output, activity period, and offspring fitness, skewed offspring sex ratios and reduced longevity (Chapter 5, Frazer, Greene & Gibbons 1993; Janzen 1994; Mitchell *et al.* 2008; Wapstra *et al.* 2009; Bestion *et al.* 2015). In light of these effects, it is not surprising that many reptile species have become, or are predicted to become, extinct due to climate change (Thomas *et al.* 2004; Araújo, Thuiller & Pearson 2006; Whitfield *et al.* 2007; Bickford *et al.* 2010; Reading *et al.* 2010; Sinervo *et al.* 2010; Böhm *et al.* 2013; Bestion *et al.* 2015). Furthermore, a great many more reptile species are classified as Data Deficient and are yet to be assessed (IUCN 2011; Meiri & Chapple 2016). To address the information gap, research is needed which gathers data necessary for realistic predictions of climate change effects on reptile species (Chapters 4 and 5, Böhm *et al.* 2016).

### *1.2 Potential for physiology to mitigate or enhance climate change effects*

Data on basal physiological traits are increasingly useful for comparative studies into climate change effects. This is made possible because of the development of techniques which utilise this data to predict potential effects of climate change on species’ activity, life history, distribution and persistence (Chapter 5, Thomas *et al.* 2004; Sinervo *et al.* 2010; Huey *et al.* 2012; Hoffmann, Chown & Clusella-Trullas 2013; Kearney *et al.* 2014; Sunday *et al.* 2014; Walker, Stuart-Fox & Kearney 2015). In the second chapter of my thesis, I examined

variation in critical thermal minimum and maximum limits and evaporative water loss rates among a widespread lowland species, *N. ocellatus*, and two range restricted highland species, *N. microlepidotus* and *N. greeni*, in a laboratory setting. Each of these thermal traits are likely to play a major role in determining the effects of warming temperatures on organismal fitness (García-Muñoz & Carretero 2013; Guillon *et al.* 2013). I found that the widespread lowland species had significantly higher critical thermal minimum and maximum limits and a significantly lower evaporative water loss rate than either highland species (Chapter 2). Inter-specific differences among these species in physiological traits appear to be environmentally driven as in other taxa; the highland species inhabit sites with lower minimum temperatures and higher relative humidity than the widespread lowland species (Chapter 2, Sunday, Bates & Dulvy 2011). Future studies could take advantage of sympatric populations of widespread lowland and highland *Niveoscincus* species to explore and standardise the effect of elevation on the physiological traits of these species. Variation in the thermal tolerances of these closely related species highlight the importance of using species-specific traits for predicting the biological effects of rising temperatures and increasing demands on water balance occurring under climate change (Bindoff 2010; Field *et al.* 2014a). A growing number of studies are using these traits in isolation (e.g. Chapter 2, below) or alongside a host of other factors to determine their potential to dictate species' activity periods, habitat suitability, persistence and distribution under climate change (as in Chapter 5 and in Buckley 2008; Kolbe, Kearney & Shine 2010).

I determined the potential for variation in thermal tolerance to drive differences in activity time available to widespread lowland and highland *Niveoscincus* species under climate change. To achieve this, I tested the frequency with which the thermal limits of these species were exceeded by historical and projected air temperatures from 1960 – 2100. Both widespread lowland and highland species were predicted to experience a decline in the frequency of air temperatures below their  $CT_{min}$ . The highland species were not predicted to experience air temperatures in excess of their  $CT_{max}$  at their respective study sites throughout the 21<sup>st</sup> century. However, air temperatures in excess of the widespread lowland species'  $CT_{max}$  were predicted to occur on 1 or 2 days from 2068 – 2096. In the absence of behavioural responses (e.g. seeking thermal refuges, Chapter 3) high temperatures may impact the persistence of the widespread lowland species at low altitude sites, because rare extreme temperatures can be more important to extinction risk than average temperatures (Parmesan,

Root & Willig 2000; Hoffmann 2010). However, given these species demonstrate behavioural plasticity in response to changes in the thermal environment (Chapter 3, below), and given the limited occurrence of lethally high temperatures predicted across this period, it is unlikely the occupation of low altitude sites by the widespread lowland species will be reduced.

I estimated the change in available activity time according to minimum and maximum temperatures selected for activity from 1960 – 2100. All three species were predicted to experience an increase in the number of days on which air temperatures exceed temperatures selected for activity. However, this change was offset by an increase in the number of days on which air temperatures were above the minimum temperature selected for activity across this period. Consequently, the overall effect of projected climate change on these species activity is likely to be a net gain in available activity period (Chapters 2 and 5). The realised fitness consequences of increasing available activity periods will depend on the interaction between climate change and other related elements. In particular, the potential for lizards to exhibit behavioural plasticity and take advantage of an increase in available activity period (Chapter 3) and climate-mediated changes in competition among widespread lowland and highland *Niveoscincus* species (Chapter 4).

### *1.3 Potential for behavioural and body temperature responses to the thermal environment*

An increasing number of researchers are highlighting the potential for behavioural plasticity to mediate the effects of climate on species physiology (Huey & Tewksbury 2009; Kearney, Shine & Porter 2009; Sunday *et al.* 2014). To avoid overheating under higher temperatures or exposure to lethally cold temperatures most species are dependent on behavioural responses, such as retreating to thermal refuges. Yet behavioural plasticity is an often overlooked aspect determining the vulnerability of species to climate change (Kearney, Shine & Porter 2009; Huey *et al.* 2012). In particular, the extent to which individuals vary their behaviour in response to changing temperature is poorly understood, and we know little about the extent to which behavioural plasticity differs both within and among species (Janzen & Morjan 2001; Doody *et al.* 2006; Warner & Shine 2008; Angilletta Jr, Sears & Pringle 2009; Uller *et al.* 2011; Cadby, Jones & Wapstra 2014; Buckley, Ehrenberger & Angilletta 2015). I examined inter- and intra-specific variation in behavioural and selected body temperature responses to basking opportunity between low and high altitude populations of two widespread lowland species, *N. ocellatus* and *N. metallicus*, and two highland species, *N. microlepidotus* and *N.*

*greeni* (Chapter 3). I found that individuals from populations historically exposed to warm and less variable environments basked less than individuals from populations inhabiting sites with low and highly variable temperatures. Furthermore, all of the populations examined displayed plastic behavioural responses to the thermal treatments, reducing time spent basking in response to high basking opportunity. Thus differences in basking time among species and populations were in the same direction as short term responses to the basking treatments. This suggests that plastic responses to current thermal environments may drive adaptive genetic divergence in basking behaviour among populations. Behavioural responses to the thermal environments translated into different effects on selected body temperature between species. While the widespread lowland species reduced their selected body temperatures when exposed to prolonged basking opportunity, the highland species maintained consistently high body temperatures regardless of basking opportunity. High altitude populations and species appear to have responded to selection to maximise basking time and selected body temperatures to reduce the physiological effect of low temperatures within harsh highland conditions (Uller *et al.* 2011; Cadby, Jones & Wapstra 2014). The *Niveoscincus* genus illustrates the potential for closely related species and even populations within the same species to possess divergent phenotypic responses to changes in the thermal environment. Together, these results indicate that *Niveoscincus* species and populations have the potential to buffer short-term changes in the environment with plastic behavioural responses (Kearney, Shine & Porter 2009; Hof *et al.* 2011). The next step for predicting the long term potential for these species to cope with climate change is to incorporate this behavioural plasticity and effects on physiology into models of climate change impacts.

#### *1.4 Potential for climate change to alter competition between altitudinally interacting species*

The net outcome of behavioural buffering of warming temperatures and increases in available activity periods is that both widespread lowland and highland *Niveoscincus* may benefit from predicted climate change. However, competitive interactions among widespread lowland and highland *Niveoscincus* species may alter the extent to which the benefits of warming temperatures have an effect at the population and species level (e.g. changes in abundance and distribution). Widespread lowland and highland species have overlapping habitat requirements and compete for basking sites within narrow 50 m altitudinal zones (Melville & Swain 1999b; Melville & Schulte 2001). At present, the upper range margin of annually reproducing widespread lowland *Niveoscincus* appears to be limited by the effect of low

thermal opportunity on birthdate, and subsequent birthdate effects on offspring fitness, where late-born offspring have reduced survival (Wapstra *et al.* 1999; Atkins, Jones & Guillette Jr 2006; Pen *et al.* 2010; Wapstra *et al.* 2010; Uller *et al.* 2011). In contrast, the lower range margin of biennially reproducing highland *Niveoscincus* species appears to be limited by competition from neighbouring widespread lowland *Niveoscincus*, resulting in a narrow zone of overlap. Greater activity periods could enable earlier parturition by widespread lowland *Niveoscincus* species, which would provide neonates with more time for food acquisition and growth prior to winter, resulting in improved chances of survival through their first hibernation (Atkins, Swain & Jones 2006; Ozgul *et al.* 2010). As highland *Niveoscincus* have effectively half the reproductive output of their lowland conspecifics, these species may be outnumbered and outcompeted by widespread lowland *Niveoscincus* under projected climate change.

Inter-specific interactions are increasingly recognised as playing a central role in mediating species climate change response (Jankowski, Robinson & Levey 2010; Godsoe, Murray & Plank 2015), yet are generally omitted from species distribution models (Guisan & Thuiller 2005; Wisz *et al.* 2013; Godsoe, Murray & Plank 2015). I took a spatially-explicit individual-based modelling (IBM) approach to examine the effects of competitive interactions and temperature-dependent processes on the abundance, persistence and distribution of interacting populations of a widespread lowland species, *N. ocellatus*, and an highland species, *N. microlepidotus*. I ran the model under historical and projected climate change and examined short (2010 – 2100) and longer term (2100 – 2300) changes in population dynamics and demography (Chapter 4).

From 2010 – 2100 the IBM predicted that the beneficial effects of warming temperatures on widespread lowland offspring survival would facilitate an increase in the abundance and the upper range margin of this species. The upper range margin of this species was expected to increase at a rate of 1.0 – 1.7 m per decade during this period. Interspecific competition for basking sites intensified, increasing the density dependent mortality experienced by both widespread lowland and highland species as a result. As the highland species did not experience improved offspring fitness under warming temperatures, increased mortality drove a concomitant decline in the abundance of this species. The highland species lower range margin retracted at a rate of 2.1 – 3 m per decade from 2010 – 2100. From 2100 – 2300 the



rate of upward movement in the widespread lowland species upper range margin increased to 2.2 – 3.4 m per decade. The rate of retraction of the highland species lower range margin also increased to 3.1 – 3.4 m per decade. The increased rate of change in the range boundaries of these species occurred despite the climate being projected to reach a new steady state equilibrium post 2100.

The mismatch between the widespread lowland species newly available climate space and realised distribution was a result of density dependent demographic processes (e.g. mortality and dispersal) slowing the realised rate of change in the upper range margin of this species. Slow dispersal rates and high mortality, along with short activity periods in temperate regions, appear to limit the response of the distribution of small lizard species to climate change (Chapter 4, Araújo & Pearson 2005; Araújo, Thuiller & Pearson 2006). In contrast, other taxa such as plants and birds, show a greater ability to track changes in available climate niche (Araújo & Pearson 2005). My model illustrates the potential for the biological effects of climate change to continue to manifest long after the initial perturbation, as effects at the individual level take time to filter up to the population and species level.

### *1.5 A process-explicit approach to predict species responses to climate change*

To realistically predict the effects of projected climate change on the life history, distribution and persistence of species under projected climate change, ideally we should model the impact of projected climate change on a full range of species traits (e.g. activity, fecundity, and longevity) and life history processes (e.g. growth and gestation length). Projections should incorporate data on environmental biophysics together with the behaviour, physiology, operative body temperature and ecology of the organism (Huey & Slatkin 1976; Tracy & Christian 1986; Buckley 2008; Kearney, Shine & Porter 2009). Mechanistic species distribution modelling is an emerging approach able to incorporate such data to describe fundamental linkages between an organism and its environment into a spatially-explicit framework (Dormann *et al.* 2012; Kearney, Matzelle & Helmuth 2012). Mechanistic species distribution models (SDMs) can incorporate the potential for behavioural compensation for temperature increases (Chapter 3, Kearney, Shine & Porter 2009) alongside physiological constraints on these buffering traits (e.g. critical thermal limits and the energetic costs of staying in the shade, Chapter 2, Sinervo *et al.* 2010).

I pioneered the use of a newly released mechanistic SDM, NicheMapR (<https://github.com/mrke/NicheMapR>), to examine the processes underlying the activity, life history and distribution of a widespread lowland species, *N. ocellatus*, and a highland species, *N. microlepidotus* exposed to past and projected climates (Chapter 5). I first ran my model using historical climate data at a low and a high altitude site in Tasmania. This allowed me to interpret and explore the adaptations which have enabled species of this genus to colonise some of the coldest habitat inhabited by lizards in the world. The model predictions suggest that exposure to different local climatic regimes drive the observed differences in the activity and life history of populations and species inhabiting low and high altitude sites. Specifically, activity, litter size, reproductive frequency and growth were predicted to be reduced at high compared to low altitude sites, as is observed in high altitude populations of *N. ocellatus* and *N. microlepidotus* (Olsson & Shine 1998; Wapstra *et al.* 1999; Wapstra & Swain 2001a; Atkins *et al.* 2007). However, the model over-predicted the effect of climate on the life history traits of lizards at high altitudes, which suggests that high altitude populations buffer climate effects on fitness related traits, potentially via metabolic cold adaptation. My hypothesis is in line with a recent study, which found that high altitude populations of *N. ocellatus* increase metabolic efficiency under low temperatures (Yuni, Jones & Wapstra 2015). Future studies could perform sensitivity analyses to determine whether adjustment to the thermal response curve, to upregulate metabolic efficiency under low temperatures, can explain the ability of high altitude populations to reduce the effect of exposure to the cold alpine environment on life history.

To examine the potential effects of climate change on these species activity and life history, I reran the model of low and high altitude populations of the widespread lowland species and the highland species under a moderate, yet realistic scenario of climate change for 2080 (3°C temperature rise). The model predicted that warming temperatures would have a number of fitness benefits for both widespread lowland and highland *Niveoscincus* species. Specifically, the model predicted that both the widespread lowland and highland species would grow more quickly to a greater maximal size, reach maturity at an earlier age and exhibit increased reproductive frequency and output under higher temperatures. Shifts in phenology to earlier parturition were also projected, which are likely to enhance offspring fitness by increasing time to put on condition prior to hibernation (Atkins, Swain & Jones 2007). Only the low altitude population of the widespread species was projected to experience a fitness cost of

warming temperatures, with longevity predicted to decrease by one year. Broadly, my findings are in line with a switch to a “live fast, die young” life history strategy exhibited by *Zootoca vivipara* experimentally exposed to warming conditions (Chamaille-Jammes *et al.* 2006; Bestion *et al.* 2015). For *Z. vivipara* exposed to warmer temperatures, a shortened lifespan was attributed to unmet increases in energetic requirements. In contrast, the reduction in the lifespan of the widespread species found here was a result of the acceleration of metabolic senescence under higher temperatures. In the absence of mitigating factors (e.g. competition), shifts in life history under warmer temperatures would result in greater fitness for both widespread lowland and highland *Niveoscincus* species, increasing the abundance of these species under future climates.

To explore the potential for climate change to drive changes in distribution, I simulated the model of the high altitude population of the widespread lowland species across an altitudinal transect on Mount Wellington, Tasmania. When exposed to historical climates, the model predicted the widespread lowland species would be limited to altitudes up to ~1010 m above sea level. This was due to the detrimental effects of low temperature on gestation length, parturition date, and reproductive output. When the model was rerun under a severe (yet realistic, 3°C) scenario of climate change in 2080, warming temperatures were predicted to increase offspring viability and reproductive output. As a result, increasing temperatures were predicted to enable the widespread lowland species to inhabit the entire available altitudinal range (<1200 m a. s. l.) by 2080, depending on the ability of this species to keep pace with expanding available climatic range (Chapter 4). My thesis suggests that widespread lowland *Niveoscincus* species will adjust to a new climatic envelope and experience range expansion through invasion of increasingly high altitude areas under warming temperatures (Parmesan *et al.* 1999; Bonino *et al.* 2015). This has been found to be the case for several other reptile species, including fourteen *Liolaemus* lizard species in Patagonia (Bonino *et al.* 2015). The next step would be to rerun this model at hundreds of sites across Tasmania under climate change to forecast likely patterns and processes in life history and distribution at the whole landscape scale. NicheMapR provides a promising and accessible avenue for future studies into the biological effects of climate change.

### 1.6 The future for *Niveoscincus* species: climate change induced threats and opportunities

Overall, my work agrees with the general expectation that reptile species (i.e. highland *Niveoscincus*) are under considerable threat from changing environmental conditions (Araújo, Thuiller & Pearson 2006; Raxworthy *et al.* 2008b; Sinervo *et al.* 2010; Foufopoulos, Kilpatrick & Ives 2011). However, the majority of work on reptile taxa to date emphasizes that the threat from climate change derives from increasingly stressful physiological conditions and restricted activity periods under warming temperatures (Williams, Bolitho & Fox 2003; Raxworthy *et al.* 2008b; Huey *et al.* 2009; Sinervo *et al.* 2010; Kearney 2013). This is especially likely to be true for tropical reptile species, whose thermal preferences have become canalized under historical selection regimes (Deutsch *et al.* 2008; Tewksbury, Huey & Deutsch 2008; Sinervo *et al.* 2010; Huey *et al.* 2012). In contrast, exposure to fluctuating temperatures experienced under past climates appears to have positioned *Niveoscincus* species to tolerate (Chapter 2), and respond positively to (Chapters 3 – 5) changes in their thermal environment. My work emphasizes the potential benefits of warming temperatures in increasing the rate of physiological processes and extending activity periods for a group of temperate lizard species. These changes are predicted to result in improved fitness, including increased fecundity and reproductive frequency for both widespread lowland and highland lizard species (Chapters 2, 4 and 5). Fitness benefits have been found for a number of other temperate reptile species, highlighting the role of exposure to different historical climates in shaping effects of contemporary climate change (Chamaille-Jammes *et al.* 2006; Deutsch *et al.* 2008; Sunday *et al.* 2014; Brusch IV, Taylor & Whitfield 2016).

For highland *Niveoscincus* species, the threat from climate change derives from the downstream effects of climate change on, and responses of, neighbouring competitors (Seebacher, White & Franklin 2015). Over the long term, upward encroachment by the widespread lowland species is predicted to drive the highland species into a slow acting extinction vortex. My thesis underscores the importance of biotic interactions as a key determinant of the vulnerability of species to climate change. In our case study, we found that biotic interactions not only have the potential to enhance the effect of climate change, but changed the predicted effect of climate change from increased fitness to increased vulnerability. Despite receiving increasing recognition as a major determinant of species outcomes under climate change, the majority of studies which extrapolate species distributions under novel conditions omit biotic interactions (Urban, 2015; Aruajo and Luoto

2007). To ensure the biological realism and predictive accuracy of future predictions, new techniques need to be developed which incorporate biotic interactions within a broader mechanistic framework. I discuss a potential method to integrate competitive interactions with mechanistic processes into next-generation models below.

As interactions with other species renders an increasing number of species at risk of extinction, particularly along altitudinal gradients (Jankowski, Robinson & Levey 2010; Meier et al. 2011; Gifford & Kozak 2012; Greenwood & Jump 2014), the key question is no longer whether such changes will manifest, but how soon. Given that greenhouse gas emissions continue to follow the most extreme climate scenarios, my predictions (particularly of climate reaching a new equilibrium post 2100) err towards a conservative outlook. As a result, shifting distributions may occur more rapidly than predicted in my thesis. I recommend ongoing population monitoring and the development of improved modelling techniques to better understand the future of unique highland members of the *Niveoscincus* genus. Practical management techniques to preserve highland *Niveoscincus* need to receive consideration within the public forum. Candidate techniques include assisted colonisation, preservation of gene pools and captive management are on the agenda for discussion in Australia (e.g. Mitchell *et al.* 2012; Dade, Pauli & Mitchell 2014; Seddon et al. 2015), but a full discussion of possible strategies are outside the scope of this thesis. The next step is to prepare my data for use in the public sector to inform conservation management decisions and prioritise species for conservation management.

### *1.7 Synthesis of available approaches for predicting biological responses to climate change*

To effectively mitigate climate change impacts on natural systems, conservation action must be informed by reliable predictions of species vulnerabilities based on the relevant scientific data (Figure 1, Meineri *et al.* 2015). Despite rapid advances in the field of ecological modelling, forecasting the long-term effects of climate change on species' life history, distribution and persistence remains a challenge (Rocchini *et al.* 2011; Moudrý & Šímová 2012; Feeley 2015; Godsoe, Murray & Plank 2015; Qiao, Soberón & Peterson 2015; Zurell *et al.* 2016). The last fifteen years have seen an exponential increase in both the number and citation of papers on methodological aspects of SDMs (Cayuela *et al.* 2009; Barbosa & Schneck 2015). However, in recent years a series of published studies have highlighted the weaknesses, misuses and sources of uncertainty inherent in such models (Rocchini *et al.*

2011; Moudrý & Šímová 2012; Godsoe, Murray & Plank 2015). The majority of SDMs ignore the potential for plastic phenotypic responses and interspecific interactions to alter the effect of climate change on biodiversity (Pearson & Dawson 2003; Urban, Zarnetske & Skelly 2013; Mason *et al.* 2014; Godsoe, Murray & Plank 2015) or rely on broad-scale patterns in niche conservatism (Tewksbury, Huey & Deutsch 2008; Huey *et al.* 2009; Buckley & Kingsolver 2012). As I found, these omissions and assumptions are likely to result in erroneous predictions of climate change effects on species' persistence and distribution (Thuiller *et al.* 2008; Meier *et al.* 2010; Meineri, Skarpaas & Vandvik 2012; Giannini *et al.* 2013). Here, I briefly review existing computer-based modelling approaches used to predict changes in species range dynamics, and highlight future applications and directions for forecasting climate change effects on species life history, distribution, abundance and persistence.

The extensive diversity in ecological contexts and broad range of human-induced environmental changes, together produce a multitude of possible future outcomes reminiscent of Darwin's old Indian ruins. When combined with a lack of data availability, shortage of modelling expertise, limited availability of high resolution climate projections and strict modelling frameworks, the obstacles to realistically forecasting species' vulnerabilities to climate change are manifold. Consequently, there is no one-size-fits all methodological approach to forecasting the responses of species to climate change. However, a recent review on the subject has now made available a detailed decision key of modelling platforms suitable for modelling demographic-based species range dynamics (Figure 1 in Lurgi *et al.* 2015). This will certainly assist researchers in narrowing down their choice of the most appropriate tool for their needs. As for the development of new platforms, some taxa e.g. *Niveoscincus* species, would benefit from more sophisticated mechanistic approaches with improved and expanded empirical frameworks which complement the current benefits of available mechanistic SDMs. However, these situations are rare owing to the hurdles listed above, particularly modelling expertise and data availability. Recent developments in the modelling field include the release of a simplified version of MORPH (an individual-based foraging model, Stillman 2008; West *et al.* 2011) and the release of NicheMapR into the public domain. It has been proposed that MORPH and NicheMapR will be extremely powerful when used in combination, by accounting both for thermodynamic processes along with foraging and dispersal behaviour (Ehrlén & Morris 2015). These advances, in combination with

growing efforts to overcome modelling challenges (e.g. accelerated data collection), are likely to facilitate progress in the fields of both conservation planning and modelling in the near future.

An alternative to developing more highly structured modelling platforms is to base conservation management decisions on several existing approaches in tandem (e.g. individual-based demographic models and mechanistic SDMs). This is often more informative than using one model in isolation, because the utility of different methods depends on the variables considered and capacity of the modelling framework to capture the drivers underlying species distributions. For example, correlative SDMs are well suited to capturing a wide range of processes implicitly present in the data which affect the spatial distribution of a species. In contrast, the process explicit nature of mechanistic SDMs facilitates identification of the relationships between organisms and their environment by capturing the relationships between key variables. With few assessments of the accuracy of SDMs (mechanistic, correlative or otherwise) predictions into novel environments, the most robust course is to consider the predictions of multiple modelling frameworks when practicable. Different modelling frameworks can be used to answer complementary questions (Kearney, Wintle & Porter 2010; Dormann *et al.* 2012; Meineri *et al.* 2015). For example, I used an individual-based demographic model to simulate changing species interactions and dispersal, to suggest mid (2010 – 2100) and long term (2100 – 2300) trends in species abundances and distributions under climate change across a mountain top. These predictions hinged on a well-known pathway for temperature effects on fitness (i.e. relationships between temperature and birthdate, and birthdate and offspring fitness) and incorporated a range of demographic processes including dispersal dynamics, competitive interactions and density dependent mortality. This model provided insight into population and species scale effects, including revealing the dampening effect of demographic processes on the rate of movement into newly available climate niche space. In contrast, the mechanistic model took a first principle thermodynamic niche approach to explicitly model the effect of numerous climatic parameters on a range of fitness related traits throughout the life cycle. This approach identified changes at the individual level and quantified the effect of warming temperatures on the fundamental niche, and has the potential to simulate broad scale changes in available niche habitat. Together, the use of multiple models provides more detailed and reliable insight

than any single model approach, and lends confidence to conclusions by considering a wide range of mechanistic and demographic elements at multiple spatial scales.

An emerging ‘whole ecology’ approach utilises a dynamic metamodel approach to incorporate the multiple mechanisms, scales and drivers of species distribution, range dynamics and extinction risk (Brook *et al.* 2009; Fordham *et al.* 2013). A metamodel links components of a complex system as discrete individual models, and governs data flow between these models and the sequence of events simulated (Lacy *et al.* 2013; Prowse *et al.* 2013). Metamodels have been used to understand historical extinctions and to produce contemporary extinction risk assessments (Lacy *et al.* 2013; Prowse *et al.* 2013; Shoemaker *et al.* 2014; McCallum 2015; Miller *et al.* 2016). For example, a metamodel approach to incorporate a predator-herbivore-vegetation dynamic has successfully been used to recreate the extinction of the thylacine, *Thylacinus cynocephalus*, where a single model approach could not (Prowse *et al.* 2013). An advantage of the metamodel approach to species risk assessment is in allowing diverse threats to interact non-linearly across multiple spatiotemporal scales (Prowse *et al.* 2013). As a result, metamodels have the potential to identify synergistic drivers of extinction risk which can accelerate at-risk species, such as highland *Niveoscincus*, towards extinction (Brook, Sodhi & Bradshaw 2008; Brook *et al.* 2009; Mokany & Ferrier 2011; Prowse *et al.* 2013). A meta-modelling approach which combines a mechanistic SDM with a spatially-explicit IBM could simultaneously test the opposing fitness effects of warming temperatures on physiology and changing competitive interactions with dominant lowland competitors to quantify the degree and level of risk highland *Niveoscincus* species face from climate change. Additional development to better assess the potential for synergistic effects between climate change and other processes such as habitat loss and degradation on *Niveoscincus* species, would allow a more holistic representation of the threats which need to be considered and managed for the conservation of these species (Brook, Sodhi & Bradshaw 2008). Metamodels provide the next necessary step towards better understanding and predicting the effects of environmental change on the life history, abundance, distribution and persistence of these species into the future.



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